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Editorial

Welcome to this the fourteenth volume of the *Journal of Cetacean Research and Management*. This volume contains sixteen papers covering a wide range of conservation and management issues.

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G.P. DONOVAN
Editor

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Beaked whale strandings on the coast of Australia in comparison to those of other cetaceans

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ABSTRACT

Beaked whale (Ziphiidae) strandings on the coast of Australia are examined in comparison to five other odontocete (toothed whale) species and two mysticetes (baleen whales) representative of non-Ziphiids found stranded in Australian waters. Ninety percent of reported beaked whale strandings involve a single animal. Seven beaked whale stranding events of three or more individuals have been recorded from 1871 to 2010, with a maximum in any event of 6. The five non-Ziphiid odontocetes had maximum numbers in a stranding of 13, 51, 65, 200, and 250, and a combined total of 66 events with 10+ in a stranding. The mysticetes had almost exclusively single strandings. Similar trends for the Ziphiids and other cetaceans are generally observed worldwide, although larger numbers of Ziphiids have stranded elsewhere. Continental scale geographical stranding patterns are similar for the Ziphiids, the five non-Ziphiid odontocetes, and the two mysticetes, although not for the same reasons. Reported strandings predominantly occurred around the southern half of Australia south of 20°S. On average around three times as many beaked whale stranding events per month occurred for the period January to April than for July to December. The monthly trend for beaked whale strandings follows the seasonal cycle of sea temperatures, indicating a relation to oceanic phenomena, rather than to the often invoked effect of increased observer effort in months with warmer air temperatures. Some single and dual beaked whale strandings which include a female may be related to use of shallow sheltered waters for calving and subsequent resting.

KEYWORDS: BEAKED WHALE; STRANDINGS; AUSTRALASIA

INTRODUCTION

This paper examines spatial and temporal characteristics of strandings of beaked whales around Australia (Fig. 1). Beaked whales are medium sized marine mammals of about 4 to 13m length, belonging to the order Cetacea, suborder Odontoceti (the toothed whales), and family Ziphiidae. Beaked whales constitute one-third of all species of small cetacean in the Australian region, but very little is known of their numbers, biology, or conservation status (Ross, 2006). However, in the 'Action Plan For Australian Cetaceans', Bannister *et al.* (1996, pp.40–41) have provided a synopsis of the general distribution of beaked whales around Australia in relation to habitat. The diet for some species in other world areas is composed of squid, fish, and occasional crustaceans, apparently obtained from on or near deep seabeds associated with canyons and slopes (MacLeod *et al.*, 2003). Blainville's beaked whales (*Mesoplodon densirostris*) have been observed to dive up to 1,200m for prey, and Cuvier's beaked whales (*Ziphius cavirostris*) up to 1,900m (Tyack *et al.*, 2006). Some non-Ziphiids are also deep divers, for example a sperm whale dive to 1,169m has been recorded (Miller *et al.*, 2004). However, Blainville's and Cuvier's beaked whales appear to be the deepest known divers of all marine mammals.

In recent years, beaked whales have received an increasing amount of attention from the research community, conservation groups and defence organisations. This focus has arisen because of mass strandings of beaked whales in some widely separated Northern Hemisphere areas being causally linked with use of naval active sonar, particularly for frequencies 1–10 kHz (Frantzis, 2004; Jepson *et al.*, 2003; Johnson *et al.*, 2004; Piantadosi and Thalmann, 2003; Rommel *et al.*, 2006). It is a matter of concern to the Royal Australian Navy (RAN) that their activities should not disturb marine mammals. Policy directives have been derived with community consultation (The Maritime Activities Environmental Management Plan) specifically aimed at minimizing or curtailing the use of active sonar when marine mammals are likely to be present (Cole, 2008). The RAN have commissioned passive acoustic surveys prior to, during, and after naval exercises in the Coral Sea (Cato *et al.*, 2009) in order to monitor and avoid marine mammals, particularly beaked whales. Passive acoustics can detect beaked whales without disturbing them by listening to and identifying the stereotyped chirps they make during feeding dives (e.g. Hamilton and Cleary, 2010). To make informed decisions on possible relations between strandings of beaked whales and anthropogenic activities (no occurrences of which have been observed about Australia; Commonwealth of Australia, 2008), information is also needed on factors such as stranding rates, and whether or not strandings have geographical or seasonal trends. This information is currently unknown, and is the focus of the present paper.

Related strandings of two or more whales, excluding mother-calf pairs, occur infrequently, and so are regarded as anomalous. Consequently so-called mass strandings of cetaceans can involve as few as two animals which beach some time and distance apart. For example D'Amico *et al.* (2009) define a 'mass' stranding as two or more cetaceans beaching within six days and 74km, excluding mother-calf pairs. D'Amico *et al.* (2009) quote an average worldwide mass stranding rate for beaked whales of 2.3 events per year for 1950 to 2004, and four per year for 1985 to 2004. Ross (2006) states that false killer whales (*Pseudorca crassidens*) are 'prone' to mass stranding on Australian coasts based on an average of one such event every 2.5 years. These numerically low rates of occurrence set the context for any analysis of strandings.

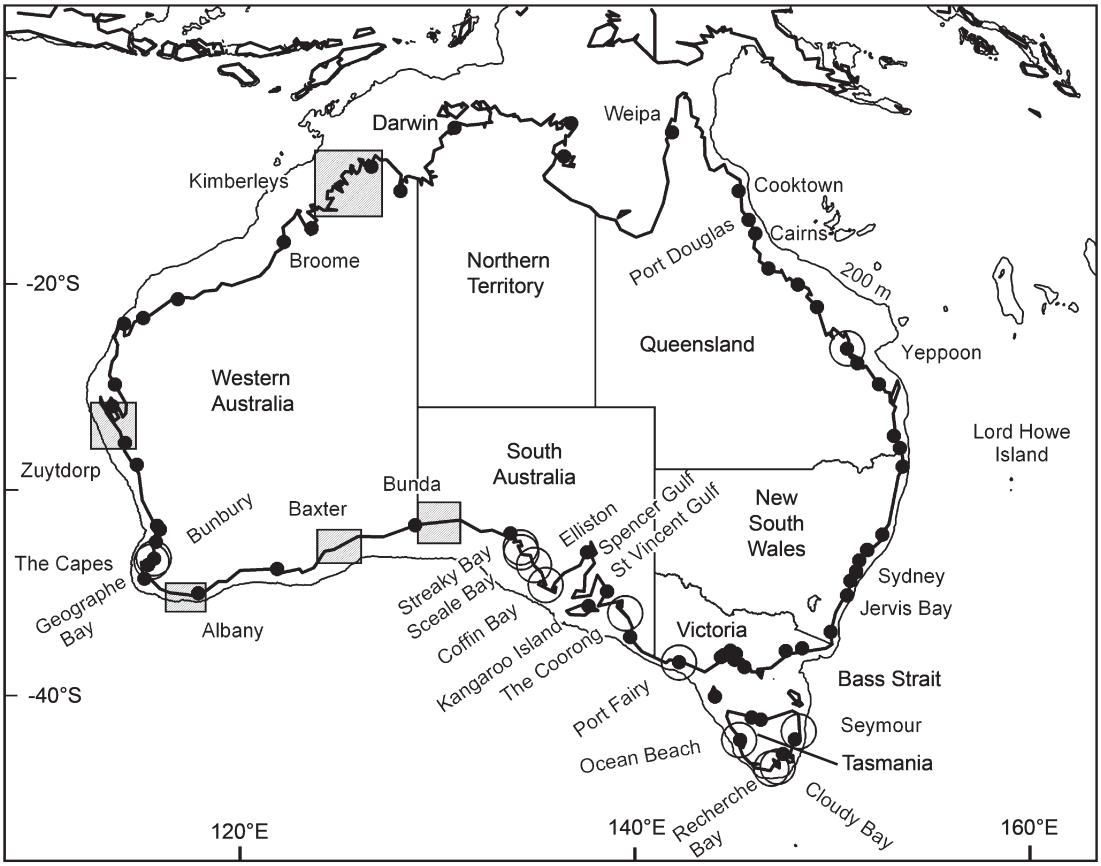

Fig. 1. The Australian coastline, states, and selected place names and population centres. Sea cliffs and rocky areas are outlined with rectangles.

In view of the infrequency of occurrence of mass strandings, this paper examines the beaked whale stranding record for the entire Australian continent, including single strandings. The authors are unaware of previous work directed specifically to beaked whale strandings around Australia as a whole. Some details of beaked whale strandings around Australia were compiled by Kemper and Ling (1991) in an examination of cetacean strandings in South Australia, and D'Amico *et al.* (2009) included Australian beaked whale mass strandings in a global examination. A true picture of beaked whale stranding behaviour around Australia can only be gained when the whole continent is examined and when the proportion of single to mass strandings is known.

The primary questions in the study addressed in this paper are as follows: Are there spatial or temporal patterns to beaked whale strandings? Do the various beaked whale species have different stranding patterns? How many beaked whales are typically involved in a stranding? Noting that an examination of the stranding patterns of beaked whales in isolation may not be particularly meaningful, how do the stranding patterns of beaked whales compare to those of other cetaceans?

One topic is of special interest. In a companion analysis, Hamilton and Lindsay (2014) found that sites of non-Ziphiid odontocete mass strandings of 10 or more individuals were strongly associated with sandy bays (this applied to at least 34 of the 36 sites and 64 of the 66 events recorded over 143 years), particularly those with headland-bay character. A description of headland-bays is given here in 'Materials and Methods'. Hamilton and Lindsay (2014) did not specifically examine beaked whale strandings because all such events involved less than 10 individuals. A further question is thus: Do beaked whales also typically mass strand in headland-bays?

MATERIALS AND METHODS

Database of stranding records

Three hundred and thirty-one beaked whale (Ziphiid) stranding records and 386 stranding records representative of non-Ziphiids were compiled into the authors' database. Attributes recorded were Species, Season, Month, Year, Australian State, Locality name, Latitude, Longitude, Position quality indicator, Number stranded, Status (live – found alive, or active stranding observed; passive – carcass found; unknown/uncertain – skeletal material, not recorded, or doubt as to the veracity of the status), General observations (e.g. sex, age, evidence of shark attack, disease), and Source of the record, including the authority for the identification.

Beaked whale stranding reports were obtained from the Australian, South Australian, and Queensland Museums, the Tasmanian Museum and Art Gallery, and OZCAM (Online Zoological Collection of Australian Museums). Other sources were the Commonwealth of Australia strandings database[1], research papers and annual reports of the

[1]Commonwealth of Australia. 2010. National Whale and Dolphin Sightings and Strandings Database. Department of Environment, Water, Heritage and the Arts. [Retrieved 11 February, 2010 from *http://data.aad.gov.au/aadc/whales/*]

International Whaling Commission (IWC). In addition, if judged to be of sufficient quality, data from 'non-scientific' sources such as press and internet reports were used; great care was taken to verify the latter sources using cross-checks, photographs and noting the authority for the identification. Photographs of strandings from internet and press reports sometimes enable very good positions to be obtained. However, in one case a photograph of stranded odontocetes from 2008 was reused for a stranding at the same site in 2011. Australian stranding records for the selected species in the authors' database date back to year 1868 for the sperm whale and 1871 for beaked whales and extend up to 2010.

Active or live strandings are of primary relevance for analysing causes of beachings related to cetacean behaviour. However, coupling of the low stranding rate of cetaceans with the need for strandings to be noted by human observers provides only a limited database. Carcass strandings and strandings of unknown status may be valuable in reinforcing the general geographical patterns observed for live strandings. Fresh carcass strandings are also useful for examinations of seasonality.

The quality of positional information associated with strandings is uneven, as is the spatial and temporal sampling. Analyses must be made with some circumspection, and only very clear trends, if any exist, are likely to have meaning. For example, we did not attempt to read too much regarding long term variation into records with irregular time series, but seasonality was sometimes very obvious for composite data. Geographical co-ordinates in the publicly available Commonwealth of Australia database are mostly too inaccurate for site specific analyses. Latitudes and longitudes are rounded to the nearest half-degree. This means that strandings up to 1.4 degrees (155km) removed from each other can be assigned the same position. Some positions are more than 3 degrees from the actual stranding site. Co-ordinates were assigned for specifically named sites such as beaches and other locations from RAN Hydrographic Office bathymetry charts (WGS84 datum) but in some cases the position is not known accurately enough for site specific analyses.

A confounding factor in strandings is the number of cetaceans killed intentionally or unintentionally by humans. At least 25% of recorded cetacean mortalities in South Australia for 1985–2000 were directly human caused (Kemper *et al.*, 2005) although beaked whales did not appear in this category. Entanglements and captures were excluded from the database. The quality control and data gathering methods used makes the database probably the most comprehensive and verified Australian beaked whale stranding record compiled to date.

Beaked whale stranding records

The database contains 331 records (single and mass strandings) for 12 beaked whale species and an 'Unknown' species category. A total of 308 records were identified to species level (Table 1). For descriptions and behavioural details of the beaked whale species in Table 1, see Culik (2004).

Non-beaked whale stranding records

Seven non-Ziphiids were included as representative of the non-beaked whale species found stranded in Australian waters. Both suborders of Cetacea (Odontoceti or toothed whales and Mysticeti or baleen whales) were included to provide balanced sampling. Two of the seven were mysticetes of the family Balaenopteridae, namely the humpback whale (*Megaptera novaeangliae*) and the Antarctic minke whale (*Balaenoptera bonaerensis*). The other five were odontocetes belonging to two separate families, Physeteridae for which the sperm whale (*Physeter macrocephalus*) is the sole member, and Delphinidae including the long-finned pilot whale (*Globicephala melas*), killer whale (*Orcinus orca*), false killer whale (*Pseudorca crassidens*), and melon-headed whale (*Peponocephala electra*). All non-beaked whale stranding records were identified to species level. These included 143 sperm whale records, 112 long-finned pilot whale records, 58 Antarctic minke whale records and 48 humpback whale records (a total of 361). Only mass strandings were included in the database for the false killer whale (20 events), melon-headed whale (3 events), and killer whale (2 events). The non-Ziphiid Odontoceti (and Mysticeti) species were broadly selected as having sufficient records for analysis, and as having different mature adult size, for example, sperm whale/long-finned pilot whale for the odontocetes, and humpback/minke for the mysticetes. This was to examine possible differences in stranding behaviour caused by size to factors such as agility in shallower waters, habitat/feeding behaviour, and efficiency and acoustic frequency of vocalisations.

Table 1

Beaked whale species and numbers in stranding events around Australia for 1871 to 2010 ordered by total number of strandings.

Beaked whale species	Scientific name	Single	Dual	Triple	Four	Six	Totals
Strap-toothed beaked whale	*Mesoplodon layardii*	94	10	3	–	–	107
Gray's beaked whale	*Mesoplodon grayi*	57	8	1	1	1	68
Cuvier's beaked whale	*Ziphius cavirostris*	38	2	–	–	–	40
Blainville's beaked whale	*Mesoplodon densirostris*	21	3	–	–	–	24
Unknown	–	21	2	–	–	–	23
Andrew's beaked whale	*Mesoplodon bowdoini*	19	1	–	–	–	20
Southern bottlenose whale	*Hyperoodon planifrons*	19	–	–	–	–	19
Hector's beaked whale	*Mesoplodon hectori*	8	2	–	–	–	10
Arnoux's beaked whale	*Berardius arnuxii*	7	–	–	–	–	7
Ginkgo-toothed beaked whale	*Mesoplodon ginkgodens*	5	–	–	–	–	5
Shepherd's beaked whale	*Tasmacetus shepherdi*	3	–	1	–	–	4
True's beaked whale	*Mesoplodon mirus*	3	–	–	–	–	3
Longman's beaked whale	*Indopacetus pacificus*	1	–	–	–	–	1
Total		**298**	**28**	**5**	**1**	**1**	**331**

Headland-bays

A headland-bay is a geomorphological coastal unit for which wave and swell action form a bay downswell of the headland with a characteristic log-spiral shape (Fig. 2). Many headland-bays have a headland at both ends, not a single headland. Bay width was measured from headland to beach end for the single headland case, and headland to headland when two were present. Bay indentation distance was measured as the maximum value to shore perpendicular to the line specifying the bay width. Hamilton and Lindsay (2014) noted that the more classically shaped headland-bays have width to indentation ratio greater than 2, with indented bays having ratio less than 2, allowing an initial differentiation of bay types through examination of coastal charts. Indented bays can also have significant headland-bay character. For these cases the log-spiral shape is present in the planform, but a second headland, usually secondary in comparison to the other, introduces indentation on the other side of the bay. Australian headland-bays typically have fine sandy beaches and offhsore seabed slopes of less than 0.5° (Hamilton and Lindsay, 2014).

RESULTS

Geographical stranding patterns

Broadscale geographical patterns for all species examined

The continental scale geographical distribution of all Ziphiid and non-Ziphiid strandings shows a simple pattern (Fig. 3a). Reported strandings occur predominantly in the southern half of the Australian continent south of 20°S, including all round Tasmania. The stranding patterns are generally the same for whales thought to use echolocation for navigation (i.e. the beaked whales, Fig. 3b, and the five non-Ziphiid odontocete species, Fig. 3c), and those which may not (the two mysticetes, Fig. 3d). Beaked whale strandings plotted by status (live/active, carcase/passive or unknown) (Fig. 4) show the same stranding patterns as Fig. 3. More strandings for all Ziphiid and non-Ziphiid species are reported for southwestern Australia, mid to eastern South Australia, and on the east coast of Tasmania, than elsewhere. There is only one reported beaked whale stranding between 120.12–130.3°E, 32–34°S along the high-cliffed rock coast of southern Australia. North of a stranding at 17.8°S, 122°E near Broome, Western Australia the only recorded strandings for the selected species are on the northernmost shoreline of the Northern Territory, with six events noted between 130.3°E to 136°E, these being three beaked whales, two sperm whales (Chatto and Warneke, 2000, have four), and a humpback whale. Strandings are also recorded on islands in Bass Strait, and on oceanic islands remote from Australia, namely Lord Howe, Heard (53°S, 72°30'E), and Macquarie Islands (54.62°S, 158.861°E).

Strandings of individual Ziphiid species are charted in Fig. 5, and strandings of the five non-Ziphiid odontocetes in Fig. 6. There are some regional differences between strandings of beaked whale species, although they are not marked. Blainville's beaked whale strandings mostly occur on the east coast; Cuvier's mostly strand about Tasmania and the Capes (Cape Naturaliste and Cape Leeuwin, Western Australia); and southern bottlenose beaked whales strand mostly in South Australia. Gray's and strap-toothed beaked whales have a wider stranding distribution than other Ziphiids, resembling those of the sperm whale and long-finned pilot whale.

Beaked whale stranding locations

The object of this section is to examine beaked whale stranding locations to see if they have any characteristics in common, and to see if beaked whales strand at the same type

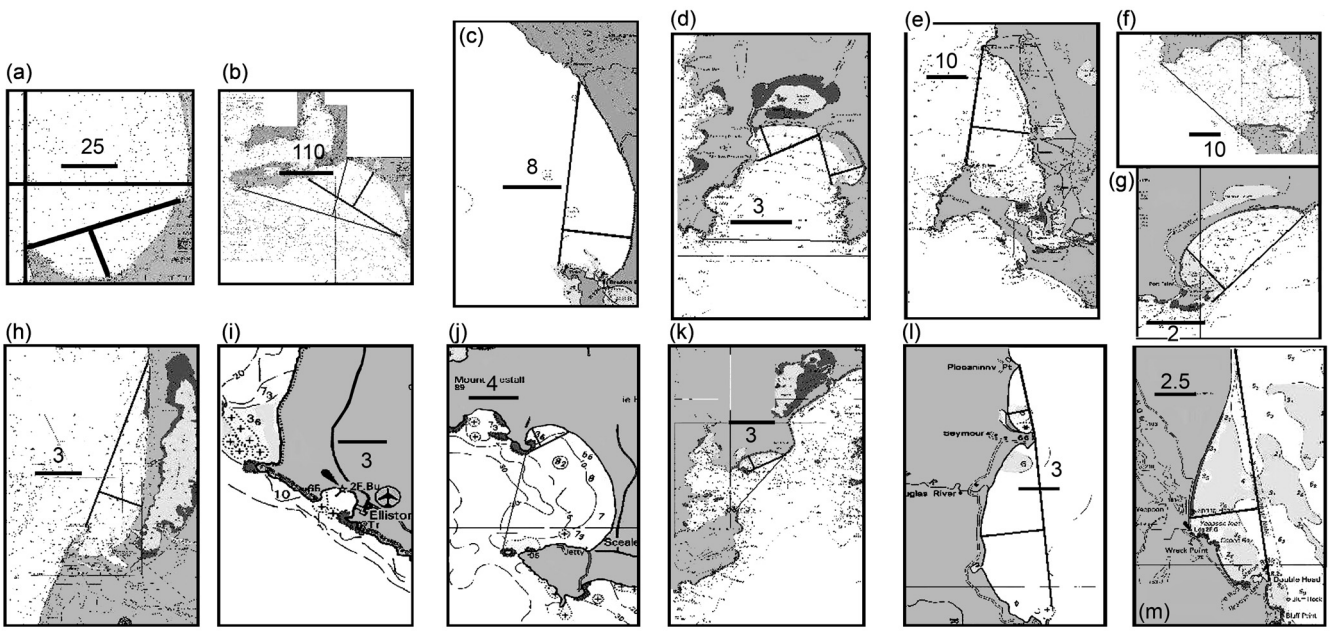

Fig. 2. Planforms of 13 Australian sites with three or more beaked whale stranding events (see Fig. 1 for locations). Twelve are headland-bays and one is an indented bay. The sites are (a) Geographe Bay, (b) the Coorong, (c) Ocean Beach, (d) Cloudy Bay, (e) Coffin Bay, (f) Streaky Bay, (g) Port Fairy, (h) Bunbury, (i) Elliston, (j) Sceale Bay, (k) Recherche Bay, (l) Seymour, (m) Yeppoon. Horizontal scale bars show distance in km. Sites (a)–(c), (e), (g)–(h), (l)–(m) are headland-bays. Geographe Bay, Ocean Beach, and Port Fairy approach prototype or more classically shaped headland-bays in planform. Sites (d)(f)(j)(k) are indented bays with headland-bay character or interior headland-bays. Site (i) is an indented bay. Straight lines drawn on the planforms define bay width and indentation distance perpendicular to bay width.

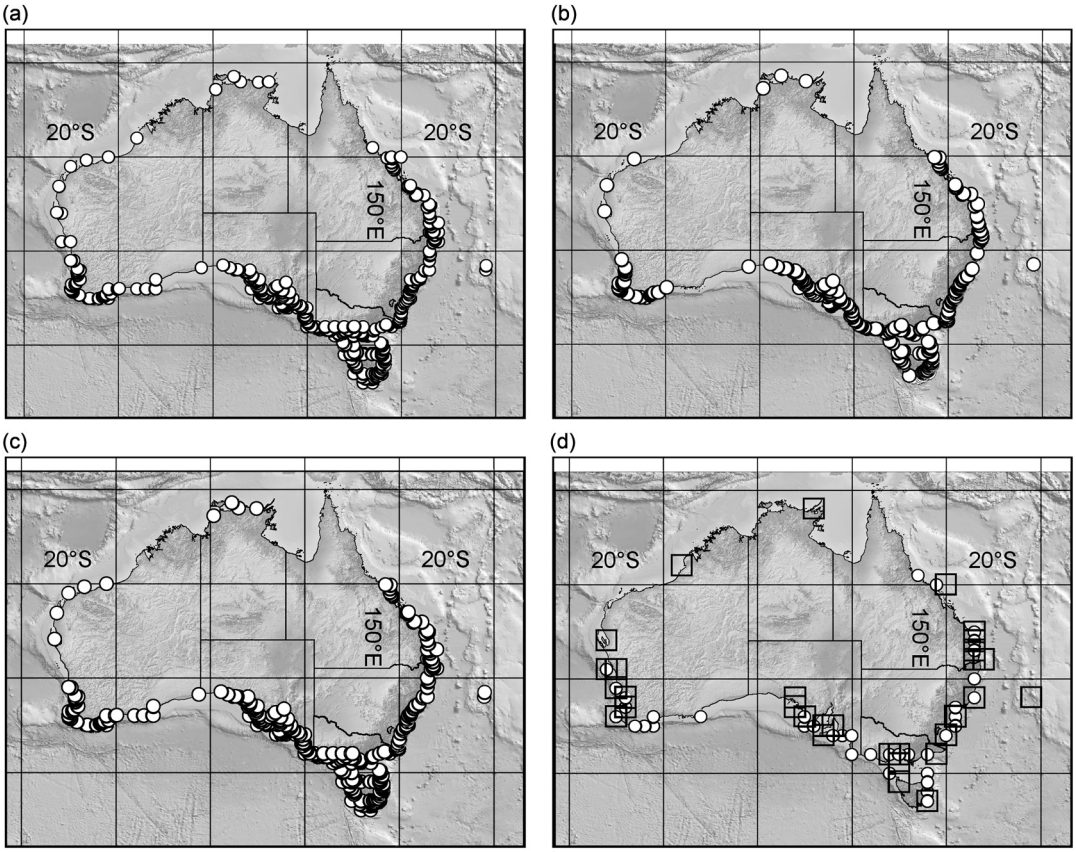

Fig. 3. Locations of strandings (live, passive, and unknown status) of beaked whales (Ziphiidae), and of seven selected non-Ziphiid species (five odontocete species and two mysticete species) on the Australian coastline. Bathymetry is from Kilgour and Hatch (2002).
(a) Combined strandings of all species (717 reports in total).
(b) Beaked whale strandings (331 in total).
(c) Strandings of five non-Ziphiid odontocetes (280 in total). Single and mass strandings for the long-finned pilot and sperm whale, and mass strandings only for the false killer whale, killer whale, and melon-headed whale.
(d) Mysticete strandings (106 in total). Antarctic minke whale (□), humpack whale (○).

of locations as other cetaceans. Sites with more than one stranding event are more likely to provide reliable information of this kind. The location of many sites are not well known, and this hampers spatial analysis. Only seven beaked whale stranding events have three or more animals in a stranding (Table 1). Six have good positional information and all are in bays (Fig. 7). Five are in headland-bays (Mandurah, Geographe Bay (2 events) and Denmark in Western Australia; and Victor Harbour in South Australia), and one is in an indented bay with interior headland-bays (Cloudy Bay, Tasmania). Of 28 dual strandings (mother-calf pairs included), half are located in bays (two are indented headland-bays, and 12 are more classically shaped headland-bays). The remainder are not well enough located for site specific analyses, but it appears that three are probably in a headland-bay, and seven are not or probably not in a headland-bay. Of the 28 dual strandings, 3 are not a mother-calf pair, 6 are a mother-calf pair, 11 include a female, and 8 have no details on age or sex. Those with a female or no details on sex could be mother-calf pairs, so that 20 to 90% of cases might not be defined as mass strandings.

There were 45 sites with two or more beaked whale stranding events, including single strandings, accounting for 124 of all 331 (37%) Ziphiid stranding events. Thirteen of the 45 sites (29%) had at least one known live beaked whale stranding event. Seventeen of the 45 (38%) also had strandings of non-Ziphiid odontocetes, and 10 of these 17 also had mysticete strandings. Three of the 45 (17%) also had a single stranding of a mysticete and no non-Ziphiid odontocete strandings. The 45 sites include larger coastline areas with a common geomorphology such as Geographe Bay (Western Australia) and Cloudy Bay (Tasmania, Fig. 2), rather than being specific beaches or sites. At least 28 of 45 (62%) are bays of some type, including 25 headland-bays or bays with headland-bay character in planform, and 3 indented bays. Five are capes, 4 are points, 1 is a port, and 6 have no indication of coastal type. It is not known if the strandings on capes and points are associated with headland-bays, because no indication is given on which side of these features the strandings occurred.

Thirteen (29%) of the 45 sites (Fig. 2) have three or more beaked whale stranding events, accounting for 60 of the 331 events (18%). Five of the 13 have one or more live beaked whale stranding event. All 13 sites are bays of some kind, at least nine of which have strong headland-bay character. The sites (Fig. 2) are Geographe Bay[2] in Western Australia (11 events), The Coorong[3] in South Australia (6), Ocean Beach[2] in Tasmania (6), Cloudy Bay[2] in Tasmania (6), Coffin Bay[3]

[2]These sites also have one or more mass strandings of ten or more non-Ziphiid odontocetes.
[3]These have one or more non-Ziphiid odontocete strandings of less than 10 animals.

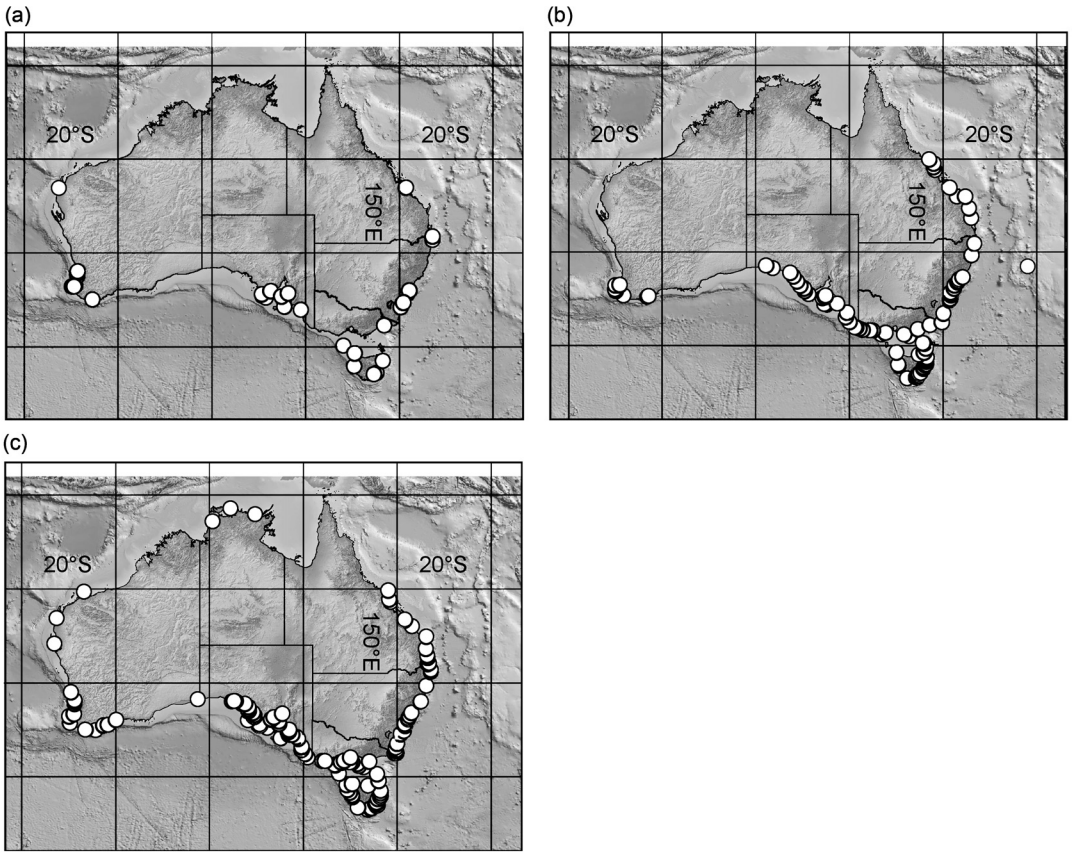

Fig. 4. Stranding locations of beaked whales (Ziphiidae) on the Australian coastline by status (live, passive, and unknown).
(a) Observed live strandings.
(b) Passive (carcass) strandings. Some would have been live strandings.
(c) Unknown stranding status. Skeletal material, or status not recorded.

in South Australia (5), Streaky Bay[3] in South Australia (4), Port Fairy[3] in Victoria (4), and three each for Bunbury (Western Australia), Elliston (South Australia), Sceale Bay (Victoria), Recherche Bay (Tasmania), Seymour[3] (Tasmania), and Yeppoon (Queensland). Bunbury could be counted as part of Geographe Bay, which is directly to its south, but it is a small headland-bay in its own right, and has been counted separately.

Hamilton and Lindsay (2014) noted 36 locations around Australia with one or more mass stranding of ten or more of the five non-Ziphiid odontocetes, with 66 such events in total. Nine of those sites also had one or more beaked whale stranding events. The nine sites are Cheynes Beach and Geographe Bay (both in Western Australia), and Cloudy Bay, Marion Bay, Ocean Beach, Perkins Bay, Pieman Heads, Sandy Cape and Tatlows Beach (all in Tasmania). Pieman Heads is an indented bay, Cloudy Bay is an indented bay with interior headland-bays, and the other seven sites have a strong headland-bay character.

Mysticete stranding locations

This section examines whether mysticetes strand in particular types of locations, and whether or not these are the same types of locations as the odontocetes. Twelve of 40 (30%) humpback whale stranding sites were headland-bays in planform or had headland-bay characteristics, 3 were deeply indented or complex coastlines (which can be viewed as topographic traps) and 9 were relatively featureless straight coastlines. These counts include live and passive strandings. The remaining 16 sites were named as points, capes, peninsulas, river mouths, lake entrances or inlets, and nearshore islands or reefs. In contrast, 36 of 42 (86%) minke whale strandings sites were headland-bays in planform or had some headland-bay character, 3 were topographical traps, and 3 were featureless. Of 16 live minke whale stranding sites, 12 had headland-bay character, and 3 were topographic traps.

Numbers in strandings

Beaked whales

Beaked whales stranded singly for 295 of 331 records (89% of recorded events). There were 35 events with 2 or more in a stranding (Table 1). Of these, seven have 3 or more individuals, with a maximum of 6 beaked whales in a single event. All 19 southern bottlenose beaked whale strandings were for a single individual. Four other species have also recorded single strandings only, but with 7 or fewer occurrences (Table 1).

Non-Ziphiids

The two balaenopterids had almost exclusively single strandings (minke whales 57 of 58 and all 48 humpback strandings). Eight of 48 humpback (17%), and 11 of 58 minke strandings (19%), were recorded as calves or subadults. These are lower bounds, since many records do not have details on age or length. In contrast, mass strandings of high numbers of individuals were recorded for the five non-Ziphiid odontocetes: 250 for false killer whales, two

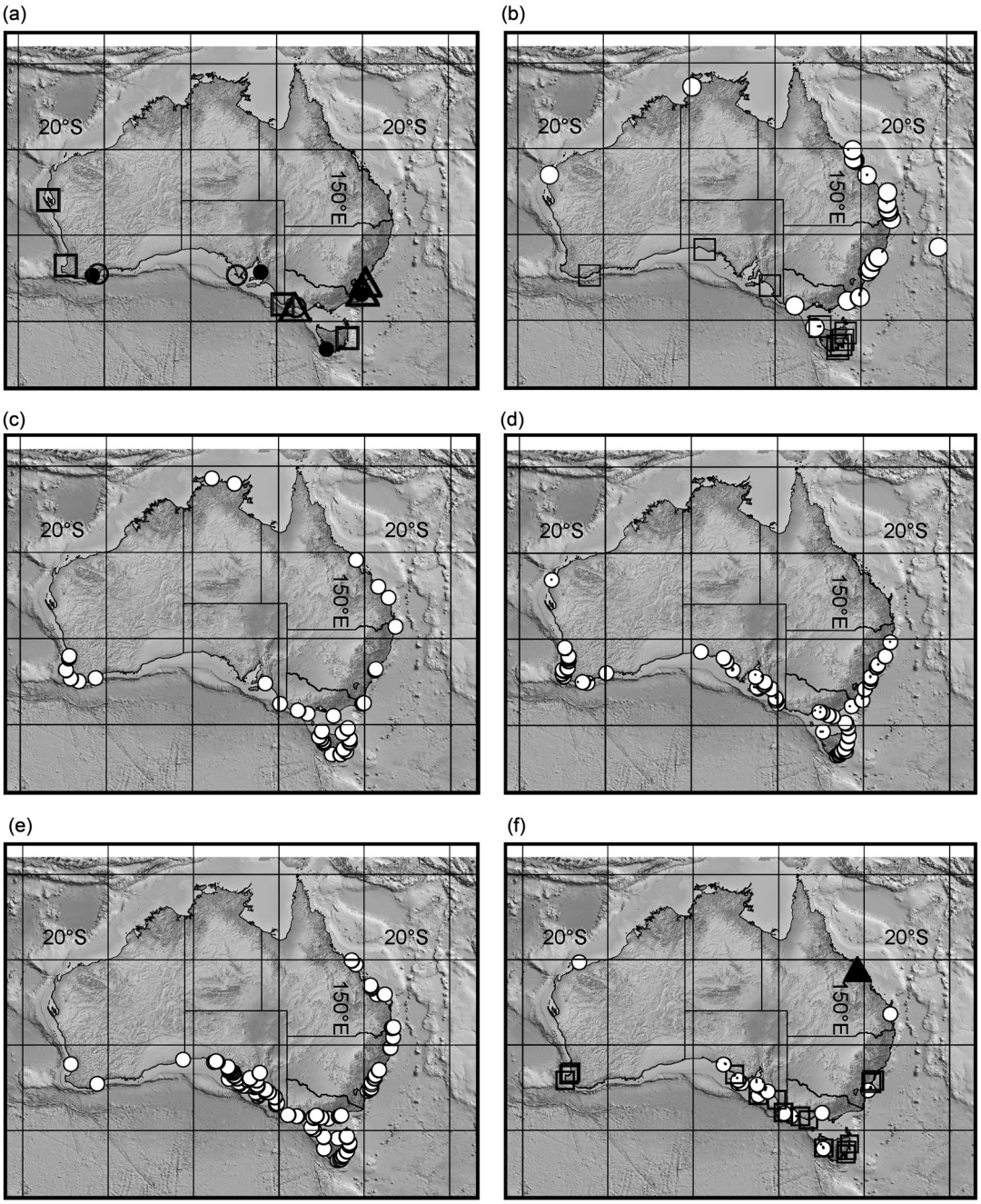

Fig. 5. Stranding locations of twelve beaked whale species around Australia (live, passive, and unknown status).
(a) Arnoux (●), Ginkgo-toothed (Δ), Shepherd's (□), True's (○).
(b) Blainville's (●), Hector's (□).
(c) Cuvier's.
(d) Gray's.
(e) Strap-toothed.
(f) Andrew's (□), Longman's (▲), Southern bottlenose (●).

events of 200 or more for long-finned pilot whales (one in South Australia, and one in Tasmania), 65 for sperm whales, 51 for melon-headed whales and 13 for killer whales. There were 66 strandings of 10+ individuals for the five non-Ziphiid odontocetes.

Temporal variation and seasonality

Total numbers of strandings in the database for all species examined (Ziphiid and non-Ziphiid) for the periods March to May, June to August, September to November, and December to February were 139, 130, 152 and 210. December to February (summer) was the only period with no recorded strandings north of 23°S, although few strandings for the selected species were recorded for those latitudes. Results of seasonal analyses obtained from a limited database must be made with some caution. If four three-monthly seasons are examined, and if it is considered that ten or more observations are required per season to have some chance of statistical reliability, then at least 40 observations are required for seasonal examinations. Not all species have this number of stranding records. The consideration of noteworthy examinations of seasonality below does not imply that they are statistically significant.

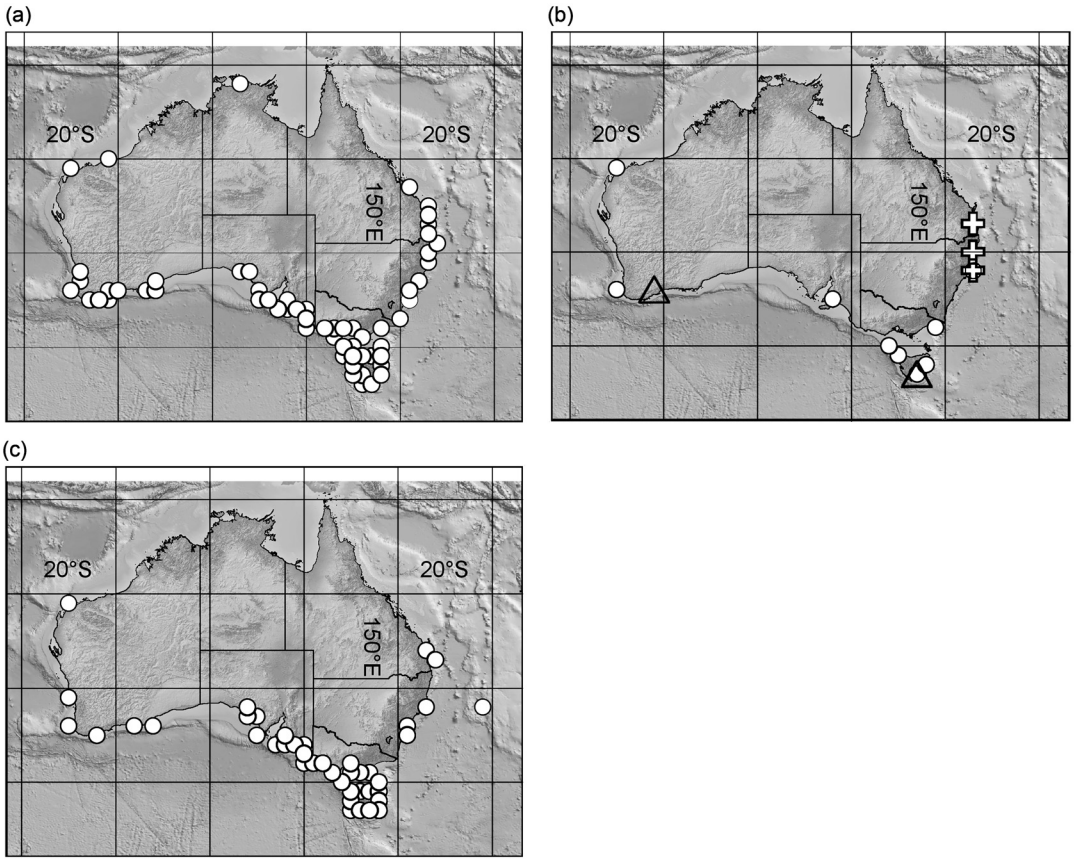

Fig. 6. Stranding locations of five non-Ziphiid odontocetes.
(a) Sperm whale. Single and mass strandings.
(b) Mass strandings of false killer whales (●), killer whales (Δ), melon-headed whales (✣).
(c) Long-finned pilot whale. Single and mass strandings.

Beaked whales

The highest number of beaked whale stranding records for the period 1869 to 2010 was 15 in 2005. Beaked whale strandings by month are shown in Fig. 8; there were 278 of known month and 53 of unknown month. The figure shows monthly aggregate totals for years 1869 to 2010, not monthly averages. For January to April the average aggregate total per month is 41, three times the average aggregate total of 13 events per month for July to December. Of 41 known live beaked whale strandings with known stranding month, 38 were for December to April, and none were for June to September. Of 10 live beaked whale strandings from Coffin Bay (135°15'E) to the southern Coorong (138°E) in South Australia, including the north side of Kangaroo Island, two were for November–December, and eight for January–February.

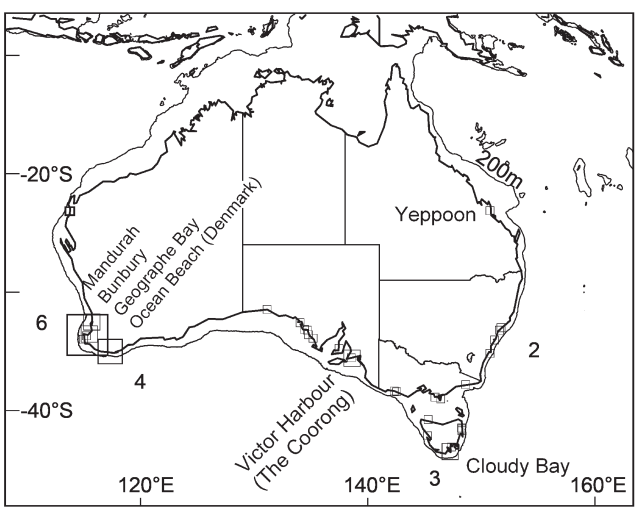

Fig. 7. Locations of stranding events of two or more beaked whales. Mother-calf pairs are not excluded. Numerals show the numbers in a stranding for the different sized open square symbols. The maximum in an event is 6 off Western Australia.

The data for two beaked whale species with more than 15 records showed clear seasonality in strandings. The strap-toothed beaked whale stranded 68 of 95 times (72%) over 1974–1984 in January to April. Gray's beaked whale stranded 29 of 60 times (48%) for 1990–2005 in December–January, and 48 of 60 times (80%) for December to April. No obvious seasonality was noted for strandings of Blainville's beaked whale (18 records), southern bottlenose beaked whale (15 records), or Cuvier's beaked whale (33 records for 1918–2009). For 1944–2007 Andrew's beaked whale stranded 10 times in January to June and once each in August, November and December. Of nine strandings with known month for Hector's beaked whale for 1990–2005, all but one in October were for February to April. All five Arnoux's beaked whale strandings are for December to February. All five Ginkgo-toothed beaked whale strandings for 1974–2009 were for May to August. Of the five Queensland stranding events north of 23°S (for 19.9 to 21.25°S) for June to August, three events were beaked whales (one Cuvier's and two strap-toothed). The others were a minke and a juvenile humpback.

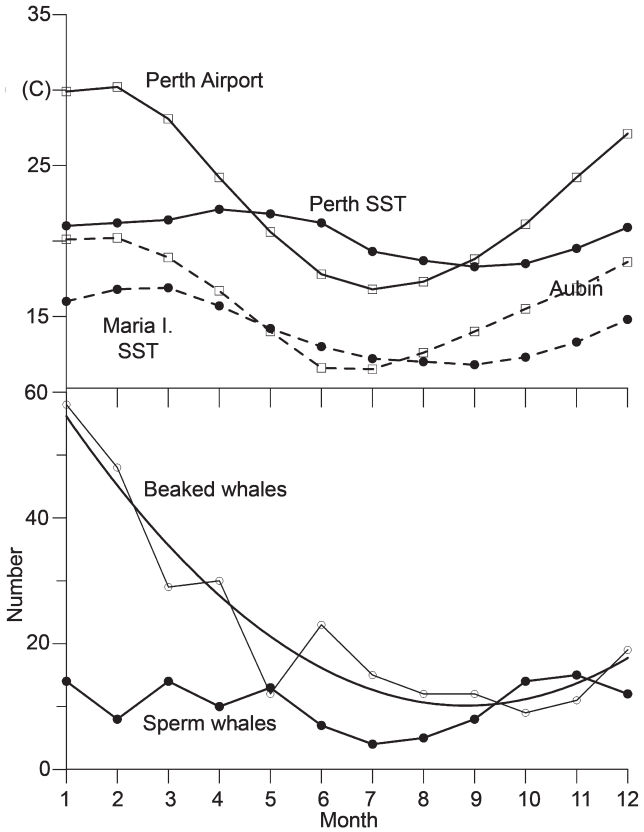

Fig. 8. Top panel: The yearly cycles of sea and air temperatures for the oceans off Perth (Western Australia), and Maria Island (Tasmania) (42.66°S, 148.02°E). The air temperatures are measured by land stations. Aubin is 31km from Maria Island. SST = sea surface temperature. Bottom panel: Total numbers of strandings by month for sperm whales, and for all beaked whale species combined.

For the 29 years from 1982–2010, 31 events were reported involving two or more beaked whales in a stranding (one per year), including mother-calf pairs. Without mother-calf pairs the rate may well be half this, but the information is insufficient to examine this point.

Non-Ziphiid odontocetes

For the 124 sperm whale records with known stranding month (Fig. 8), a lower number of total strandings occurred in June to September for the 101 years from 1909–2009 (an average aggregate total of 6 strandings per month compared to 12.5 in other months). Long-finned pilot whales (108 records) mostly stranded in October to March over years 1917–2009 (an average aggregate total of 13 events per month compared to 5 for other months). False killer whale strandings peaked in June and July for 1936–2009 (9 of 17 mass strandings were in these two months). The three melon-headed whale mass strandings for 1959–1988 were in July–August.

Mysticetes

For the period 1919–2006, humpback whales stranded more often in the months July to December (an average aggregate total of 6.5 per month, with a broad peak for October–November of 9.5 per month), than in January to June (an average aggregate total of 1.7 per month). For 1946–2005 minke whales stranded a total of 47 times over July to October, and 10 times in other months.

DISCUSSION

Geography, habitat and migration

The majority of strandings for beaked whales and the seven other selected cetacean species occur around the southern half of the Australian continent. Evans *et al.* (2005) have previously noted higher frequencies of strandings on the southernmost areas of Southern Hemisphere land masses. Only 6 of 717 strandings for the selected species are north of 17.8°S, all in the Northern Territory; three were beaked whales. The lack of northern stranding records does not appear to be due simply to a lower density of observers in tropical Australia, as a stranding record has been maintained. Chatto and Warneke (2000) list 57 cetacean strandings, including dolphins, in the Northern Territory from 1948 to 1999, including mass strandings of 54, 40 and 21 short-finned pilot whales (*Globicephala macrorhynchus*) from 1984 to 2004.

Relation of strandings to the distribution of live cetaceans

If the stranding data reflect distribution, all species examined appear to be infrequent visitors to Australia's tropical north. This is reasonably certain for the two mysticetes. The overall stranding patterns for the humpback whales are consistent with north/south migratory movements between Antarctic feeding grounds and subtropical breeding areas adjacent to the Australian coast, coupled with following of shorelines to the breeding grounds. Latitudes 15–18°S are the general northern limit of humpback whale migration routes to calving grounds for both Western Australia (Jenner *et al.*, 2001) and eastern Australia (Australian Government, 2004; Gales *et al.*, 2010). It appears that humpback whales do not stray in numbers much farther north than these latitudes. Humpback whales have been sighted in the Great Barrier Reef lagoon of Queensland as far north as 12°S (Kaufman *et al.*, 2010), but only two live sightings of humpbacks are recorded for the Northern Territory, with another in the Gulf of Carpentaria between the Northern Territory and Queensland[4]. No strandings have been noted for north Queensland towns such as Cairns, Port Douglas, Cooktown and Weipa (Fig. 1).

The general distributions for the five non-Ziphiid odontocetes (false killer, killer, longfinned pilot, melonheaded and sperm whales) are not well known, with most available information coming from strandings. Morrice *et al.* (2002) compiled killer whale sightings around Australia, from which they describe sightings in latitudes 0–25°S as rare. Killer whale sightings around Australia (Morrice *et al.*, 2002, their fig. 1) have the same general distribution as cetacean strandings in Fig. 3(a). Information on Ziphiid distributions is particularly dependent on strandings. As a point of interest, there are only four reported strandings of Shepherd's beaked whale, and these are widely separated from each other (Fig. 5(a)). In a remarkable coincidence, a pod of 12 Shepherd's whales was sighted near the stranding site in western Victoria in February 2012[5].

Shelf width

Extensive areas shallower than 200m occur over northern Australia (Fig. 1), and deep feeding cetaceans might be

[4]*http://data.aad.gov.au/aadc/whales/species_sightings*
[5]*http://www.antarctica.gov.au/science/cool-science/2012/whale-trackers-make-rare-sighting#prettyPhoto* [Accessed 13 November 2012]

rarely found in such areas. In contrast, the edge of the continental shelf is close to the coast for much of eastern and western Australia south of 25°S. To explain the more frequent Cuvier's beaked whale strandings in Tasmania compared to South Australia (see Fig. 5), Kemper and Ling (1991) proposed that the wide South Australian shelf and possible deep feeding behaviour in underwater canyons might keep beaked whales farther offshore than the narrow Tasmanian shelf. Tyack *et al.* (2006) have tracked Blainville's and Cuvier's beaked whales to over 1,200m and 1,900m deep respectively during feeding dives, supporting this idea. D'Amico *et al.* (2009; p.459) suggested worldwide beaked whale strandings occur where the 1,000m depth contour is close to shore (within 80km).

However, the wide continental shelf from 18–23°S on the east coast of Australia is not associated with an absence of strandings of the deep diving Blainville's and Cuvier's beaked whales (Figs 3, 4, 5). It is also noted that the South Australian shelf is up to 190km wide where Ziphiids have stranded (Fig. 3b). Kemper and Ling (1991) noted that more southern bottlenose beaked whales stranded in South Australia than Tasmania (see Fig. 5f). These observations imply that factors additional to shelf width may be important in determining where some beaked whale species strand. This is discussed further below.

Coastline characteristics

CLIFFS AND ROCKY COASTS

Hamilton and Lindsay (2014) noted a visual correlation between the absence of strandings and the presence of rocky sea cliffs which run unbroken for hundreds of kilometres on the coasts of Western Australia and South Australia (the Zuytdorp, Albany, Baxter, and Bunda cliffs) (Fig. 1). This was attributed to the reduced number or absence of beaches in these cliffed areas. If whales did strand at rocky cliffs it is unlikely they would be seen. They may well also keep a safe distance from the cliffs, being alerted by wave noise. Across much of northern Australia there may be a correlation between the lower numbers of strandings with rocky or reefy coasts, rather than with cliffs. In particular, the entire Kimberley coast of northwest Australia (15–18°S) is shown as rocky in Sharples *et al.* (2009), and there are no stranding records there, despite it being adjacent to humpback whale breeding grounds. Short (2006) describes laterite rocks and reef flats as common along the Northern Territory coast, with coral reef structures located immediately seaward of at least 1,430 beaches from the Kimberley area to Cape York. Most are barrier reefs backed by a lagoon and lower energy beaches. Only 16% of the bedrock-dominated Kimberley coast is sandy (Short, 2006). Elsewhere in Australia sandy beaches occupy between 38–66% of each state coastline (Short, 2006), indicating a potential for more strandings to be noted in those areas.

COASTLINE COMPLEXITY

Kemper and Ling (1991) noted a relatively low occurrence of cetacean mass strandings on the New South Wales coastline, possibly because of the relatively uncomplicated nature of the coast, whereas Tasmania showed many examples of strandings associated with complex topography (Nicol, 1986). The database has 71 strandings of two or more individuals (mother-calf pairs included) for Tasmania, and 6 for New South Wales for the five selected odontocetes. With islands included, this indicates that dual strandings upwards have occurred more than 4.6 times per length of coastline for Tasmania than for New South Wales. Coastline complexity clearly plays some part in cetacean strandings. However, headland-bays dominate the Australian mass stranding record for 10+ in a stranding (Hamilton and Lindsay, 2014), and these have relatively low complexity compared to re-entrant bays and bays with indentation ratio less than 2. This indicates that coastline complexity is not necessarily the major factor in mass strandings.

Many larger mass stranding events for the five selected non-Ziphiid odontocetes are associated with headland-bays or bays with headland-bay character (Hamilton and Lindsay, 2014). It is not possible from the available data to properly examine any relationship of beaked whale strandings with headland-bays, since there are too few mass strandings of beaked whales involving three or more individuals and dual strandings have insufficient information on sex to eliminate mother-calf pairs. What can be said is that (a) beaked whales have stranded in several headland-bays where larger mass strandings (10+ in a stranding) of other odontocetes have occurred and (b) with an increase in the number of beaked whales in a stranding event, or in the number of beaked whale stranding events at a site, the correlation with headland-bays also increases. At least 25 of 45 beaked whale strandings (56%) of two or more individuals (mother-calf pairs included) occurred in bays with headland-bay character, with three in indented bays. At least 9 of the 13 sites (69%) with 3 or more beaked whale stranding events have significant headland-bay character (Fig. 2). Five of 7 sites (71%) with three or more beaked whales in a stranding event were in a headland-bay, with one in an indented bay with interior headland-bays (Cloudy Bay), and one site poorly located.

Mass strandings

It is commonly reported that odontocetes often mass strand in high numbers, but that mysticetes do not (e.g. Sergeant, 1982), primarily related to social structure (see below). The Australian non-Ziphiid odontocete and mysticete strandings in our database follow this pattern. The two mysticetes had almost exclusively single strandings, and the five non-Ziphiid odontocetes had maxima of 13 to 250 in a stranding, with 66 strandings of 10+ individuals. However, the Ziphiid strandings do not follow this pattern. They fit between these two extremes.

D'Amico *et al.* (2009) list 136 worldwide beaked whale strandings of two or more individuals from 1874–2004, including Australian data. Forty-three of the 136 (32%) involved more than three animals, with ten of these for thirteen or more animals. D'Amico *et al.* (2009) observed 15 to be the usual worldwide maximum in a single event for any beaked whale species, with a maximum ever recorded of 28 Gray's beaked whales in a single event in 1874 at Chatham Island, New Zealand. Of the 35 Australian events with 2+ in a stranding, seven have more than 2 individuals, with a maximum of 6 in a single event (Table 1). Beaked whales stranded singly for 89% of recorded events (Table 1). Some beaked whale species have only single stranding events

around Australia to date (Arnoux's, Ginkgo, Longman's, southern bottlenose, True's). Only Gray's, Shepherd's, and strap-toothed beaked whales have recorded strandings of more than two individuals.

Worldwide strandings of two or more beaked whales for 1950–2004 totalled 126, or 2.3 a year on average (D'Amico *et al.*, 2009). This is a lower bound, since some will not be discovered or recorded. For the 29 years from 1982–2010, Australia recorded 31 events involving 2+ beaked whales in a stranding (one per year), including mother-calf pairs. Without mother-calf pairs the rate may well be half this, but the information is insufficient to examine this point.

Species size, social group size and inshore-offshore species

There is no obvious correlation in the present data of whale species size with numbers in a stranding. The maximum numbers in strandings of any particular odontocete species in the Australian data matches two factors observed elsewhere in the world. One is the typical size of their pod or social group, and the degree of social cohesion within the group (Whitehead, 2003). The second factor is that offshore species live-strand more frequently than inshore species, with the implication that the offshore species may not have learned to navigate in coastal waters (Klinowska, 1985). For example, often killer whales live close to shore (e.g. Tyack *et al.*, 2006) and are not typically involved in mass strandings. In line with this observation, Morrice *et al.* (2002), and Ross (2006) state that killer whales rarely strand around Australia, with only three mass strandings noted (our database has two).

Humpback whales migrate northwards along the Australian east coast for several weeks in austral winter months in an almost continuous stream of individuals, with the peak northwards migration in June–July (Franklin *et al.*, 2011). They regularly occupy shallow areas such as Hervey Bay in Queensland, which is less than 18m deep, often with calves (Franklin *et al.*, 2011). They occasionally intrude into shallow enclosed areas with depths less than 30m such as Jervis Bay, New South Wales and sometimes Sydney Harbour (pers. obs.). However, the seasonal presence of large aggregates of humpback whales in shallow coastal waters has not led to mass strandings. This is probably because the amount of time spent close to shore on seasonal migrations habituates them to the presence of land from birth, and to navigating along coastal routes. When in coastal areas they can therefore be regarded as an inshore species, together with calves still 'learning the road' which are more susceptible to stranding mishaps, particularly during the return to Antarctica in October–November.

Seasonality in strandings

Summer beaked whale strandings

Beaked whale strandings overall occurred more for January to April than in other seasons (Fig. 8), and no live strandings were recorded for June to September. The exception is the Ginkgo beaked whale, for which all five strandings were in cooler months (May to August). The 101 year record for sperm whales (which are also deep diving odontocetes) does not show an enhancement in summer strandings (Fig. 8). Summer stranding of beaked whales would not be expected to relate to seasonal availability of prey, if beaked whales always feed at great depth. The circulations and properties of waters at 1,000m about Australia are generally decoupled from surface waters, and variations in temperature, salinity, and nutrients at 1,000m are small compared to differences in near surface waters. Prey at 1,000m would not be expected to be subject to the degree of seasonality in primary productivity of near surface waters.

Ross (2006) notes that the strap-toothed beaked whale may use waters adjacent to the continental slope for calving, but gives no evidence for this. Our database suggests another possibility. In South Australia in December–January one live straptooth beaked whale mother-calf pair stranded in Spencer Gulf, and one live pregnant Arnoux's beaked whale female stranded in St. Vincent Gulf. The gulf waters are less than 30m deep, far less than the 1,000 to 2,000m that some other beaked whale species are reported to dive to for food, and 200km distant from the edge of the continental shelf. It was earlier noted that of 29 dual beaked whale strandings, five were a female-calf pair, one included a calf, and ten others included a female. Four were not a female-calf pair, and nine had no identification on sex. The data suggest that beaked whales possibly frequent shallow or sheltered inshore waters for calving and subsequent resting of mother-calf pairs, rather than areas adjacent to the continental slope. This would potentially explain why beaked whales are not restricted to waters deeper than the continental shelf, despite their reported deep diving feeding behaviour.

Seasonality in mysticete strandings

The peak of the northwards migration of humpbacks along Australia's east coast is in June–July (Franklin *et al.*, 2011). Humpback strandings peak in July and October, indicating the northern migration and the southwards return to Antarctica. The spatial distribution of minke strandings is similar to that of the humpbacks (Fig. 3d), but strandings peak in June and September, indicating a migration cycle one month ahead of the humpbacks.

Seasonality in non-Ziphiid odontocete strandings

An interesting finding from the database is the much lower stranding rate of sperm whales around Australia in June to September over 101 years (half that of other months, see Fig. 8). This may indicate that a significant proportion of sperm whales which are usually present about Australia move away from Australia in June, returning after September. It is known that groups of larger male sperm whales move from Antarctic latitudes to equatorial regions at this time of the year for the winter breeding season, after which they return to Antarctic latitudes in summer (Culik, 2010). The coincident decrease in strandings suggests a similar movement of sperm whales away from Australia to deeper waters such as the warmer water breeding grounds, but whether of females and/or males cannot be determined from our data. Long-finned pilot whales strand in highest numbers from October to March in a quite different seasonal pattern than sperm whales. False killer whale mass strandings rise to a peak over May–June–July. This is possibly related to the peak migration time of mysticetes, which can form their prey.

Relation of strandings to sea temperatures

Evans *et al.* (2005) presented evidence of a 12–14 year periodicity in strandings for recently deceased or live cetaceans about Tasmania and Victoria. They postulated that this periodicity might relate to zonal trends in wind strengths, which cycle across quasi-decadal time scales. They found some correlation between the periodicity and years with stronger local winds in August (Southern Hemisphere winter). They loosely associated the periodicity with higher numbers of summer strandings, postulating these as being caused by enhanced winter productivity in coastal regions, caused by the stronger winds, bringing whales northwards.

Kemper and Ling (1991) tentatively associated a rise in summer stranding events for southern states with observer effort and Evans *et al.* (2005) invoked observer effort to explain lower numbers of winter strandings. However, the seasonality observed in the present paper, particularly for beaked whale strandings, corresponds more to seasonality in ocean temperatures, not to the summer air temperatures which may bring more observers to beaches and coasts (Fig. 8). Although the peak in January–February for beaked whale strandings shown in Fig. 8 is likely enhanced by observer effort, the expected corresponding enhancement is not seen in November–December, which are at background levels. While observer effort is a factor in reporting of strandings, it is apparently over-ridden for beaked whales by the correlation with sea temperatures.

There is a substantial lag of two to four months in ocean near-surface temperatures compared to air temperatures in southern Australian latitudes (Fig. 8). Two factors drive the lag. One is the thermal lag or thermal inertia of water compared to air, causing water to retain heat content far longer than air. The second is due to polewards flowing warm boundary currents on both sides of Australia, which bring warm subtropical waters to southern latitudes some months after they first arise from strong solar heating at latitudes 10–15°S.

The wind-driven subtropical circulation gyre of the South Pacific Ocean transports warm waters southward along the east Australian coast in the East Australian Current (EAC), a western boundary current. In the southern portions of the gyre, sea temperatures lag air temperatures because of the time taken to transport waters from one location to another. The EAC turns seawards near the latitude of Sydney, but some or all of this current or warm water rings spawned by it sometimes move southwards along the Australian coast to eastern Tasmania and much farther southwards (Harris *et al.*, 1987). Southern latitudes off south-eastern Australia consequently experience their warmest ocean temperatures in February–March, not mid-December to January (a two month lag), and their coolest ocean temperatures in or around September, not June–July (a three month lag). Maria Island (42.633° S, 148.083° E) off east Tasmania shows this pattern (Fig. 8, also see Harris *et al.*, 1987 and Ridgway, 2007).

A warm current also flows polewards off Western Australia, but is driven by sea surface height differences between the tropics and waters south of Australia, rather than being part of the wind driven Indian Ocean gyre. The Leeuwin Current brings highest near surface ocean temperatures to the Perth region of Western Australia in April–May (a four month lag), with coolest temperatures in September, not in June (a three month lag) (Hamilton, 1986; Rochford, 1984). This effect may continue eastwards. Continuations of the Leeuwin Current flow eastwards round The Capes into the Great Australian Bight to as far eastwards as Tasmania (Australian Government, 2007). Maps of the lag of sea surface temperature compared to air temperature for the Australian region are found in Li *et al.* (2013).

CONCLUSIONS AND SUMMARY

Information on strandings around Australia of beaked whales compared to other selected cetaceans are summarised as follows.

(1) Twelve species of beaked whales have stranded around Australia (Table 1). The maximum number of cetaceans observed in any one stranding event around Australia for 1868 to 2010 (143 years) is much less for beaked whales (maximum of 6), and two mysticete species (humpback (1) and Antarctic minke whales (2)), than for five species of non-Ziphiid odontocetes: false killer (250), long-finned pilot (200 to 250), sperm (65), melon-headed (51) and killer whales (13). The number of recorded beaked whale events with three or more in a stranding is seven, compared to 66 non-Ziphiid mass strandings with 10+ in a stranding for the five odontocetes just named. This makes it difficult to establish patterns of stranding behaviour for beaked whales. It is believed that the typical size of a species' pod or social group, and the degree of social cohesion within the group, is related to the maximum numbers in strandings (Whitehead, 2003). This would imply that beaked whales around Australia have smaller pods than the five selected non-Ziphiid odontocete species, but it may also be that as deep diving feeders they do not usually inhabit shallow waters in groups.

(2) For single strandings upwards, beaked whales have the same continental scale stranding patterns around Australia as the five non-Ziphiid odontocetes and the two mysticetes listed in the previous paragraph. Reported strandings predominantly occurred in the southern half of the Australian continent south of 20°S. For the humpback whale this appears related to their usual northern limits of migration along both the eastern and western coastlines of Australia to sheltered warm-water breeding grounds. For the non-Ziphiid odontocetes, this may occur because they strand more often than elsewhere in headland-bays (Hamilton and Lindsay, 2014). Wave and swell conditions south of 20°S are conducive to formation of headland-bays. Headland-bays are not numerous north of 20°S because Southern Ocean swell and swell from other latitudes is attenuated by greater travel distances, wide continental shelves and barrier reefs. Some beaked whale species strand on a particular part of the Australian coastline, for example Blainville's whales predominantly strand on the east coast. There are some indications that beaked whale strandings may occur more often in headland-bays, as for the five selected non-Ziphiid odontocetes, but this remains to be confirmed. There is an indication that Antarctic minke whales may also strand predominantly in headland-bays, whereas the humpback whale seemed

to strand almost anywhere. Although the causes for strandings of mysticetes and odontocetes may be different, the coincidence in their overall geographical stranding patterns allows subsequent more detailed examination and comparison of the characteristics of their stranding sites to be performed without complication.

(3) Of the six beaked whale species which exhibit apparent seasonality in strandings, five have most strandings in February–March (Andrew's, Arnoux's, Gray's, Hector's, strap-toothed), and a lower number of strandings in or about September, whereas all five Ginkgo strandings were in May to August. While observer effort will influence these numbers, they conspicuously lag the warmer air temperatures which affect observer movements to or from coastal zones by two to four months, and are directly correlated with the seasonal cycle of sea temperatures about southern Australia. The observed seasonality in beaked whale strandings is then indicated to be related to oceanographical factors, not solely to observer effort, as might be expected for aquatic organisms.

Grouping the stranding data for all beaked whale species overcomes some of the difficulties of having lower numbers of mass strandings to analyse than for other odontocetes about Australia, and brings out some seasonality very strongly. Comparing the composite behaviour with that of other cetaceans also allows more confidence to be placed in some observations. For example, the maximum number of beaked whales in stranding events about Australia is much lower than for five other odontocete species, and is higher than two mysticetes. Seasonal stranding patterns and stranding site characteristics of beaked whales around Australia are generally aligned more with those of other odontocetes than those of mysticetes. In general terms the examination indicates that sites of repeated beaked whale strandings, and sites of mass strandings of beaked whales, can be expected to be associated with the same coastal conditions on the average as mass strandings of other odontocetes around Australia, i.e. sites with a sandy headland-bay character, rather than the straight featureless coastlines often seen for the single stranding behaviour of humpback whales.

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Age classification of bowhead whales using recursive partitioning

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ABSTRACT

An algorithm was derived for using morphometric data to classify bowhead whales into three age brackets: over 90 years ('very old'); 60–90 years ('old'); and under 60 ('younger'). Recursive partitioning was applied to a subset of the data from post mortem examinations. This subset consisted of whales with higher quality data scores and with either estimated ages or characteristics of very old animals such as: near-maximum body length and baleen length; heavy scarring; and ancient weapons embedded in them. Statistical analysis suggested that for males, body length and peduncle girth provide the most useful information for this age classification. For females, anterior flipper length and body length were the key variables for classifying age. If anterior flipper length is not available for females, then body length, baleen length and peduncle girth may be used to classify age.

KEYWORDS: CLASSIFICATION TREES; MORPHOMETRIC GROWTH; BOWHEAD WHALE; POPULATION PARAMETERS; NORTHERN HEMISPHERE; ARCTIC; WHALING – ABORIGINAL; AGE DETERMINATION

INTRODUCTION

The subsistence harvest of bowhead whales (*Balaena mysticetus*) in the Bering-Chukchi-Beaufort (BCB) Seas stock provides important nutritional and cultural needs for several coastal Alaskan native communities and Russian native communities in the Chukotka region. The Alaska Eskimo Whaling Commission (AEWC) locally manages the harvest through an agreement with the US National Oceanic and Atmospheric Administration (NOAA). The hunt has been the subject of scientific scrutiny from both the US and international scientific community since the 1970s. In 1977, the International Whaling Commission (IWC) set a zero catch limit for the hunting, citing concerns about the population size and increased hunting mortality. Following this, in 1978 at an IWC special meeting, a quota system for the hunt was established. The quota was uninterrupted until 2002, gradually increasing as better information on population size and rates of increase became available (IWC, 1986, pp.17–18; 1989, p.20, p.50; 1992, pp.27–28, p.49, pp.61–62; 1995, pp.21–23, pp.73–75). However, at the 2002 IWC meeting (Shimonoseki, Japan), the quota renewal was blocked based on concerns about possible stock sub-structure within the BCB bowhead whale population (IWC, 2003, pp.18–22).

At the 2004 annual meeting of the IWC, the US committed to conducting bowhead whale stock structure research. Elements of the stock structure programme were discussed during the 2004 meeting of the IWC Scientific Committee (IWC, 2005a, pp.23–24; 2005b).

Givens *et al.* (2004) provided some of the first genetic evidence of population structuring in BCB bowhead whales. They also found evidence of age related genetic structuring termed 'generational gene shift' (GGS) and concluded that:

> 'As yet, it is impossible to determine if observed differences among groups are attributable to:
>
> (1) a single stock exhibiting generational gene shift;
>
> (2) a sub-stock harvested around St. Lawrence Island;
>
> (3) two stocks having different temporal migration patterns past Barrow;
>
> (4) inadequate data with small sample sizes consisting of unrepresentative whales and potentially unreliable genetic loci; or
>
> (5) some combination of the above.'

Jorde *et al.* (2007) also found evidence of temporal genetic structure in whales migrating past Point Barrow in autumn. This structure could be related to age classes since there is stock size/age structure in both the spring and autumn migration, and the magnitude was unclear. Givens *et al.* (2010) used a larger data set, but were unable to detect multiple populations in the western Arctic bowhead whale population, although the population was distinct from those in the eastern Canada and in the Okhotsk Sea. They also did not incorporate the temporal structure suggested by Jorde *et al.* (2007).

Interpretation of genetic data from samples collected during the bowhead whale hunt is complicated by two factors: (1) the population is out of genetic equilibrium resulting from a recent history of a large reduction (from commercial whaling) followed by a rapid expansion; and (2) the hunt is known to be non-random with respect to age (smaller animals are often preferred) (Archer *et al.*, 2010). To aid in interpreting empirical data, simulations were conducted to emulate the population dynamics and the sampling. The latter required age estimates of the whales sampled (B. Taylor, pers. comm.; Martien *et al.*, 2007).

Expected patterns of genetic heterogeneity can be computed under the age model and compared to previously observed data (Archer *et al.*, 2010). Relevant cohorts for this comparison are 'very old', 'old' and 'younger' whales. The 'very old' whales were mostly born before 1909, which was near the end of commercial hunting and represents whales

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with a genetic structure which pre-dates the potential genetic bottleneck caused by commercial whaling. It is estimated that the whales in this group were believed to be at least 90 years old when harvested. 'Old' whales are defined to be between 60 and 90 years in age. All others are 'younger' whales.

More generally, age classification based on basic morphometric data can provide valuable input to models and analyses that rely on age information for bowhead whales lacking more direct estimates of age. The research summarised in this paper was motivated by such bowhead whales.

METHODS

A subset of the bowhead whale harvest database maintained by the North Slope Borough (1976–2005) was used. The variables included in this study were: whale identification code; an assessment of the data quality; sex; body length; length of longest baleen plate; testis length; anterior flipper length; peduncle girth; white peduncle patch; white eyebrow; corpora count; estimated age; aging technique; and verbal comments describing other characteristics of note. In addition, ratios of morphometric measurements were also included. These were peduncle girth/body length, anterior flipper length/body length, peduncle girth/anterior flipper length and baleen length/body length.

A subset, with 74 females and 49 males, was selected according to the following criteria. Whales were included that had the highest data quality scores (1 and 2; scale 1–5), estimated age or age category, and data on at least two morphometric measurements. Due to the small number of 'very old' whales, and because the goal was to classify whales into the three age cohorts of Martien *et al.* (2007), whales were also included in the dataset that did not have estimated ages, but that were believed to be particularly old based on verbal comments from scientists and hunters. Suitable comments included 'stone point in blubber' since it is acknowledged that hunting with stone harpoon points ceased in ~1880 with the advent of alternative weapons for hunting. Thus a whale with a stone point in its blubber must have been very old, and certainly alive before 1909. Whales with extreme corpora counts (e.g. whale 89B3, with corpora count 41) or testes sizes (e.g. whale 95B7, testis length 110 cm) also were classified as 'very old'.

Recursive partitioning (Clark and Pregibon, 1992) is a statistical method for classifying multivariate data points into categories; in the case of this study, age is divided into three bins referred to hereafter as age classes. The ability to predict membership in more than two categories gives recursive partitioning a critical advantage over categorical data methods (such as logistic regression) that only apply to two categories (Neter and Wasserman, 1974). The input covariate data may be qualitative or quantitative. The output dependent variable is categorical.

The recursive partitioning-algorithm creates a classification tree by a series of binary splits of the data based on covariate values. At each branching node of the tree, the data are partitioned into two subgroups based on a binary split at a selected value and covariate. The covariate and the splitting value for a node are selected to maximise the impurity reduction, which is measured as the sum over category 'i' of the simple Gini index $f(p_i) = p_i(1 - p_i)$ (Breiman *et al.*, 1984). Here p_i is the proportion of individuals placed into category 'i' that actually belong in category 'i'. For example, if individuals A1, A2, A3, B1 and B2 are split into group A = {A1,A2} and group B = {A3,B1,B2} then the value of the Gini index would be $(1)(1 – 1) + (2/3)(1 – (2/3)) = 0.22$. If all individuals at a node are correctly categorised, then the impurity is zero. Ideally, the final subgroups at the end of the splitting process would each contain individuals from only one of the categories.

In recursive partitioning a tree can be 'grown' and/or 'pruned'. In addition, to limit overspecification, *minsplit* is a parameter that can be set as the minimum number of observations that must exist in a node, in order for a split to be attempted (Therneau and Atkinson, 2006, function *rpart.control*). For this study, *minsplit* = 5 was used. Pruning is the removal of nodes to simplify a tree (Breiman *et al.*, 1984). For the present analysis the trees branched on only a small number of variables, resulting in simple trees (see Figs 1–3), therefore pruning was not needed.

Using recursive partitioning, individuals with only partial information can be included. Any individual with missing information for some covariate(s) is not used in setting the

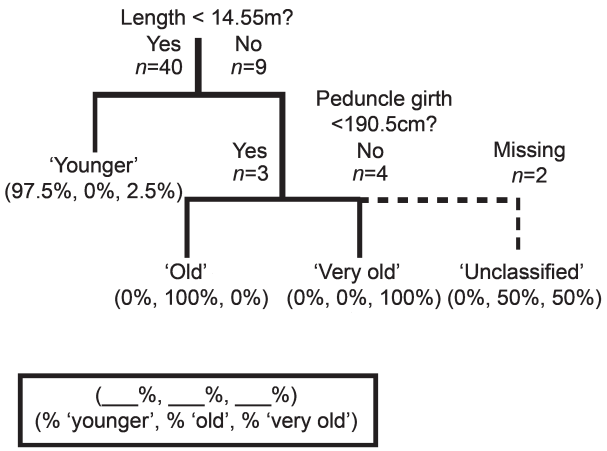

Fig. 1. Partition for age classification of male bowhead whales using body length and penduncle girth.

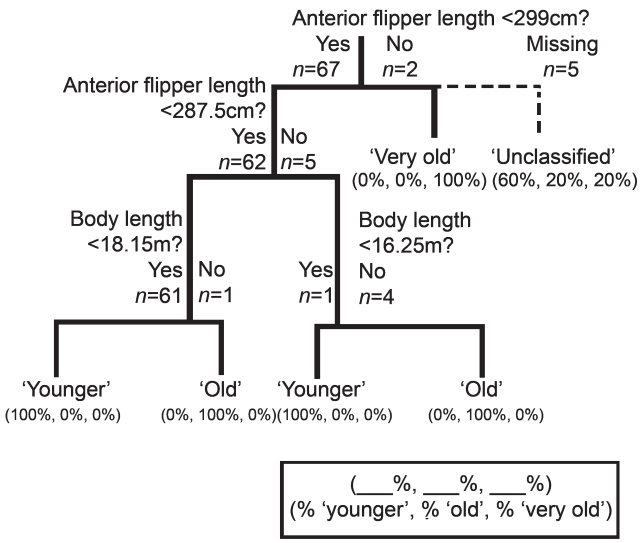

Fig. 2. Partition for age classification of female bowhead whales using anterior flipper length and body length.

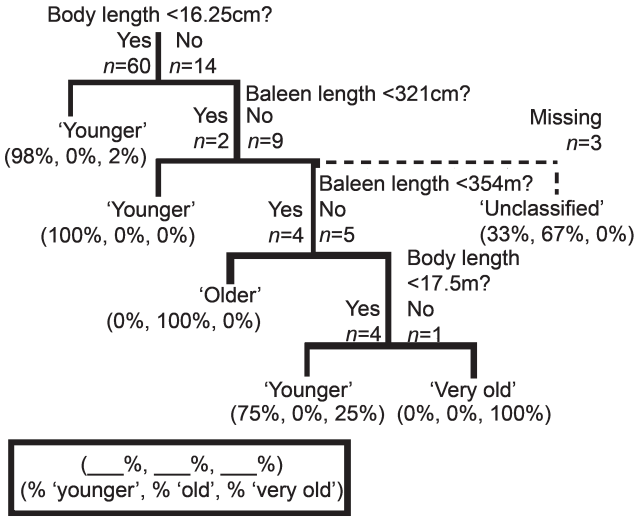

Fig. 3. Partition for age classification of female bowhead whales using body length, baleen length and penduncle girth.

split value for covariate(s) that it is missing, but that individual is included in setting the split values when the relevant covariate data are available. That is, if the peduncle girth measurement for a whale is available, but baleen length is missing, then that whale would be included in setting a split value based on peduncle girth, but could not be used in setting a split value based on baleen length. If a whale is missing a covariate value at any node of the classification tree, then it is classed as 'unclassified'.

Recursive partitioning was implemented using the *rpart* algorithm in the R statistical package (Therneau and Atkinson, 2006). Males and females were analysed separately because growth curves differ noticeably for the two sexes of bowhead whales (Lubetkin *et al.*, 2012); one goal of the study was to partition these whales into age categories based on morphometric measurements that vary with sex (Lubetkin *et al.*, 2012). Separate models are appropriate.

Cross validation provides an assessment of how well a procedure will perform on future data. Assessment of whether a whale is classified correctly via partitioning is based on the estimated age or age class in the data set. For brevity herein this is termed 'actual' age class. 'Leave-one-out cross validation' was used to assess the recursive partitioning modelling algorithm for these data. A partition is computed on the full data set, excluding one observation. It is then determined whether the resulting partition correctly classifies the excluded observation. This process is iterated for each observation in the data set. In addition, the resulting partitions were compared to see how they varied with the slightly reduced data sets. Leave-one-out cross validation is computationally time consuming for large data sets, but feasible for the present data.

Ovarian corpora counts are likely good predictors of age for females (George *et al.*, 2011). Graphical data exploration suggests that females were categorised less successfully than are the males using the variables at hand, except for corpora counts. In the current data set, the age values of many of the females, and of all of the older females, were estimated based on corpora counts. Therefore, it would be circular and not valid to use corpora counts for determining the age class of females.

RESULTS

Males

Based on recursive partitioning of the 49 male bowhead whales in the data set, the initial division was based on body length. The 40 whales with body length less than 14.55m were classified as 'younger'. All 39 of the whales with estimated ages less than 60 years were successfully partitioned off in this step. The longer whales (length at least 14.55m) were classified at this point as 'very old'. This group subsequently underwent a second split based on peduncle girth. The three whales with peduncle girth <190.5cm were reclassified as 'old' (aged 60–90 years), and the four with peduncle girth >190.5cm remained classified as 'very old' (aged over 90 years). Thus all four whales classified as 'very old' and all three classified as 'old', were correctly identified at this final step. In this group of longer whales, one 'very old' and one 'old' were missing peduncle girth data and therefore were 'unclassified'. The classification algorithm consisting of these two splits, based on body length and peduncle girth, correctly classified all but one of the 47 male whales in the data set that had body length less than 14.55m, peduncle girth recorded or both.

The one 'very old' whale (95B16) that was not classified correctly measured 14.1m in length with a peduncle girth of 169cm. It was noticeably the smallest 'very old' whale. The others measured from 15.2 to 17.7m in length, with peduncle girths from 193 to 230cm. Whale 95B16 was aged via aspartic acid racemisation (George *et al.*, 1999) to be 91 years (standard error = 16 years) and was at the low end of the 'very old' age category. The field notes for whale 95B16 were done later and said 'morphometric data suspect' because the examiners were inexperienced – thus in further analyses, this whale should probably be excluded from the dataset.

The classification tree is displayed in Fig. 1 and summarised in Table 1. In interpreting Fig. 1, it can be seen that in the leftmost end node, the partition has classified 40 whales as 'younger'. The vector (97.5%, 0%, 2.5%) under the corresponding end node indicates that 97.5% (39 out of 40) of these whales were estimated to be 'younger'. Similarly 0% (0 out of 40) were estimated to be 'old' and 2.5% (1 out of 40) were estimated to be 'very old'. The vectors under the other end nodes similarly give the age classification percentages.

Empirical probabilities (proportions) are also given in the Table 1. They are P('actual' class i|partitioning based class j). For example, the 40 whales classified via partitioning as 'younger' (up to 60 years) are represented in the 'younger' row for age class via partitioning; 39 of them were actually 'younger' and one was actually 'very old' (over 90 years). Thus, in the 'younger' partitioned row of Table 1, 39 of 40, or 97.5% of the whales were actually 'younger'. This was similar for the other age classes too.

Graphical displays of the data are useful for evaluating the validity of the partitioning results. Fig. 4 shows body length versus peduncle girth for the 47 male bowhead whales with sufficient data to be classified. The points are coded by age class. It is readily apparent from this plot that body length and peduncle girth would be good predictors for age class. The dotted lines added to the plot indicate the subgroupings from the recursive partitioning algorithm. Whales with points

Table 1
Empirical classification counts for male bowhead whales, based on body length and peduncle girth.

Age class via partitioning	'Actual' (estimated) age class			
Count (% within estimated age class)	Under 60 years 'younger'	60–90 years 'old'	Over 90 years 'very old'	Total
Under 60 years 'younger'	39 (97%)	0 (0%)	1 (2.5%)	40
60–69 years 'old'	0 (0%)	3 (100%)	0 (0%)	3
Over 90 years 'very old'	0 (0%)	0 (0%)	4 (100%)	4
Unclassified due to missing data	0 (0%)	1 (50%)	1 (50%)	2
Total	39	4	5	49

to the left of the vertical dotted line were classified as 'younger'. The crosses indicate the whales that actually were 'younger'. From Fig. 4 it can be seen that all of the 'younger' whales were correctly classified by the recursive partitioning algorithm. Whales with points to the right of the vertical dotted line and below the horizontal dotted line were classified as 'old'. The circles indicate the whales that actually were 'old'. Whales 95B7 ('very old') and 83G1 ('old') are missing from the plot since their peduncle girth measurements are missing. The algorithm classified all whales in the upper section of the plot as 'very old'. The whales classified in the data set as 'very old' correspond to the triangular plot points. The triangular point outside this region corresponds to a 'very old' whale classified as 'younger' by recursive partitioning.

Cross validation analysis for males yielded that six of the 49 leave-one-out iterations resulted in misclassifications and two resulted in 'unclassified' status due to missing data. In the full dataset procedure, one of the 49 whales was misclassified and two were unclassified (see Table 3). The resulting classification tree was the same as that from the full data results in 44 of the 49 leave-one-out runs. In four of the remaining five runs, the cut-off values differed slightly (differences of up to 0.25m for length and up to 5.5cm for peduncle girth). All the misclassified individuals were 'near the border'. These data partition so finely that leaving one out along the boundary between adjacent categories could result in a slight shift in the algorithm's cut-off values, causing the left-out observation to be misclassified into the adjacent category. This would not be surprising in any data set, especially in this analysis where some age classes have few members.

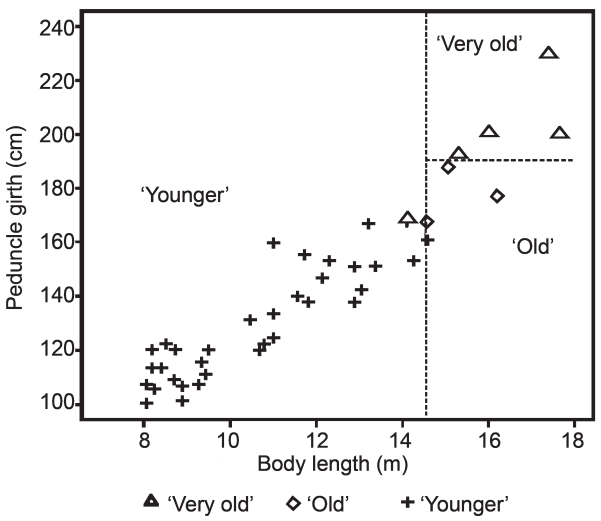

Fig. 4. Body length versus penduncle girth for 49 male bowhead whales.

Females

For the 74 female whales in the data subset, the first two binary splits were based on anterior flipper length. The first is at 299cm, and the second at 287.5cm. Five of the 74 females were missing anterior flipper values and therefore could not be classified. Further divisions within the resulting groups of the remaining 69 whales classify individuals based on body length. Within the 287.5–299cm flipper length group, individuals at least 16.25m in length were classified as 'old' (60–90 years). The shorter individuals were classified as 'younger' (under 60 years). Within the <287.5cm flipper length group, individuals that were at least 18.15m in length were classified as 'old' (60 to 90 years). Again, the shorter individuals were classified as 'younger' (under 60 years). The resulting classification tree is shown in Fig. 2. It yielded perfect classification for the 69 female whales having anterior flipper data.

In recognition that not all whales have anterior flipper length measurements, which was the first variable used in this classification tree, a second binary tree was made for when this information was unavailable. The resulting tree (Fig. 3) used body length at the first split and then baleen length. Classification results are summarised in Table 2. This tree yields correct classifications for 69 of the 71 whales in

Table 2
Empirical classification counts for female bowhead whales, based on body length and peduncle girth.

Age class via partitioning	'Actual' (estimated) age class			
Count (% within estimated age class)	Under 60 years 'younger'	60–90 years 'old'	Over 90 years 'very old'	Total
Under 60 years 'younger'	64 (97%)	0 (0%)	2 (3%)	66
60–69 years 'old'	0 (0%)	4 (100%)	0 (0%)	4
Over 90 years 'very old'	0 (0%)	0 (0%)	1 (100%)	1
Unclassified due to missing data	1 (33%)	2 (67%)	0 (0%)	3
Total	65	6	3	74

Table 3

Cross-validation results for male bowhead whales. Available numerical age estimates given for misclassified whales.

Age class via partitioning	'Actual' (estimated) age class			
Count (% within estimated age class)	Under 60 years 'younger'	60–90 years 'old'	Over 90 years 'very old'	Total
Under 60 years 'younger'	38	1	1	40
60–69 years 'old'	1 (58 years)	1	2 (160 years)	4
Over 90 years 'very old'	0	1	2	3
Unclassified due to missing data	0	1	1	2
Total	39	4	6	49

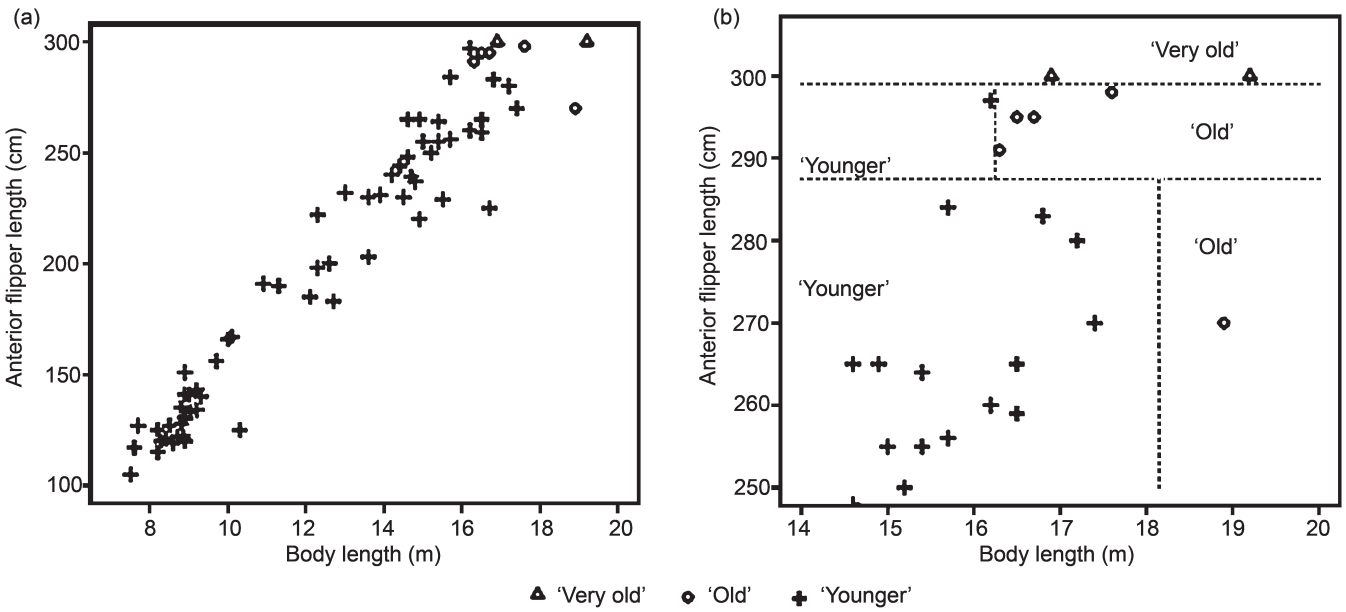

Fig. 5a. Anterior flipper length versus body length for 74 female bowhead whales.
Fig. 5b. Anterior flipper length >250cm versus body length >14m for female bowhead whales.

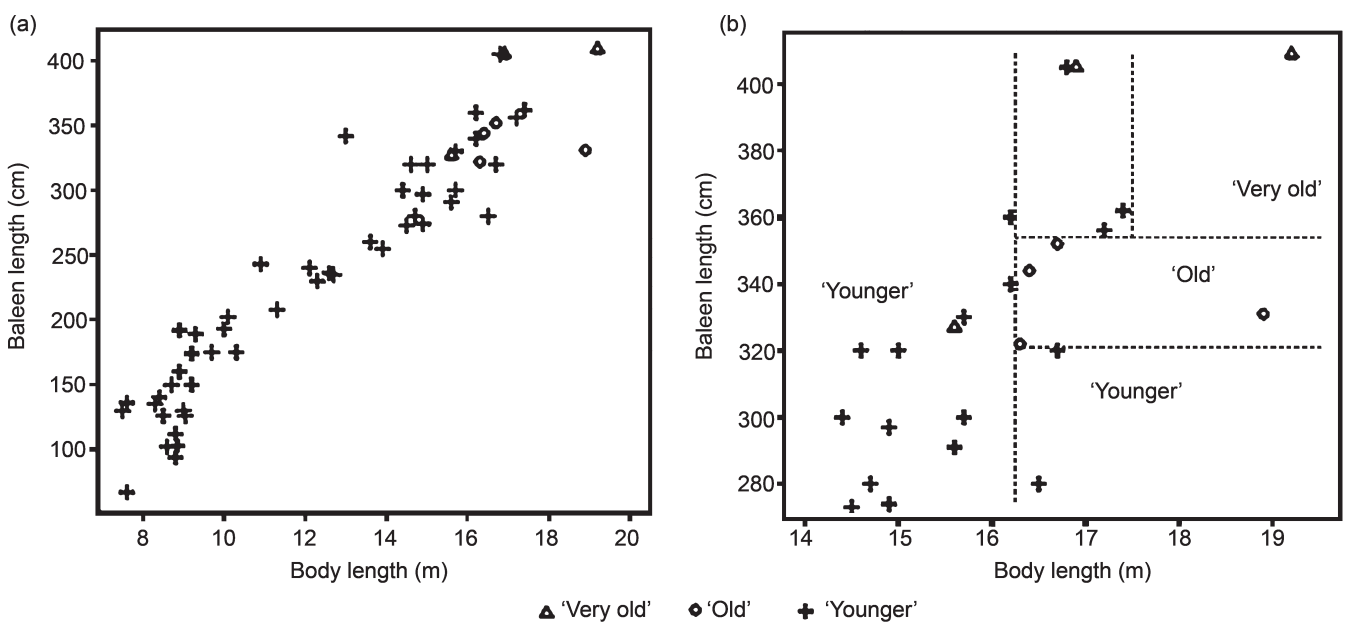

Fig. 6a. Body length versus baleen length for 74 female bowhead whales.
Fig. 6b. Body length >14m versus baleen length >275cm for female bowhead whales.

the data set having body length <16.25m, baleen lengths recorded or both.

Graphical evaluation of the results for the 69 female whales with anterior flipper length in the data set in Fig. 5a shows anterior flipper length versus body length, corresponding to the main recursive partitioning algorithm. Fig. 6a shows body length versus baleen length for these whales. These are the primary variables used in the back-up partitioning algorithm for the case when anterior flipper length was unavailable. Fig. 5b and 6b focus on the upper ranges of the displayed variables to show the partitions more clearly.

Cross validation analysis for the females using anterior flipper length and body length yielded three misclassifications in the 74 leave-one-out iterations. These corresponded to whales 82WW1, 92B2 and 92B4. The two misclassifications in the original runs were whales 92B2 and 03B9. Whales 82WW1 and 92B4 both had two of the four longest anterior flipper measurements, 298cm and 297cm, respectively. In the runs when these whales were left out, the initial split was not made that separated off the whales with longest anterior flipper length. Whale 92B2's short body length resulted in its consistent misclassification. It was shorter than all of the whales assigned to the 'old' age class, and shorter than 15% of the whales assigned to the 'younger' age class.

DISCUSSION

With so few whales in the 'very old' and 'old' age classes, it is not surprising to have slight shifts in the classification trees when one of them is removed from the data set. Changes in the classification trees and in the misclassification rates from the leave-one-out iterations were minor. The recursive partitioning algorithm appears to function well and to give reasonably stable results for age classification of the data set of bowhead whales considered.

In assessing the accuracy of the recursive partitioning algorithm for age classification, it was assumed that the age class assigned to each whale in the data set was accurate. In fact, the age classes are based on age estimates from a variety of estimation procedures including corpora counts for females, aspartic acid racemisation and field notes. Incorrect age classifications in the data set would impact the numerical assessments of the effectiveness of recursive partitioning for these data. In Tables 1 and 2 'Actual' (estimated) age class are referred to.

The recursive partitioning algorithm performs well in identifying age classes for these bowhead whales, achieving a 97–100% correct classification result for whales with key data recorded. Leave-one-out cross validation results indicate that the algorithm is reasonably stable.

These analyses were based on small sample sizes and the data in the upper age range were sparse. Several of the oldest whales did not have numerical estimates for age, but based on qualitative findings (e.g. heavily scarred) were deemed to be 'very old'. The results therefore have limited reliability, especially in the upper age range. The small numbers of 'very old' and 'old' whales likely increase sensitivity of the estimated threshold values at tree nodes, especially for those age classes of particular interest.

There are substantially more data for the younger age classes; hence, richer models could be developed for those animals (Lubetkin *et al.*, 2008; Lubetkin *et al.*, 2012). Such models could potentially yield numerical estimates of ages rather than relying on age classes and will be a subject of further research. The use of age classes in this analysis was appropriate in the present study since a primary concern was with the detection of 'very old' whales.

The morphological growth patterns are of some interest. For females, an allometric relationship was found and that suggests the pectoral limbs (flippers) for very old females are disproportionately larger than younger whales of similar body length. For males, body length and peduncle girth provide the most useful information for age classification. The latter suggests that the caudal region of old males is more robust than younger males of similar length. The evolutionary significance of these growth patterns (for both males and females) are unknown.

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Occurrence, distribution and abundance of cetaceans in Onslow Bay, North Carolina, USA

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ABSTRACT

In this paper the occurrence, distribution and abundance of cetaceans in offshore waters of Onslow Bay, North Carolina, USA is described. Between June 2007 and June 2010 monthly aerial and shipboard line-transect surveys were conducted along ten 74km transects placed perpendicular to the shelf break. In total 42,676km of aerial trackline (218 sightings) and 5,209km of vessel trackline (100 sightings) were observed. Seven species of cetaceans were observed, but the fauna was dominated strongly by common bottlenose and Atlantic spotted dolphins. Both species were present year-round in the study area. Using photo-identification techniques, five bottlenose dolphins and one spotted dolphin were resighted during the three-year period. In general, the abundance of cetaceans in Onslow Bay was low and too few sightings were made to estimate monthly abundances for species other than bottlenose and spotted dolphins. Maximum monthly abundances of bottlenose and spotted dolphins were 4,100 (95% CI: 1,300–9,400) in May 2010 and 6,000 (95% CI: 2,500–17,400) in March 2009, respectively. Bottlenose dolphins were found throughout the study area, although they were encountered most frequently just off the shelf break. In contrast, spotted dolphins exhibited a strong preference for waters over the continental shelf and were not encountered beyond the shelf break.

KEYWORDS: ABUNDANCE ESTIMATE; MONITORING; SURVEY-COMBINED; TRENDS; PHOTO-ID; ATLANTIC OCEAN; NORTHERN HEMISPHERE; ATLANTIC SPOTTED DOLPHIN; MODELLING; BOTTLENOSE DOLPHIN; COMMON DOLPHIN; RISSO'S DOLPHIN; ROUGH-TOOTHED DOLPHIN; FIN WHALE; SPERM WHALE; SHORT FINNED PILOT WHALE

INTRODUCTION

Understanding of the distribution and abundance of many populations of offshore cetaceans is limited because of the difficulty and expense of obtaining quantitative estimates of these parameters (Hammond, 2010). Surveys of such populations typically occur at very broad spatial scales, interspersed by long time periods (e.g. Hammond *et al*., 2002, 2013; Gerrodette and Forcada, 2005). Thus, there is often a spatial mismatch between available data and information needed to assess the potential impact of human activities on pelagic cetaceans in specific areas. In addition, the snapshots of cetacean occurrence and density from broad-scale surveys provide no information on potential seasonal trends in these parameters.

This paper reports the results of an intensive three-year study of the occurrence, distribution and abundance of cetaceans in Onslow Bay, North Carolina, USA, within the South Atlantic Bight. In 2005, the US Navy proposed development of an Undersea Warfare Training Range (USWTR) in this area (Department of the Navy, 2009). Relatively little was known regarding the occurrence of cetaceans in the offshore waters of Onslow Bay because most previous surveys in the South Atlantic Bight had been conducted at a very coarse spatial scale (Mullin and Fulling 2003; Garrison *et al*. 2010). To address this data limitation, an intensive survey programme was begun in June 2007. In 2009, the Navy changed its preferred site for the USWTR to an area off Jacksonville, Florida (Department of the Navy, 2009), but our surveys continued in Onslow Bay.

The proposed USWTR in Onslow Bay consisted of an area of 1,715km^2 that straddled the 200m isobath (Fig. 1). A variety of cetaceans were known or believed to occur in this area, including shelf-associated species such as Atlantic spotted dolphins (*Stenella frontalis*) and common bottlenose dolphins (*Tursiops truncatus*) and pelagic species, such as short-finned pilot whales (*Globicephala macrorhynchus*) (Mullin and Fulling, 2003; Garrison *et al*., 2010). In addition, several mysticetes, such as endangered North Atlantic right whales (*Eubalaena glacialis*), likely use portions of Onslow Bay as a migratory corridor (Schick *et al*., 2009).

A monitoring plan was developed that included monthly aerial and shipboard surveys for cetaceans and sea turtles, strip-transect surveys for seabirds and passive acoustic monitoring of cetaceans with a towed hydrophone array and a series of moored recorders. The results of three years of aerial and shipboard line-transect surveys for cetaceans, beginning in June 2007 are reported in this paper. The results of the passive acoustic monitoring programme (Hodge, 2011) and sea turtle and seabird surveys (Thorne, 2010) will be reported separately. A suite of complementary field methods (aerial surveys, vessel surveys and passive acoustics) deliberately selected to maximise the probability of detecting all cetaceans in the study area, including deep-diving and cryptic species (Barlow, 1999). To extend the time

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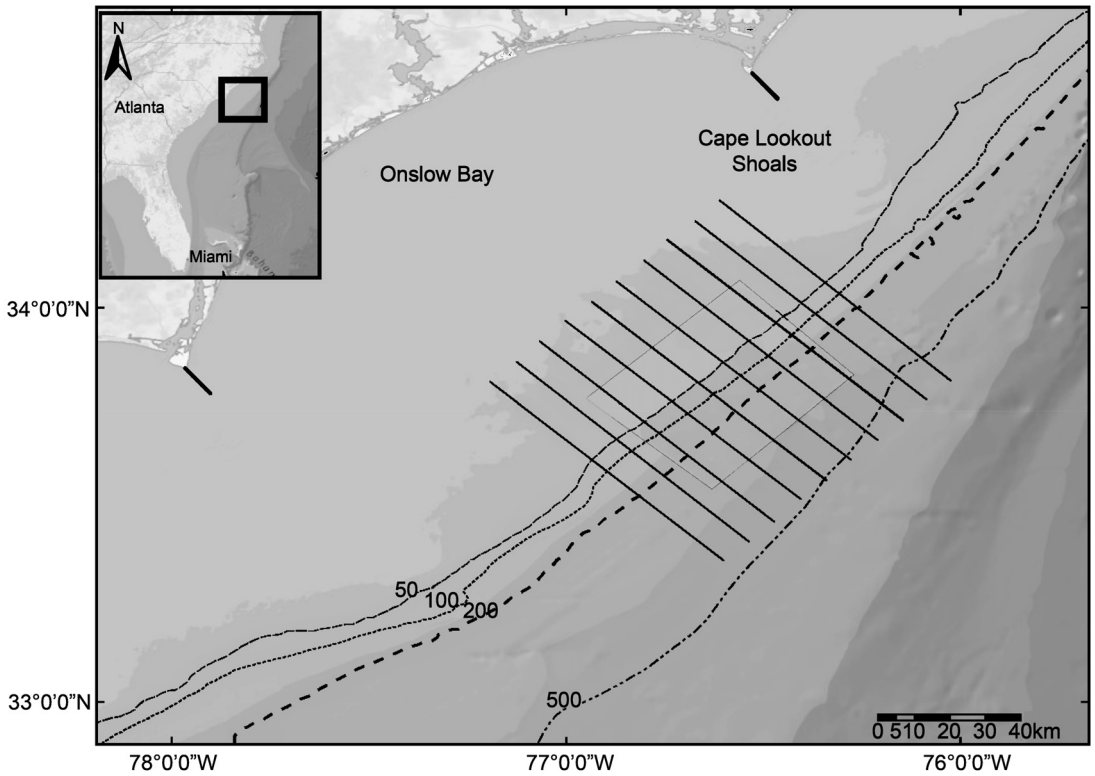

Fig. 1. The study area in Onslow Bay, North Carolina, USA, showing the tracklines used in aerial and vessel surveys. The shaded box indicates the location of the proposed Undersea Warfare Training Range (USWTR). Isobath depths are in metres. The inset shows the location of the study area within the southeastern United States. Data on the occurrence of stranded cetaceans in Onslow Bay were derived from events that occurred from Cape Lookout to Cape Fear, denoted by the two thick lines extending from shore.

series and increase the sample size of observations, an earlier series of aerial surveys conducted in this area in 1998 and 1999 was also incorporated.

The objective of the research, therefore, to provide a comprehensive description of the occurrence, distribution and abundance of cetaceans in Onslow Bay, including seasonal variation in these parameters.

METHODS

Study area

The proposed USWTR site in Onslow Bay consisted of a rectangle 46 × 37km; the center of this rectangle is approximately 90km from shore. Surveys extended beyond the proposed boundaries of the USWTR, so the total prediction area was 5,334km^2. Surveys were conducted along ten transect lines that were placed perpendicular to the coast and the shelf break, each 74km in length and spaced approximately 9km apart, in this area (Fig. 1). Both aerial and vessel surveys used the same set of tracklines.

The dominant oceanographic feature of the study area is the Gulf Stream, which meanders back and forth over the shelf break as it flows northwards. As a result of these meanders, oceanographic conditions at any point in the study area can vary considerably in only a few days. The 200m isobath bisects the study area (Fig. 1) which, therefore, included both the continental shelf and slope waters.

Aerial surveys

Aerial surveys were conducted from June 2007 to June 2010 inclusive in a *Cessna 337 Skymaster* at an altitude of 305m and a speed of 185km hr^{-1}. Surveys were conducted on days with low sea states (Beaufort 0–3) and optimal visibility. The goal was to complete a full set of ten tracklines twice each month. The earlier set of aerial surveys was conducted over a slightly different set of tracklines in the same location from September 1998 to July 1999, also using a *Cessna 337* and a similar survey protocol, except that the plane flew at 230m (McLellan *et al*., 1999). Sightings data from the two sets of aerial surveys were combined. To improve precision of the detection functions of certain species, sightings from aerial surveys for right whales conducted closer to shore by the University of North Carolina Wilmington were also incorporated (all survey results reported in OBIS-SEAMAP; Halpin *et al*., 2009).

During aerial surveys, an observer monitored each side of the plane, equipped with a GPS unit, data sheet and binoculars; each side was considered to be an independent transect. The observers recorded the start and end of transect lines, any changes in environmental variables (i.e. cloud cover, sea state, visibility and glare) and sightings of marine mammals, sea turtles and vessels. When a sighting cue was observed, the observers estimated horizontal and vertical sighting angles by eye. The aircraft then broke from the trackline and closed on the sighting location. The plane circled over the sighting to obtain photographs to confirm species identity. During each encounter, the left observer was designated as data recorder and the right observer obtained digital photographs with a Canon 40D camera and a 100–400mm image-stabilised lens. These images were used to assist with species identification (see below), refine estimates of group size and confirm sightings of calves. A best estimate of group size was established using both field observations

and subsequent examination of digital images. Each observer independently estimated the minimum and maximum number of animals in each sighting. Once photographs and sighting data were collected, the plane returned to the initial location on the trackline and resumed survey effort. The plane did not break from the trackline for sightings of sea turtles, other marine vertebrates (e.g. sharks and rays) or vessels.

Vessel surveys

Vessel surveys were conducted from June 2007 to June 2010, inclusive, from two platforms: the F/V *Sensation*, a 16m offshore fishing vessel and the R/V *Cetus*, a modified 12m offshore fishing vessel. These two vessels were chosen for their ability to transit rapidly to and from the study area. The target of survey effort varied over the course of the study, with a maximum goal of five transects per month during the summers of 2007 and 2008. Due to seasonal variation in sea conditions, lower targets of monthly survey effort were set during winters.

Observations were made from the flying bridge (5.0m and 4.2m above waterline for the *Sensation* and *Cetus*, respectively) using naked eye and 7 × 50 binoculars. While on effort, two observers (one port and one starboard) scanned constantly from straight ahead to 90° abeam either side of the trackline. A third observer monitored the trackline, coordinated with the vessel skipper and acted as data recorder. The observers rotated positions (including at least one rest station) every 30 minutes. Survey speed was approximately 18km hr^{-1}. Standard line transect sampling methods for cetaceans were used, similar to those described by Barlow (2006).

The location and species identity of each cetacean group were recorded. Each observer estimated group size independently and these estimates were averaged at the end of each survey to generate a final estimate of group size. Environmental conditions (weather, sea state, depth and sea surface temperature) were recorded every 30 minutes or whenever sighting conditions changed. All sighting and environmental observations were entered into an onboard data collection system (Vis-Survey, developed by Dr. Lance Garrison, NOAA SEFSC Miami, FL) linked to a GPS unit.

During these vessel surveys a hydrophone array (Seiche Instruments, UK) was towed approximately 150m behind the vessel. The array consisted of four elements, spaced 1.2m apart, with a flat (+/– 3dB) frequency response between 2 and 100kHz and a sensitivity of –165dB re 1V/µPa. High-frequency acoustic recordings at 192-kHz sampling rate were made on a laptop running *Ishmael* software (Mellinger, 2001) and a MOTU Traveler audio interface (Mark of the Unicorn, Cambridge, MA, USA). A trained acoustician monitored incoming acoustic signals aurally and visually via spectrograms in *Ishmael*, with the gain set to –96dB. Recordings were made directly to an external hard drive whenever calls were detected using *Ishmael*, at which point time and location were noted. The recording station was located in the main cabin of the survey vessel, isolated from the visual observers, so the acoustic and visual surveys functioned independently.

In addition, patterns of residency in the study area were monitored by identifying individual animals using photo-identification techniques. Thus, whenever possible, digital photographs were obtained for photo-identification. These photographs were also used to confirm species identification and to compare identification features with those used by the aerial survey team (see below). *Canon* or *Nikon* digital SLRs equipped with 100–300mm zoom lenses were used. All photo-identification images were graded for quality and individual distinctiveness using methods described in Read *et al*. (2003).

Species identification

Digital images of each sighting were reviewed in the laboratory to confirm species identity. During the first year aerial and shipboard observers reviewed every sighting together and established a set of diagnostic features that were subsequently used to identify each cetacean species. Common bottlenose and Atlantic spotted dolphins were sometimes difficult to distinguish from the air, particularly when groups were comprised entirely of juveniles. In addition, it is difficult to differentiate short- and long-finned species of pilot whales (*G. macrorhynchus* and *G. melas*, respectively) at sea (Rone and Pace, 2012). Thus, if species identity could not be unequivocally determined, the sighting was designated to the nearest taxonomic category (e.g. 'unidentified delphinid').

Statistical analysis

General approach

To generate density surfaces and, where possible, identify environmental variables driving patterns of animal distribution, the probability of detection associated with each sighting was estimated and then surface density per segment of trackline within the truncation distance was estimated. Detection probabilities were estimated assuming that detection of an animal on the trackline was certain (see below for a discussion of this assumption).

The survey region is heterogeneous with substantial changes in depth and the fluctuating presence of the Gulf Stream. The adjusted density data were characterised by a high ratio of zero to non-zero segments, so density was modelled with a two-stage process: (1) the probability of presence as a logistic generalised additive model (GAM); and, (2) estimated density, given that animals were present. The product of these two prediction surfaces gave an estimated relative density surface for the study area. Abundance was then obtained by numerically integrating under these surfaces. The resulting abundances do not take into account periods when animals were submerged, and therefore unavailable for detection, or imperfect detection on the trackline. Due to limited sample sizes, only bottlenose dolphins and Atlantic spotted dolphins could be modelled.

Estimation of detection probabilities

Either a hazard-rate $(1 - \exp(- y/\sigma)^{-b})$ or half-normal form $(\exp(- y^2/2\sigma^2))$ was used for the probability detection function (σ is the scale parameter) (Buckland *et al*., 2001) where y is perpendicular distance. The effects of covariates, other than perpendicular distance were incorporated, into the detection function model by setting the scale parameter to be an exponential function of the covariates (Marques, 2001). Thus, the probability of detection becomes a

multivariate function, $g(y,v)$, representing the probability of detection at perpendicular distance y and covariates v ($v = v_1,..,v_Q$ where Q is the number of covariates). The scale term, σ, has the form:

$$\sigma_k = \exp\left(\beta_0 \pi \sum_{q=1}^{Q}\left(B_q v_{kq}\right)\right)$$

and β_0 and β_q ($q = 1,\ldots,Q$) are parameters to be estimated. With this formulation, it was assumed that the covariates may affect the rate at which detection probability decreases as a function of distance, but not the shape of the detection function. In the aerial case the covariates considered were Altitude, Beaufort Sea State and Glare. In the boat case, the covariates were Species, Beaufort Sea State, Group Size and Visibility.

A backward, stepwise selection procedure (starting from the previous best model) was used to decide which covariates to include, with a minimum Akaike's Information Criterion (AIC) inclusion criterion. All initial model selection was performed in the program *Distance* (v5.0; Thomas *et al*., 2002) and re-fitted the final selected models using a set of customised functions (mrds v.1.3.8) in *R 2.9.2* (*R* Developmental Core Team, 2009). This facilitated estimation of variance within *R* (see below).

In general, rates of encounter rates with cetaceans were very low during the 2007–10 surveys, so detection probabilities were estimated by augmenting sightings with data gathered from the same aerial platform during surveys carried out closer to the coast and another set flown near Wallops Island, Virginia in 1998 and 1999 (McLellan *et al.,* 1999). Additional shipboard sightings were also incorporated, using the same methodology and observers, from the F/V *Sensation* obtained during a brief survey off Cape Hatteras, where cetacean densities are much higher, in 2007. All dolphin species were grouped into a single guild of delphinids to estimate detection functions and then evaluated species as a covariate when fitting the detection function. There were too few sightings to estimate density for species other than bottlenose and spotted dolphins.

Estimation of density surfaces

A modified version of the 'count model' of Hedley *et al.,* (1999) was implemented to model spatial distribution. The response variable for this model was a density based on the estimated number of individuals for a small segment i of trackline, $\hat{N}_i$, calculated using an estimator similar to the Horvitz-Thompson estimator (Horvitz and Thompson, 1952), as follows:

$$\hat{N}_i = \sum_{j=1}^{n_i} \frac{s_{ij}}{\int_o^w \hat{g}(y,v_{ij})\pi(y)dy}, \qquad i = 1,\ldots,T,$$

where, for segment i, $\int_0^w \hat{g}(y,v_{ij})\pi(y)dy$ is the estimated probability of detection of the jth detected pod, n_i is the number of detected pods in the segment and s_{ij} is the size of the jth pod. The total number of transect segments is denoted by T. By assumption, $\pi(y)$, the probability density function of actual (not necessarily observed) perpendicular distances is uniform up to the truncation distance; this is satisfied by locating transects randomly.

Having obtained the estimated number of individuals in each segment, the density in segment i, $\hat{D}_i$, from $\hat{N}_i/a_i$ where a_i is the area of segment i was estimated. Segment area was calculated as the length of the segment multiplied by twice the truncation distance used to model the detection function. The survey tracklines were initially divided into distinct segments based on effort and sighting conditions. Long segments were divided and a variety of segment lengths from 5 to 13km were evaluated; 10km was chosen as an appropriate compromise between maximising the ratio of non-zero to zero segments, maintaining environmental resolution and giving some measure of spatial independence (see Results).

In most cases, the number of segments with detections was extremely low, which made fitting of models difficult, so a variety of alternative approaches were explored. Zero-inflated methods were investigated, but these proved impossible to implement successfully with the dataset. Therefore, a two-stage process was implemented: the presence or absence of animals in a particular segment was modelled using a logistic GAM and then non-zero density was modelled in each segment again with a GAM but now assuming a Gamma error structure. The predicted probability of the presence of animals in a segment was multiplied by the predicted non-zero density in that segment to obtain the predicted density of animals. This two-stage process may introduce a potential bias in that absences (zeros) are over-represented because some observed zeros were not true absences, but simply segments of low density where animals were present but not observed. Perfect correction for under detection is not possible given the absence of a $g(0)$ estimate.

The following covariates were included in the models: sea surface temperature (Temp); depth (Depth); day of year (Dayofyear); and year of survey (Year). Dayofyear was considered as a cyclic cubic spline, so the second derivative of the curve for Dayofyear met at the beginning and end of the year. Sea surface temperatures were collected during shipboard surveys, but for the aerial survey and prediction grid temperatures[5] were obtained at 1-degree and weekly resolutions (Reynolds *et al*., 2002). Depths were obtained from ETOPO2 at 2-minute resolution[6]. Year was trusted as a factor rather than a continuous variable because of the break in surveys between 1999 and 2007.

Temperatures and depths were associated with effort segments by finding the closest point in the temperature and bathymetry data to the midpoint of the effort segments using great circle distances (and date for temperature). Finally, Survey was incorporated as a factor to identify the survey platform (plane or boat), but only if the estimated value of the regression coefficient associated with the plane was lower than those associated with the ships, i.e. the use of Survey reflected differences in $g(0)$ between aerial and shipboard surveys.

Backwards model selection was implemented using generalised cross validation (gcv) in the *mgcv* package (v. 1.5–2) in *R* (v. 2.9.2) for covariate selection in the logistic model, augmented with diagnostic plots, using the principles described in Wood (2006). Model selection was by

[5]*http://dss.ucar.edu/datasets/ds277.0/data/oiv2/.*
[6]*http://www.ngdc.noaa.gov/mgg/image/2minrelief.html.*

generalised cross validation. All covariates were considered for inclusion in the model as 1D smooths of untransformed covariate values. A maximum of four degrees of freedom was allowed in the selection of 1D smooths for Temp, Depth and Dayofyear as the response to these variables would be unlikely to have more than two minima and maxima. The presence of unexplained spatial variation was looked for by inspection of semi-variograms of the residuals of the models. Models were fitted to all data across all years. Survey was included in all models to account for the detectability differences on the trackline between aerial and ship surveys.

Due to variation in environmental conditions along transects, it was not always split survey effort into segments of equal length (see below). Therefore, the model was weighted by segment area. The presence-only data were modelled in the same way, although sometimes simplified models were chosen for the point estimate to avoid generating spuriously high results in the bootstrap where the full range of data might not be available, leading to dubious extrapolation over the entire prediction region.

Prediction of density and variance estimation

The final models were used to predict density using a two-minute resolution prediction grid. Abundance was estimated by numerically integrating under this predicted density surface. If survey platform was included in the final model, abundance was predicted assuming the survey mode with the largest coefficient value, as this would reflect the best detection on the trackline. Predictions were made for every month of each survey year to allow comparison of seasonal trends across years.

Variance was estimated by repeating the entire abundance estimation process on a large number of samples, drawn at random from the data, to obtain a distribution of abundance estimates. Confidence intervals were derived from this distribution using the 2.5% and 97.5% percentiles to obtain the upper and lower limits. Samples were obtained by sampling transects, at random and with replacement, so that the selected effort reflected the effort in the original sample and accounted for evidence of temporal correlation in the residuals by the same sections of effort together being used. Models were refitted with the same covariates as in the original analysis but the degrees of freedom available to each smooth could be reselected, subject to the constraints mentioned above.

RESULTS

Aerial surveys

Aerial surveys of all tracklines were conducted each month from June 2007 to June 2010, with the exception of January and September 2008 and May 2010. The aerial survey covered 42,676km of trackline, with most (78%) effort occurring in Beaufort Sea States 2 and 3. An additional 12,821km of trackline were flown between September 1998 and July 1999, with effort in every month except February 1999. Taking both data sets together, 55,497km of trackline were surveyed with effort in every calendar month.

A total of 279 sightings of seven species were recorded during these aerial surveys. Atlantic spotted and common bottlenose dolphins dominated the cetacean fauna (Table 1).

Table 1

Summary of cetacean sightings in Onslow Bay, North Carolina, by platform type and period.

	Aerial surveys		Vessel surveys	
Species	1998–99	2007–10	2007–10	Total
Tursiops truncatus	39 (64%)	126 (58%)	51	216
Stenella frontalis	0	57 (26%)	36	93
Delphinus delphis	14 (23%)	1 (<1%)	0	15
Grampus griseus	3 (5%)	4 (2%)	4	11
Globicephala spp.	1 (2%)	7 (3%)	3	11
Steno bredanensis	0	3 (1%)	1	4
Balaenoptera physalus	0	1 (<1%)	0	1
Unidentified delphinid	3 (5%)	19 (9%)	5	27
Unidentified ziphiid	1 (2%)	0	0	1
Total	61	218	100	

The sightings included 22 unidentified delphinid schools and an observation of a single group of unidentified beaked whales in May 1999. In addition, an off-effort sighting of a single sperm whale (*Physeter macrocephalus*) was recorded while transiting to the offshore end of a trackline in October 2009. No mixed-species groups were observed. Species composition was similar in the 1998–99 and 2007–10 surveys, with two exceptions. No spotted dolphins were observed during the earlier surveys, but this species comprised more than a quarter of all sightings in the latter period. In contrast, common dolphins (*Delphinus delphis*) were observed in the earlier time period but not the more recent surveys. Based on the distribution of long- and short-finned pilot whales during summer (Waring *et al.,* 2011), it is likely that all pilot whales observed from June–August were *G. macrorhynchus*, but it was not possible to confirm species identity of pilot whales during these surveys.

Spotted and bottlenose dolphins were present throughout the year (Table 2). Sightings of bottlenose dolphins were recorded during every month, and sightings of spotted dolphins occurred in every month except July and December (Table 2), although this species was observed during vessel surveys in July (see below). There were too few sightings of other species seen to draw conclusions regarding their seasonal occurrence. Spotted dolphins were restricted to shelf waters; bottlenose dolphins were found over both shelf and deeper waters (Fig. 2a). Pilot whales, Risso's dolphins (*Grampus griseus*) and rough-toothed dolphins (*Steno bredanensis*) were exclusively found over the shelf break and in deeper waters (Fig. 2a). Mean (±S.E.) observed group size of bottlenose dolphins in Onslow Bay was 20.1 (±2.0) in the earlier surveys and 15.1 (±1.4) in the more recent period. Mean observed group size of spotted dolphins in Onslow Bay was 26.1 (±3.6) in 2007–10.

Vessel surveys

A total of 5,209km of vessel survey effort was recorded from June 2007 to June 2010. Most (70%) of this survey effort was conducted in Beaufort Sea States 2 and 3. A total of 95 sightings of five cetacean species and 5 sightings of unidentified delphinids was made. Species composition (Table 1) and distribution (Fig. 2b) were similar to those observed from the aircraft, with most (87%) sightings composed of common bottlenose and spotted dolphins. Mean group sizes of bottlenose and spotted dolphins were 13.8

Table 2

Cetacean sightings by month in Onslow Bay, North Carolina, from June 2007 to June 2010. Only aerial survey effort and sightings are presented. Effort is represented by the number of tracklines, indicated in the bottom row.

	Month											
Species	J	F	M	A	M	J	J	A	S	O	N	D
Tursiops truncatus	12	5	17	13	14	20	2	7	4	18	13	1
Stenella frontalis	4	9	9	6	2	8	0	6	6	6	1	0
Delphinus delphis	0	0	1	0	0	0	0	0	0	0	0	0
Grampus griseus	0	0	0	0	1	2	0	1	0	0	0	0
Globicephala spp.	0	1	0	0	2	1	2	1	0	0	0	0
Steno bredanensis	0	0	0	1	0	2	0	0	0	0	0	0
Balaenoptera physalus	0	0	1	0	0	0	0	0	0	0	0	0
Tracklines	40	30	55	50	40	62	60	60	36	60	46	30

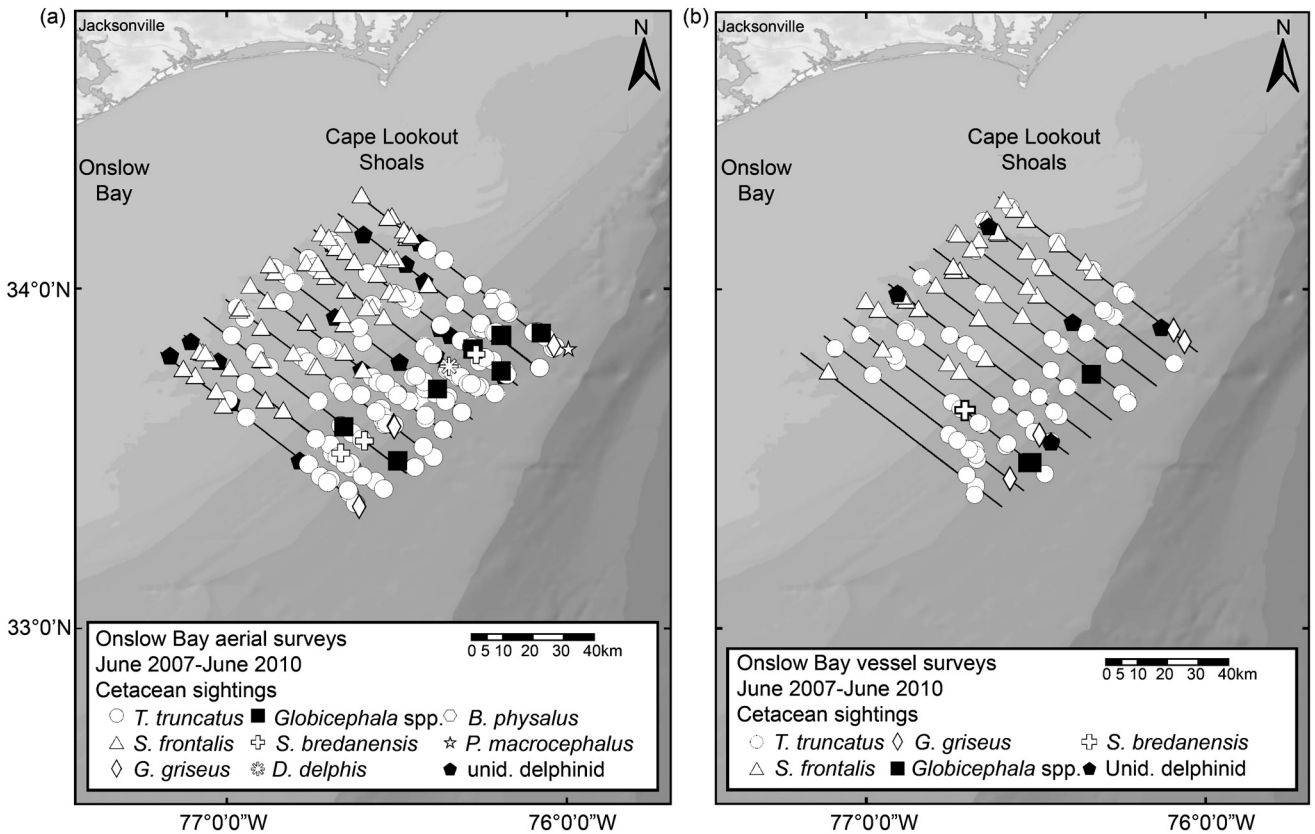

Fig. 2a. Spatial distribution of sightings of cetaceans from aerial surveys in Onslow Bay, June 2007–June 2010. The single sighting of a sperm whale was made off-effort during transit.
Fig. 2b. Spatial distribution of sightings of cetaceans from vessel surveys in Onslow Bay, June 2007–June 2010.

(±1.5) and 22.6 (±5.9), respectively. As was the case for aerial surveys, no mixed-species groups were observed.

The hydrophone array was towed on 41 days, for a total of 194.5 hours of combined visual and acoustic surveys. During these combined surveys a total of 109 acoustic detections of cetaceans were recorded; 68 were visually confirmed and 41 were not observed. Thus, most (62%) acoustic detections of cetaceans were also detected independently by the visual observers.

In total 3,169 digital photo-identification images of five species of cetaceans were obtained and the following animals were catalogued: 106 individual bottlenose dolphins; 49 spotted dolphins; 16 pilot whales; 12 rough-toothed dolphins; and 7 Risso's dolphins. Five bottlenose dolphins were resighted: (1) ID 9-016 on 25 July 2008 and 17 August 2009; (2) ID 4-002 on 15 September 2009 and 1 October 2009; (3) 1-004 on 1 October 2009 and 11 April 2010; (4) and (5) IDs 7-015 and 8-009, seen together on 28 April 2009, and seen together again on 20 April 2010. One spotted dolphin, ID 9-013, seen on 9 August 2009 and then again on 1 October 2009 (Fig. 3) was also matched. No individuals of other species were resighted, although the catalogue sizes for these species were small.

Statistical analysis

Sightings of all dolphins from aerial surveys were binned into 200m widths because of evidence of rounding and they were right truncated at 1.4km. The best fit dolphin aerial detection function was a hazard rate function including perpendicular distance, *Altitude* and *Beaufort Sea State* only

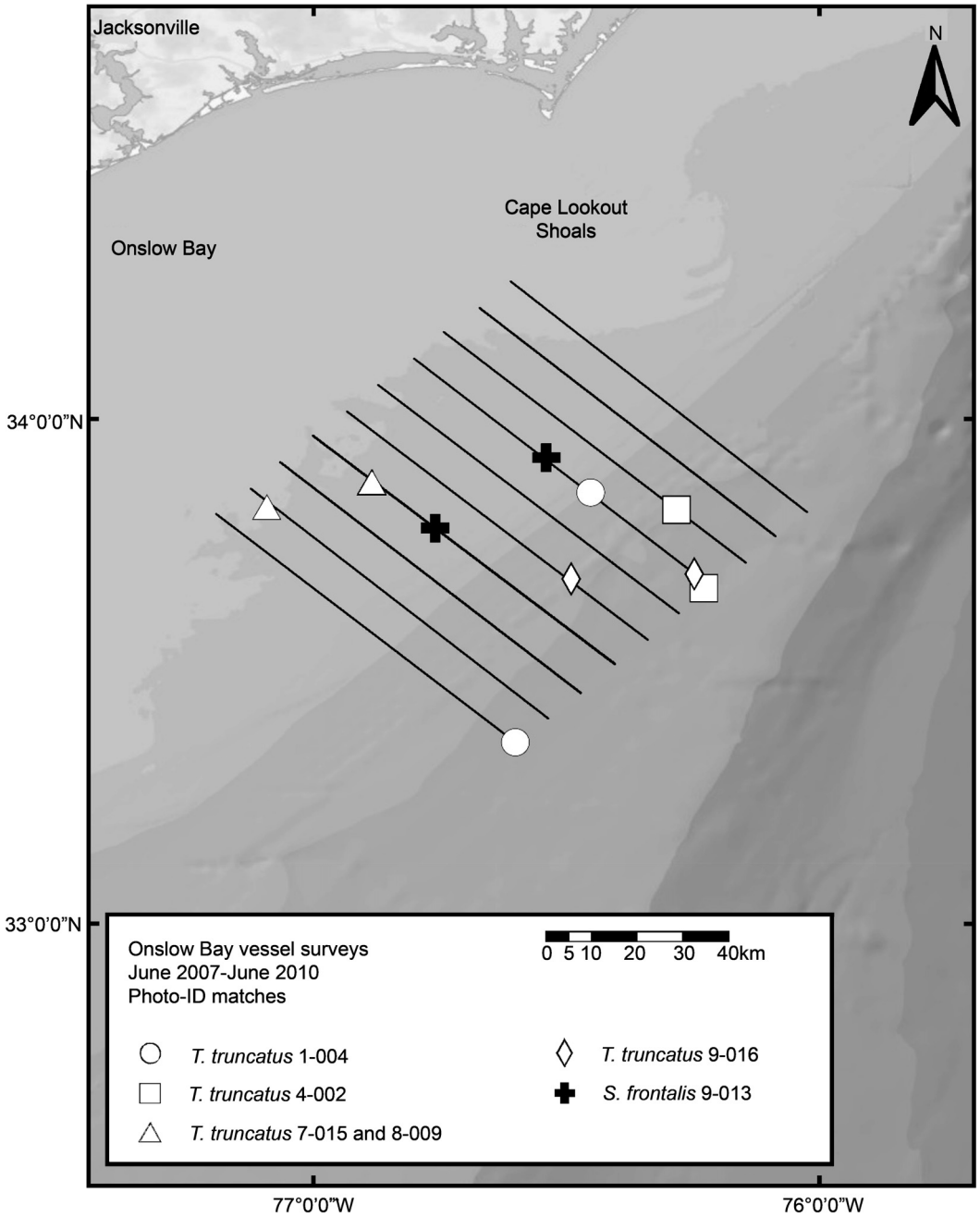

Fig. 3. Photo-identification matches of bottlenose (*Tursiops truncatus*) and Atlantic spotted dolphins (*Stenella frontalis*) in Onslow Bay, North Carolina. See text for dates of sightings.

(Fig. 4). Vessel sightings of dolphins were binned into 100-m widths and right truncated at 300m. The best fit detection function was a half-normal with Beaufort Sea State as covariate (Fig. 5).The mean aerial detection probability was 0.45 (SE = 0.02). The mean boat detection probability was 0.53 (SE = 0.05)

The tracklines for aerial and shipboard surveys were divided into 7,180 segments (5,873 aerial and 1,307 shipboard). The final fitted models for predicting density and for biological explanation are given in Table 3. Bottlenose dolphins were detected in 174 segments (2.4%). Estimated abundance of this species (rounded to the nearest hundred) varied between 600 (95% CI: 100–1,700, August 2007) and 4,100 (1,300–9,400, May 2010) (Fig. 6). These values correspond to densities of 0.117km^{-2} (95% CI: 0.016–0.323) in August 2007 and 0.767km^{-2} (95% CI: 0.238–1.768) in May 2010, respectively. Bottlenose dolphins were encountered most frequently at intermediate depths, with maximal values of presence occurring just off the shelf break (Fig. 7). Abundance varied both across and within years (Fig. 6) with peak occurrence in spring and, to a slightly lesser extent, autumn (Table 2; Figs. 6 and 7). A model assuming uniformity of density in space and time (and a boat survey) produced an abundance of 1,400 (95% CI 700–2,800) equivalent to a density of 0.268km^{-2} (95% CI: 0.127–0.529).

Spotted dolphins were detected in 78 segments (1%). Given the small numbers detected, estimates of abundance were, unsurprisingly, associated with wide confidence intervals (Fig. 8). Estimated spotted dolphin abundance varied from 0 in 1998–99 to 6,000 (95% CI: 2,500–17,000) in March 2009, which corresponded to a maximum density of 1.122 (95% CI: 0.475–3.182km^{-2}). Spotted dolphins

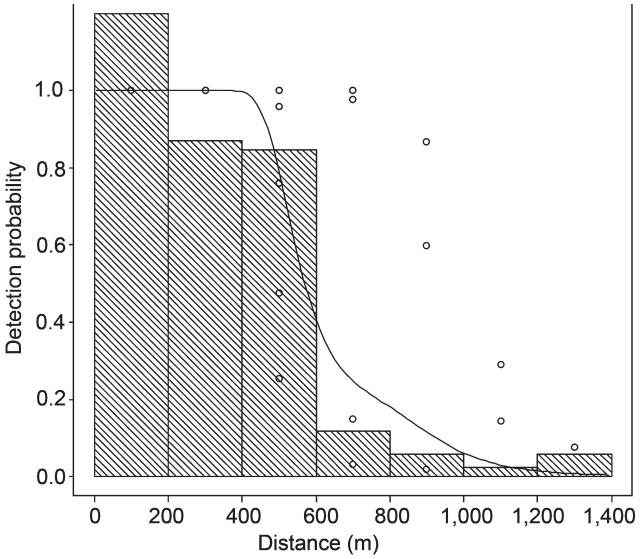

Fig. 4. Detection functions for dolphins (data binned into 200m intervals) from aerial surveys of cetaceans in Onslow Bay, North Carolina ($n = 270$) mapped over a scaled distribution of the perpendicular distances such that the area under the curve equals the area of the histogram.

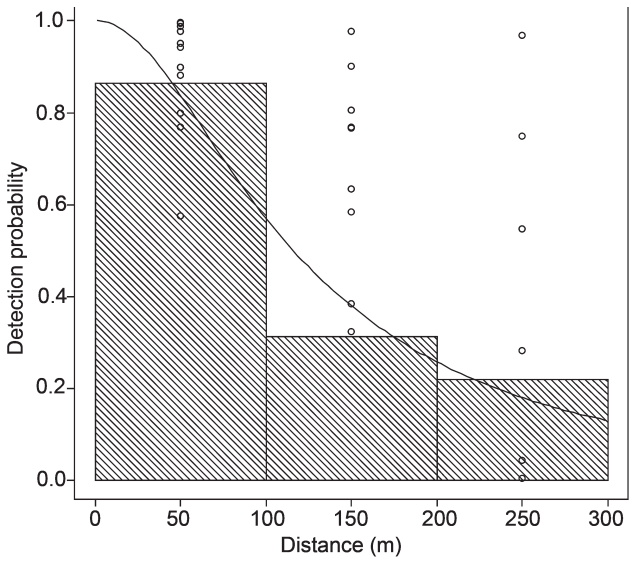

Fig. 5. Detection functions for dolphins (data binned into 100m intervals) from vessel surveys of cetaceans in Onslow Bay, North Carolina ($n = 76$) mapped over a scaled distribution of the perpendicular distances such that the area under the curve equals the area of the histogram.

exhibited a strong preference for waters over the continental shelf; their presence was not influenced strongly by either temperature or day of year, although both variables were included in the final model (Fig. 9). A model assuming uniformity of density in space and time (and a boat survey) from 2007 inclusive produced an abundance of 1,200 (95% CI 500–1,900) equivalent to a density of 0.230km^{-2} (95% CI: 0.096–0.364km^{-2}).

DISCUSSION

Occurrence and distribution

The cetacean fauna observed in Onslow Bay included both shelf and slope-associated species, but was dominated by Atlantic spotted and common bottlenose dolphins. Spotted dolphins were restricted to the continental shelf; bottlenose dolphins were the only species to occur in both shelf and

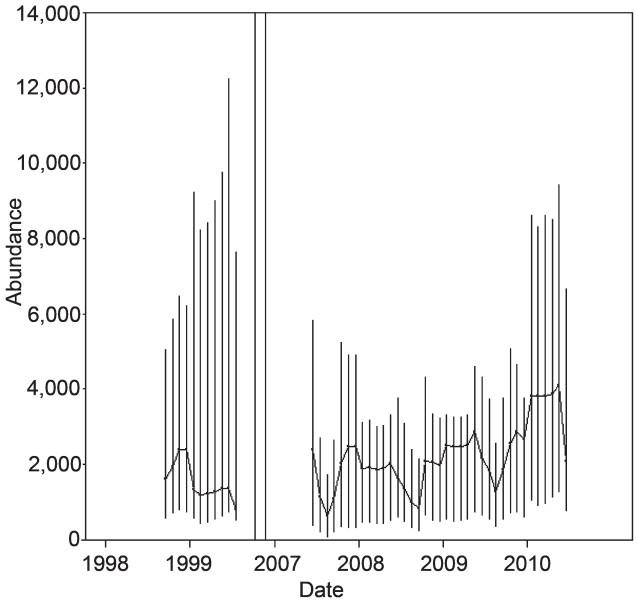

Fig. 6. Estimated monthly abundances of bottlenose dolphins (*Tursiops truncatus*), with 95% confidence intervals, in Onslow Bay, North Carolina.

slope habitats (see below). All other species occurred along the shelf break or in deeper slope waters. In total, eight species of cetaceans were observed (including the off-effort sighting of a sperm whale) and one group of unidentified beaked whales. Vessel and aerial surveys produced similar lists of species occurrence in the study area.

Fixed passive acoustic monitoring recorders in Onslow Bay also yielded detections of the calls of pygmy or dwarf sperm whales (*Kogia* spp.), minke whales (*Balaenoptera acutorostrata)* and sei whales (*B. borealis)* (Hodge 2011). Pygmy and dwarf sperm whales are noted for their cryptic behaviour, so it is perhaps not surprising that they were not observed. Despite the frequency with which these two species strand along coasts of the southeastern U.S. (see below) only a very small number of sightings have been recorded during dedicated surveys (Waring *et al*., 2011). The calls of baleen whales can travel for long distances, so it is likely that the vocalising minke and sei whales occurred outside the area surveyed (Hodge, 2011). North Atlantic right whales were not observed in the study area, although the aerial survey team recorded three sightings of right whales close to shore in November 2007, December 2008 and November 2009 while transiting to the field site.

As had been done by Pyenson (2010), species composition from the surveys was compared with a long-term data set of stranded cetaceans from the ocean beaches of Onslow Bay (Table 4). Bottlenose dolphins dominated the stranding record in Onslow Bay. Six of the eight species observed during the surveys were also represented in the stranding record and the order of frequency was identical for these species in both data sets. A number of pelagic cetaceans were recorded as strandings in Onslow Bay but not observed during the surveys – some of these cetaceans, such as pygmy or dwarf sperm whales, are known to be cryptic (see above), but many others likely occur offshore of the study area. Others, such as humpback whales, *Megaptera novaeangliae* (Swingle *et al.,* 1993; Barco *et al.*, 2002) and harbour porpoises (*Phocoena phocoena)*, are coastal species and

Table 3

Models for bottlenose and spotted dolphins in Onslow Bay, North Carolina. The term *s*() indicates a smoothed function of the variable of interest. The number after the variable name gives the realised number of degrees of freedom. The final column gives the number of the relevant figure.

Model	Terms in model	% deviance explained	Figure
Tursiops truncatus			
Logistic component	*Survey + s(Depth,4) + s(Temp,3) + Year*	4.3	6,7
Non-zero density component	*Survey + s(Depth) + Year*	24.6	6
Stenella frontalis			
Logistic component	*Survey + s(Depth,3) + s(Temp,4) + s(Dayofyear,3) + Year*	20.2	8,9
Non-zero density component	*Survey + s(Depth,4) + Temp**	36.5	8

*Linear.

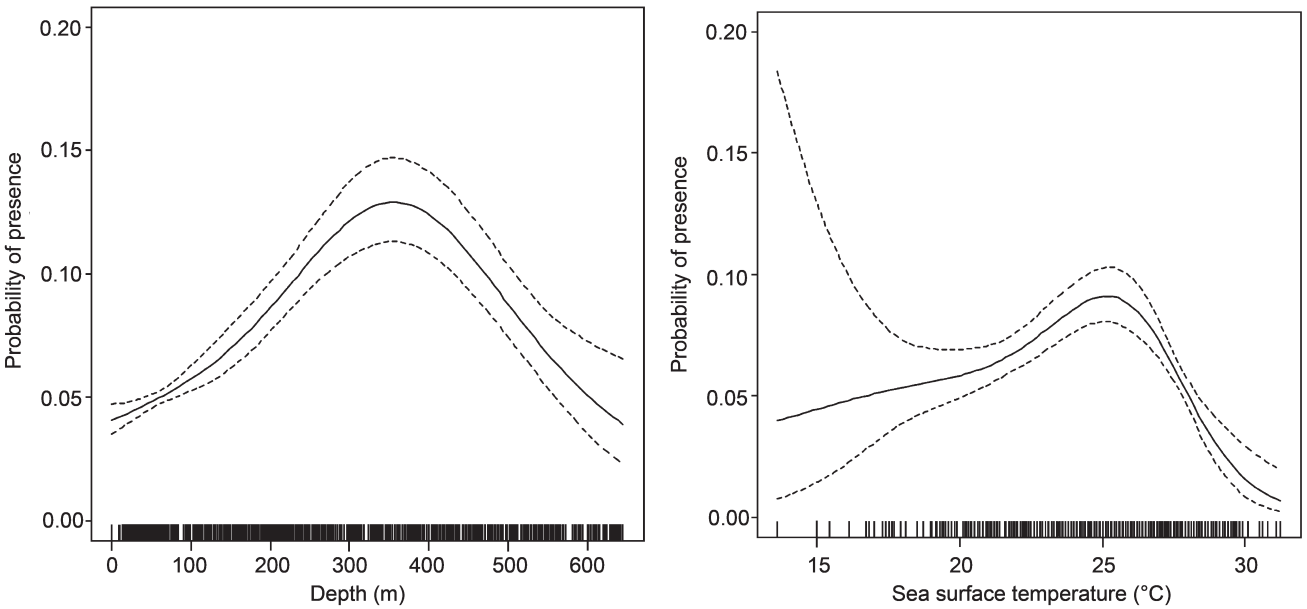

Fig. 7. Relationship between presence/absence of bottlenose dolphins and: (a) depth; and (b) sea surface temperature in Onslow Bay, North Carolina given the other terms in the model assuming a boat survey in 2010. Tick marks on the x-axis represent a datum at that covariate value. Dashed marks represent 2 standard errors lower and upper lines (approximately equal to the 95% confidence interval) associated with the uncertainty in the model only.

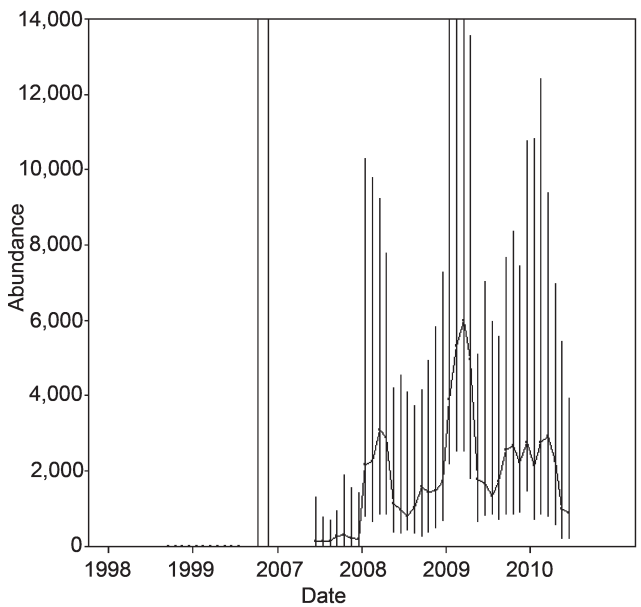

Fig. 8. Estimated monthly abundances of Atlantic spotted dolphins (*Stenella frontalis*), with 95% confidence intervals, in Onslow Bay, North Carolina.

occur well inshore of the study area. In general, there was relatively good concordance between the observations made and the stranding record.

The species composition and distribution patterns observed were similar to those recorded during previous broad-scale surveys of the South Atlantic Bight and Mid-Atlantic shelf break (Mullin and Fulling, 2003; Garrison *et al*., 2010). Surveys did not extend far enough offshore to encounter deep-diving species, such as sperm and beaked whales, on a regular basis, although single sightings of both were recorded at the offshore limit of the study area. The moored passive acoustic monitoring system recorded sperm whale clicks throughout the year in Onslow Bay (Hodge, 2011), although like the calls of baleen whales, these sounds can travel considerable distances. On 20 November 2010 an exploratory aerial survey was conducted further offshore and encountered three groups of *Mesoplodon* spp. along the 1000m isobath. It can be concluded that most beaked and sperm whales in Onslow Bay occur offshore of the boundaries of the study area and this is supported by habitat models for beaked and sperm whales in this area (Best *et al*., 2012).

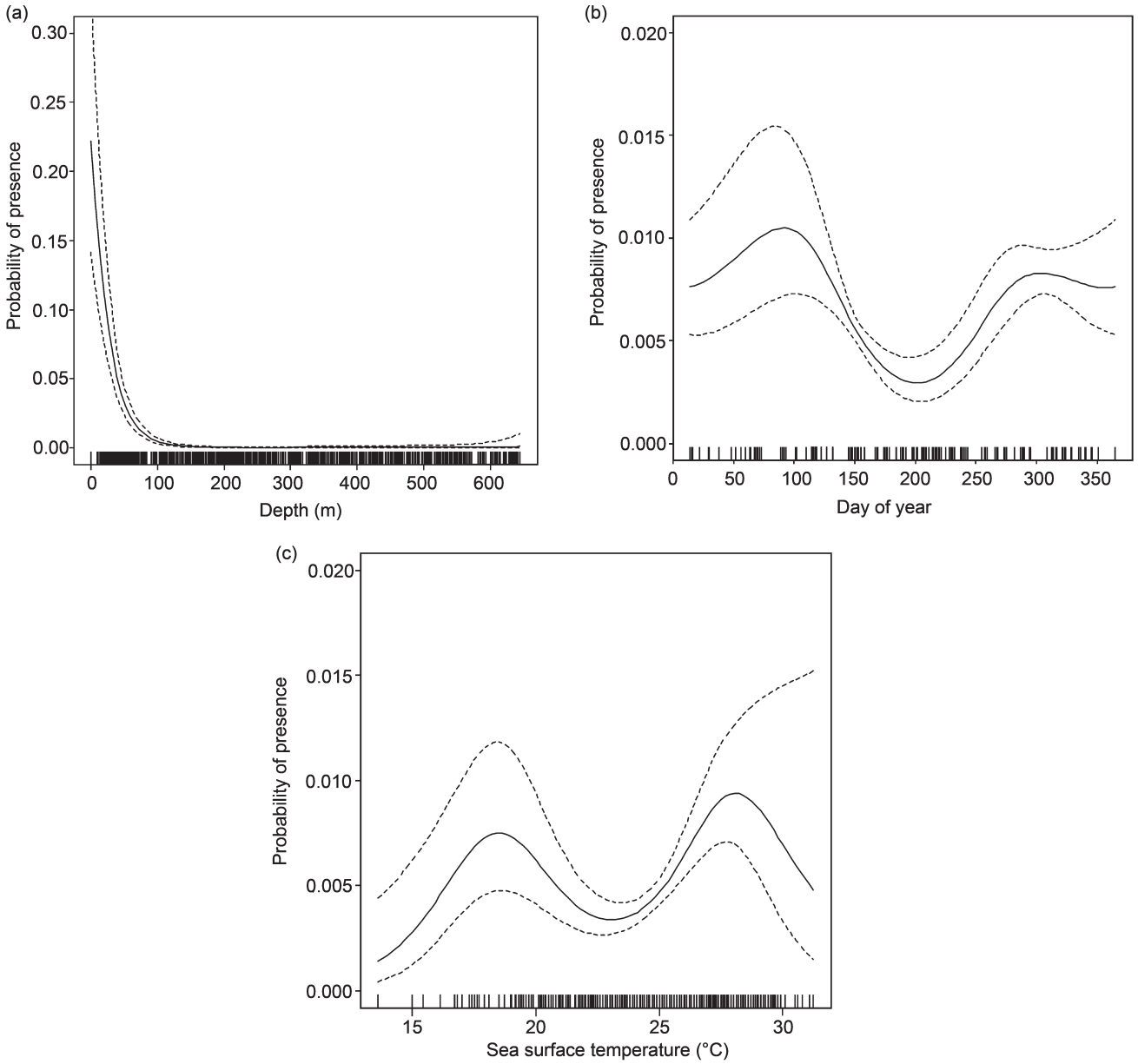

Fig. 9. Relationship between presence/absence of Atlantic spotted dolphins and: (a) depth; (b) day of year; and (c) sea surface temperature in Onslow Bay, North Carolina, given the other terms in the model assuming a boat survey in 2010. Tick marks on the x-axis represent a datum at that covariate value. Dashed marks represent 95% confidence interval associated with the uncertainty in the model only.

It is possible that the bottlenose dolphins observed over the continental shelf included both coastal and pelagic ecotypes (Mead and Potter, 1995). The two forms exhibit fixed genetic differences and probably represent distinct species (Hoelzel *et al.,* 1998); their distribution overlaps on the continental shelf south of Cape Hatteras (Torres *et al.,* 2003). The likelihood of the presence of bottlenose dolphins was greatest near the shelf break, consistent with previous observations of the offshore ecotype (Kenney, 1990). Biopsy samples and detailed photographic records of bottlenose dolphins are being collected so that the distribution of the two ecotypes in this area can be better understood.

The smaller-bodied, offshore form of Atlantic spotted dolphins (Adams and Rosel, 2006) was not observed, although these animals have been seen off Cape Hatteras, North Carolina (A.J. Read, unpublished data). Nor did we encounter several other pelagic species, such as pantropical spotted (*Stenella attenuata*) or Clymene dolphins (*Stenella clymene*), which were recorded by Mullin and Fulling, (2003). Like the deep-diving species described above, it is likely that these pelagic species occur beyond the seaward extent of the surveys.

Both bottlenose and spotted dolphins were present year-round in Onslow Bay. Despite some evidence that the probability of their presence was affected by sea surface temperature, no clear seasonal patterns in the abundance of bottlenose dolphins were observed, even though the pelagic ecotype of this species is believed to exhibit seasonal movements along the continental slope (Kenney, 1990). There was some indication of an effect of season and/or water temperature on the probability of the presence of spotted dolphins, but this effect was small compared to the overriding effect of water depth.

Approximately 5% (5 of 106) of well-marked bottlenose dolphins and 2% (1 of 49) of spotted dolphins were resighted, despite limited photographic sampling effort.

Table 4

Summary of cetacean strandings by species on the ocean beaches of Onslow Bay, NC (see Fig. 1) from September 1998 to June 2010. Strandings are presented as the number of animals. Almost all strandings involved single individuals; there was only a single mass stranding of 12 striped dolphins in the data set, indicated by the asterisk. Cetacean sightings are ordered in decreasing frequency from Table 1 with cetacean strandings following the same order of decreasing frequency.

Species	Encountered in survey area	Number of stranded individuals
Tursiops truncatus	Yes	248
Stenella frontalis	Yes	6
Grampus griseus	Yes	3
Globicephala macrorhynchus	Yes	3
Physeter macrocephalus	Yes	2
Delphinus delphis	Yes	1
Steno bredanensis	Yes	0
Balaenoptera physalus	Yes	0
Stenella coeruleoalba	No	13(*)
Kogia breviceps	No	12
Kogia sima	No	6
Megaptera novaeangliae	No	6
Phocoena phocoena	No	4
Balaenoptera acutorostrata	No	3
Feresa attenuata	No	2
Stenella attenuata	No	2
Eubalaena glacialis	No	1
Balaenoptera edeni	No	1
Peponocephala electra	No	1
Stenella clymene	No	1
Mesoplodon europaeus	?	4
Mesoplodon densirostris	?	1
Ziphius cavirostris	?	2

These resightings occurred over seasons and years, suggesting some degree of structured habitat use by individual dolphins. We are not aware of any other attempts to match images of Atlantic spotted dolphins and offshore bottlenose dolphins along the US east coast, but these findings suggest that such work could provide insight into the population structure of these species.

There were two noticeable changes in species composition between 1998–99 and 2007–10. Short-beaked common dolphins were the second-most frequently observed species in 1998–99 but were almost entirely replaced by Atlantic spotted dolphins in the more recent surveys. Only one sighting of common dolphins in 2007–2010, on 9 March 2010 was made, the same day on which the only sighting of a fin whale (*Balaenoptera physalus*) was recorded. In contrast, common dolphins were observed on 14 occasions during June, July, September and October of 1998–99. Onslow Bay represents the southern limit of the range of common dolphins in the western North Atlantic (Waring *et al.,* 2011); it is possible that this limit moves latitudinally in response to environmental variables, so that common dolphins are present in the study area during some years, but not others. Common dolphins were not observed in the broad-scale surveys of the South Atlantic Bight conducted in July and August 1998 by Mullin and Fulling (2003) but were recorded north of Cape Hatteras in June–August 2004 during the survey by Garrison *et al*. (2010). The absence of spotted dolphins in the 1998–1999 surveys in Onslow Bay is puzzling. It is possible that some of the sightings of unidentified delphinids made during 1998–99 were of this species, but only three of these sightings were recorded during the more recent surveys. It is also possible that the increase in spotted dolphin abundance (see below) over the study period represents a population incursion from more southern waters.

Abundance

The abundance of cetaceans in Onslow Bay was very low, although the data were inadequate to estimate density for species other than Atlantic spotted and bottlenose dolphins. A relatively small number of groups of these two species were encountered, resulting in wide confidence limits around the estimates (Figs. 6 and 8) and limiting the inferences that can be drawn from changes in abundance over time.

In general, the estimates of density of spotted and bottlenose dolphins are comparable with those of Mullin and Fulling (2003), who surveyed a much larger area. Atlantic spotted dolphins and bottlenose dolphins were the two most abundant species observed by these researchers, although their survey included an extensive area of pelagic habitat where coastal Atlantic spotted dolphins do not occur.

Like those of Mullin and Fulling (2003), the estimates of density presented here are negatively biased to some degree because it was not possible to meet the assumption that all groups of cetaceans on the trackline were detected (i.e. that $g(0) = 1$). Some groups of cetaceans may have been submerged as the survey vessel or aircraft transited past them (availability bias); other groups at the surface may have been missed by the observers (perception bias). The proportion of acoustic detections that were also detected visually (62%) suggests that the magnitude of this latter bias is not large, especially given that some groups of vocalising dolphins may have been out of the detection range of visual observers. The first source of bias from aerial surveys was ameliorated by forcing survey type into the models and only predicting with the factor coefficient associated with vessels (this effectively makes the $g(0)$ estimate for aircraft no more negatively biased than that for ships). It might be expected that survey platform (*Survey*) should always naturally appear in the models, as $g(0)$ should generally be higher for a ship than a plane. This was not always the case due, in part to the low power to detect this effect because of the low number of sightings. Thus, *Survey* was forced into the model for bottlenose dolphins.

Other researchers have used a variety of analytical approaches to estimate $g(0)$ directly. In vessel surveys of small delphinids (including the genera *Stenella* and *Tursiops*) Barlow and Forney (2006) estimated $g(0)$ to be 0.86 for groups of less than 20 individuals and 0.97 for groups of 20 or larger. In aerial surveys of bottlenose dolphins in California, Forney and Barlow, (1998) estimated a $g(0)$ as 0.67 for small (1–10) and 0.85 for large (>10) groups, although these values did not fully account for availability bias. Spotted and bottlenose dolphins in Onslow Bay occurred in a variety of group sizes and some groups on the trackline were not detected by our observers. Thus, the estimates of density and abundance estimates are negatively biased to an unknown degree.

Assessment of field approach

As noted above, the objective of the research was to provide a comprehensive description of the occurrence, distribution and abundance of cetaceans off Onslow Bay. A suite of complementary approaches were selected to ensure that the

presence of all cetaceans could be assessed and to maximise information collected by these different research modalities. Aerial surveys gave the advantage of relatively brief breaks in the weather, which was particularly important in winter, when survey conditions were generally poor. There have been few prior attempts to conduct regular surveys of cetaceans in the North Atlantic during winter. The surface vessels provided an independent means of assessing occurrence, distribution and abundance and, importantly, allowed investigation of patterns of residency using photo-identification methods. Merging results from the aerial and vessel surveys added a layer of complexity to the analysis, but this did not outweigh the benefit of the combined approach. Although not discussed here, the vessel surveys also allowed collection of biopsy samples that are important for studies of population structure and feeding ecology. Finally, our passive acoustic monitoring program allowed a continuous record of the presence of vocalising cetaceans in all seasons, weather conditions and during both day and night. The passive acoustic techniques also allowed determination of whether the visual surveys missed any deep-diving or cryptic species. This additional information indicated that at least some pygmy or dwarf sperm whales were present in Onslow Bay, but not detected during aerial or shipboard surveys. Despite the advantages of this complementary approach, however, the low encounter rates of cetaceans in Onslow Bay limit the statistical power with which it is possible to detect changes in density caused by anthropogenic or natural factors, given any reasonable level of survey coverage.

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Abundance and site fidelity of bottlenose dolphins in coastal waters near Panama City, Florida

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ABSTRACT

Dolphin watching and swim-with programmes are popular tourist attractions in Panama City, Florida, USA. Despite this, little is known about the population of dolphins that utilise this area, specifically St. Andrew Bay. To learn more about this population, photo-identification mark-recapture surveys were conducted between March 2004 and July 2007. The main objectives were to estimate the abundance of bottlenose dolphins inhabiting this region during this time period and to examine their patterns of site fidelity. Robust design population models were used to calculate seasonal abundance estimates, which ranged from 89 (CI 95% = 71–161) to 183 (CI 95% = 169–208) dolphins, even though 263 distinctive dolphins were identified during the study. Only 7% of dolphins (n = 18) observed were seen regularly in the study region. In addition, only 12% of dolphins (n = 30) observed had high site fidelity for the study region, while 58% (n = 153) were considered to be transient to the area. This study provides baseline information regarding dolphin abundance and site fidelity in and around St. Andrew Bay that may be used for the conservation and management of this dolphin population.

KEYWORDS: BOTTLENOSE DOLPHIN; ABUNDANCE; PHOTO-ID; SITE FIDELITY; GULF OF MEXICO; MARK-RECAPTURE; NORTHERN HEMISPHERE; NORTH AMERICA

INTRODUCTION

The presence of a bottlenose dolphin (*Tursiops truncatus*) population in St. Andrew Bay near Panama City, Florida, USA, has been well known by tourists for more than 20 years (Samuel and Spradlin, 1995; Colborn, 1999; Samuels and Bejder, 2004). Although illegal as defined by the US Marine Mammal Protection Act (as amended 2007), tourists have been swimming, feeding and interacting with this dolphin population since the 1980s either independently or as participants of swim-with or dolphin watching programmes (Colborn, 1999). Despite the popularity of dolphins in this region for tourism purposes, scientific information regarding the status and/or ecology of this population is lacking. In fact, the only scientific reports on this population include results from aerial surveys conducted in 1993 (Blaylock and Hoggard, 1994) and a few quantitative studies regarding human-dolphin interactions in this region (Samuels and Spradlin, 1995; Colborn, 1999; Samuels and Bejder, 2004).

Between 1999 and 2006, three unusual mortality events (UMEs) occurred along the northwest Gulf coast of the Florida Panhandle (NMFS, 2004; Gaydos 2006). These events appear to have been spatially and temporally correlated with blooms of *Karenia brevis*, a dinoflagellate known to cause red tide, and were associated with the deaths of over 300 dolphins (NMFS, 2004). On 20 April 2010, the *Deepwater Horizon* offshore drilling rig exploded and sank approximately 160 n.miles from Panama City. This event occurred at approximately 1,500m below sea level and discharged approximately 10 million litres of oil per day for 84 days (Mascarelli, 2010). The cumulative effect that these events, combined with anthropogenic stressors such as boating, fishing, and military activities, had on the population of dolphins in this region cannot be fully evaluated because baseline data regarding their abundance and distribution patterns does not exist.[4]

Bottlenose dolphins inhabiting the Gulf of Mexico are managed as eastern, western, and northern Gulf of Mexico 'stocks'. Within the northern Gulf of Mexico stock, a separate management boundary for dolphins inhabiting the bays, sounds and estuaries exists, although portions of the coastal stocks may co-occur with the northern Gulf of Mexico continental shelf stock. However, as noted by the US National Marine Fisheries Service, there is insufficient information available to determine the current status of bottlenose dolphins in St. Andrew Bay, and thus how the total human-caused mortality may engender a decline of the local populations.

Therefore, the objectives of this study were: (1) to estimate the seasonal abundance of bottlenose dolphins in St. Andrew Bay using photo-identification mark-recapture techniques; (2) to create a photo-identification catalogue of distinctive individuals in the region for long-term monitoring purposes; and (3) to characterise dolphin site fidelity patterns in this area.

MATERIALS AND METHODS

Study area

St. Andrew Bay (30°07'N, 85°43'W) is located on the northwest Gulf coast of Florida, USA (Fig. 1). The survey area, of approximately 323 km^2, included St. Andrew Bay and the surrounding near-shore and coastal waters of the

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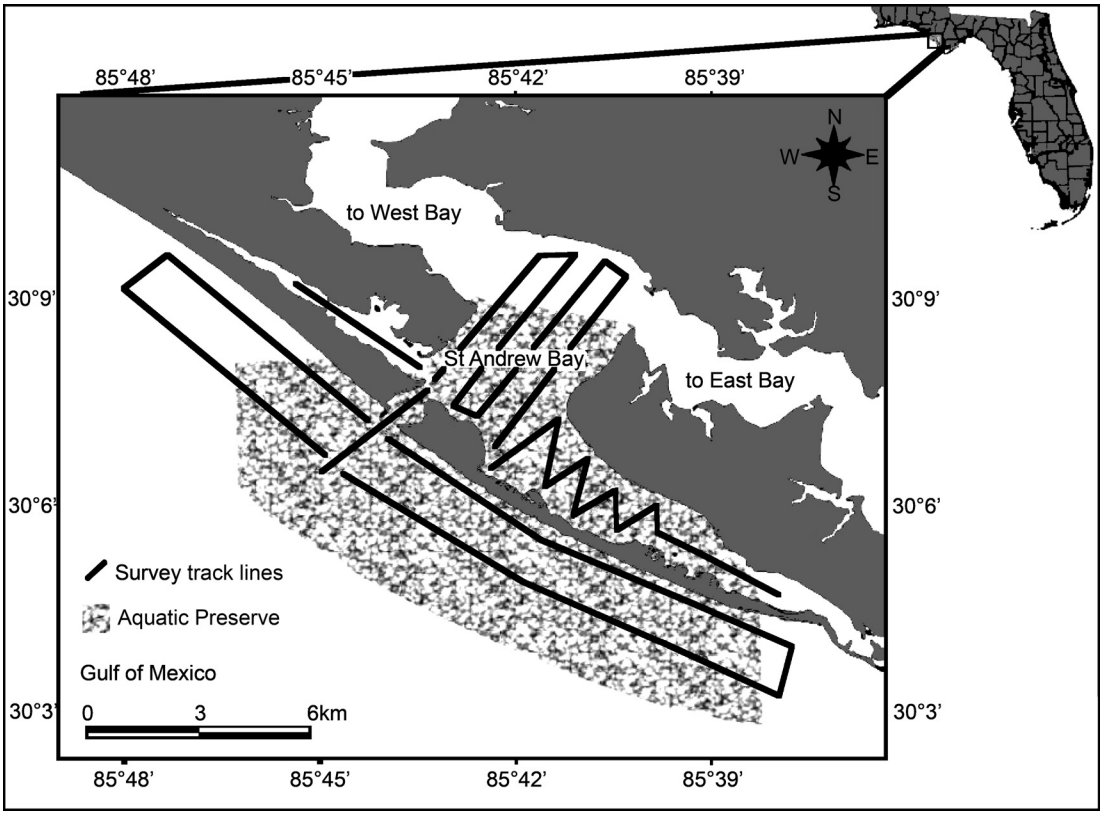

Fig. 1. St. Andrew Bay mark-recapture photo-identification survey region, including survey tracklines and the delimitation of the St Andrew Aquatic Preserve.

northern Gulf of Mexico (Fig. 1). The St. Andrew Aquatic Preserve, which aims to protect, promote and utilise indigenous marine wildlife and habitats by providing food and healthy habitats (Gardner, 1991), was included in the survey area.

Data collection

Seventeen photo-identification primary sampling periods were conducted in the study area between March 2004 and July 2007 from small boats (5–7m) powered by 55–85 horse power outboard engines between. Each photo-identification primary sampling period was 3–5 consecutive days long, which resulted in 77 independent survey days (366 total hours; Table 1).

Surveys were carried out in Beaufort sea states of ≤3 and followed predetermined track lines (Fig. 1). When a group of dolphins was sighted, the survey vessel slowly approached the group and ran parallel to their course. The location of each dolphin encounter was recorded with a GPS (*Garmin* GPSMAP 76S). Photographs were taken by one or two photographers using *Canon* EOS 350D cameras equipped with 35–80mm, or 70–300mm zoom lenses. Individual dolphins were identified daily from photographs using unique natural markings, such as nicks and notches along the dorsal fin, as well as tooth rakes marks, scratches, scars and skin lesions along the dorsal fin and peduncle (Würsig and Würsig, 1977; Würsig and Jefferson, 1990). Photographs of dorsal fins were graded on both distinctiveness of the dorsal fin (D) and quality of the photographs (Q) following Urian *et al.* (1999). Only dolphins with sufficient markings (e.g. 3–5 small to medium sized markings, one or two large markings) identified from high-quality pictures (e.g. in focus, unobscured, with the dorsal fin relatively perpendicular to the plane of the photograph) were used in the analyses (Urian *et al.,* 1999; Baird *et al.,* 2001). To minimise subjectivity and the possibility of making incorrect matches or missing matches altogether, poor-quality photographs of non-distinctive animals were not used in the analyses (Read *et al.*, 2003; Tyson *et al.,* 2011). In addition, as many distinctive features as possible were used to confirm matches (Scott and Chivers, 1990; Wilson *et al.*, 1999) and to create our photo-identification catalogue. Finally, a classification system designed by Urian *et al.* (1999) was used to facilitate the comparison of dorsal fins in the photo-identification catalogue. This method allowed us to compare distinctive individuals observed in the study area to one-another as well as to compare distinctive individuals observed in study area to distinctive individuals observed in near-by areas where similar photo-identification catalogues exist (e.g. St. Joseph Bay; Balmer *et al.*, 2008).

Table 1

Summary of mark-recapture photo-ID surveys of bottlenose dolphins in St. Andrew Bay, Florida, between 2004 and 2007.

Months	No. of days surveyed	No. of sampling periods	No. of hours surveyed	No. of sightings
Mar.–May 2004	12	4	71	139
Sep.–Oct. 2005	15	3	69	129
Nov. 2005	15	3	56	156
Jul.–Aug. 2006	15	3	68	186
Jun.–Jul. 2007	20	4	102	192
Total	77	17	366	802

Estimation of population size

Population size was estimated from mark-recapture surveys for multiple time periods (Table 1) using the robust design model (see below). To avoid problems associated with pseudo-replication (Wilson *et al.,* 1999), photo-identification surveys were not conducted every day. Encounter histories of each identified animal were created: days each animal was observed were coded as '1', while days on which each animal was not observed but the study area was surveyed were coded as '0'. Encounter histories of each distinctive individual were used to determine the abundance of dolphins inhabiting the region during each time period using the program *MARK* (White and Burnham, 1999).

The robust design model (Pollock, 1982; Pollock *et al.,* 1990) was preferred to other closed population models for the analysis because the assumptions of geographic (immigration/emigration) and demographic (births/deaths) closure were not upheld during our study period (Cooch and White, 2010). For example, six dolphins that had been freeze-branded during a health study assessment in St. Joseph Bay (located approximately 30 n.miles away) were observed in the study area. In addition to these observations, several mortalities and births were recorded during the study period. Robust design models combine characteristics of both closed and open population models by assuming that the population under study is open to gains (birth and immigration) and losses (death and emigration) between sampling periods, but that it is closed to such gains and losses during sampling periods (see Pine *et al.*, 2003 for a review). For each photo-identification sampling period, the probability of first capture (p), the probability of recapture (c), and the abundance of dolphins inhabiting the survey region (N) was estimated. Five primary sampling periods, each 3–5 consecutive days long (Table 1), were carried out during each field survey period. The abundance of bottlenose dolphins inhabiting the survey region was then estimated for each primary sampling period (N_1, N_2… N_5) (Pollock *et al.,* 1990).

The following models were used to derive estimates of abundance estimates: (1) the robust design with 'Random Emigration'; (2) the robust design with 'Markovian Emigration'; and (3) the robust design with heterogeneity (M_h; capture probability can vary for individuals). It was hypothesised that the last model would be the most appropriate model for the data set because individual dolphins in this region have been observed begging near boats (Bouveroux and Mallefet, 2008), which creates heterogeneity in capture probabilities of individiuals. This behaviour may be due to years of human interaction in this region (e.g. humans feeding and swimming with the animals) (Samuels and Bejder, 2004). Natural markings were used to identify individuals, thus initial abundance estimates pertained to the population of marked animals only. To expand these estimates to include the unmarked component of the population, the estimates were divided by the proportion of distinctive dolphins in the population (Wilson *et al.*, 1999). This proportion was calculated from the ratio of distinctive (D1 + D2) to total (D1 + D2 + D3) animals in all photographs that exceeded quality thresholds (Williams *et al.,* 1993; Wilson *et al.*, 1999; Read *et al.,* 2003; Tyson *et al.,* 2011). Variances were estimated for each estimate using the delta method and calculated 95% confidence intervals (CI) by multiplying the square root of the variance by 1.96. The standard error distribution (SE) was assumed to be the same as the estimate of the distinctive population estimate (Williams *et al.* 1993).

SITE FIDELITY

A site fidelity index was created following Balmer *et al.* (2008) so that observed side-fidelity patterns could be compared with site-fidelity patterns observed in nearby regions (e.g. St. Joseph Bay). For each sampling period each identified dolphin was placed into one of five categories based on the number of times it was sighted: Category 1 = 1 sighting; Category 2 = 2–10 sightings; Category 3 = 11–20 sightings; Category 4 = 21–30 sightings; and Category 5 = 31+ sightings. Each identified dolphin was further classified based on the number of sampling periods during which it was observed (adapted from Wilson *et al.,* 1997; Quintana-Rizzo and Wells, 2001): Category 1 = 'common', 13–17 capture occasions; Category 2 = 'frequent', 9–12 occasions; Category 3 = 'occasional', 5–8 occasions; and Category 4 'rare', 1–4 occasions.

RESULTS

Photo-identification

Between 2004 and 2007, 263 distinctive bottlenose dolphins were identified in St. Andrew Bay.

Population size

The robust closed capture model with heterogeneity was chosen as the most appropriate model for estimating dolphin abundance in this region because it had the lowest Akaike's Information Criterion (AIC) value (Table 2). With this model, it was estimated that the abundance of dolphins was 126 (SD = 8.75, CI 95% = 113–49) individuals in November 2005 and 133 (SD = 8.67, CI 95% = 121–57) individuals in September–October 2005. The highest estimated abundance, 183 dolphins (SD = 9.46, CI 95% = 169–208), occurred in June 2007 while the lowest abundance, 89 dolphins (SD = 19.34; CI 95% = 71–161) occurred in March–April 2004 (Table 2).

Site fidelity

Distinctive dolphins were observed during each of the 77 photo-identification surveys. Forty-two percent (n = 110) of animals were observed only once in the study region, while 7% (n = 18) were observed more than 21 times. Two individuals were observed more than 35 times (Fig. 2).

Seventy-five percent of dolphins observed were considered to be in the 'rare' category (n = 197), 11% were considered to be in the 'occasional' category (n = 29), 7% were considered to be in the 'frequent' category (n = 18) and 7% were considered to be in the 'common' category (n = 18). Twelve percent of dolphins (n = 33) were seen in all four years and thus were considered here to be high site fidelity, while 58% (n = 154) were observed during only one year and were therefore defined as transients (Table 3).

The annual variation in the proportion of dolphins observed is seen in Fig. 3. Three quarters of dolphins were seen one to five times. More dolphins were observed five

Table 2

Mean estimates of population size for each sampling period. The standard deviation (SD), 95% confidence interval (CI 95%), and AIC values are included for each model.

Models, robust design	Mar.–May 2004	Sep.–Oct. 2005	Nov. 2005	Jul.–Aug. 2006	Jun.–Jul. 2007
With heterogeneity	89	133	126	125	183
AIC: 4,199.14					
SD	*19.34*	*8.67*	*6.89*	*8.75*	*9.46*
CI 95%	*71–161*	*121–157*	*115–143*	*113–149*	*169–208*
Markovian emigration	67	112	109	105	151
AIC: 4,615.92					
SD	*2.1*	*2.58*	*2.24*	*2.9*	*1.98*
CI 95%	*64–74*	*109–121*	*106–116*	*101–114*	*146–155*
Random emigration	77	115	122	130	154
AIC: 4,722.37					
SD	8.23	4.35	6.80	10.70	3.38
CI 95%	67–104	110–129	113–140	116–159	148–164

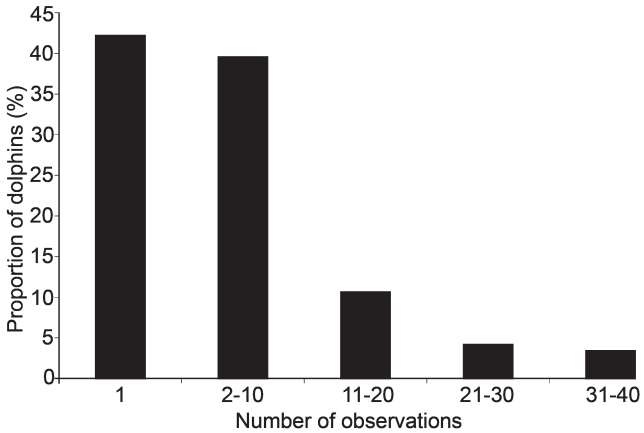

Fig. 2. Proportion of individuals observed in the study area based on their total number of observations.

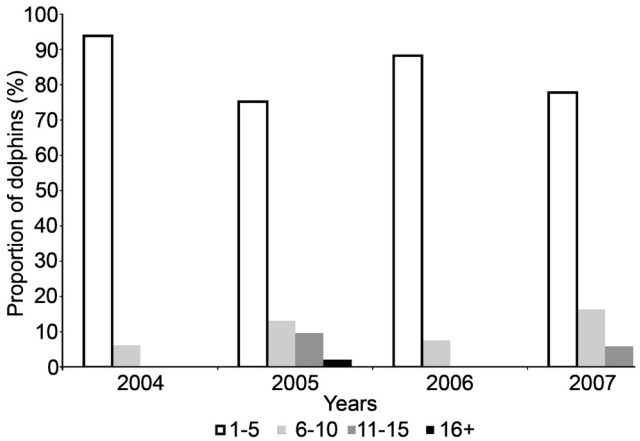

Fig. 3. The proportion of dolphins observed each study year and the number of times they were observed.

times or more during the autumn of 2005 (24.7%, $n = 65$) and summer of 2007 (22.2%, $n = 58$) than during any other season.

DISCUSSION

The highest and lowest abundance of dolphins were estimated during June 2007 and April–May 2004, respectively. Similar fluctuations have been reported in coastal waters of Texas (Shane, 1980), the Gulf of California (Ballance, 1990), Ireland (Rogan *et al.,* 2000), Scotland (Wilson *et al.,* 1997; Culloch, 2004) and Louisiana (Hubard *et al.,* 2004). Fluctuations in dolphin abundance have been attributed to spatial variations in local conditions, which result in certain areas being more suitable for mating, foraging, or predator avoidance (Wells *et al.,* 1980; Rogan *et al.,* 2000; Culloch, 2004). Balmer *et al.* (2008) found that bottlenose dolphins in St. Joseph Bay were also seasonally variable in abundance. They recorded the highest abundance of dolphins in May 2005 and the lowest in July 2005.

Table 3

The number and percentage of distinctive dolphins observed during the study.

	One year	Two years	Three years	Four years
No. of dolphins sighted	154	47	29	33
% of dolphins sighted	58.55	17.87	11.02	12.54

While confident conclusions regarding seasonal variations in dolphin abundance in St. Andrew Bay cannot be made because the region was surveyed only once each season, the abundance of dolphins did appear to fluctuate seasonally, which is similar to patterns of dolphin abundance observed in other regions (Shane, 1980; Ballance, 1990; Wilson *et al.,* 1997; Rogan *et al.,* 2000; Culloch, 2004; Hubard *et al.,* 2004). The results presented here are the opposite of those found in St. Joseph Bay, which had a lower abundance rate in June and a higher abundance in April and May 2004 (Balmer *et al.,* 2008). This difference may be explained by movements of dolphins between St. Joseph Bay and St. Andrew Bay. Indeed, of the 263 dolphins identified, six had previously been freeze-branded by researchers in St. Joseph Bay in April and July 2005 (Balmer *et al.,* 2008). In addition, a comparison of both photo-identification catalogues (St. Joseph Bay versus St. Andrew Bay) revealed that 69 individuals were observed in both study areas.

Coastal bottlenose dolphins may be year-round residents, such as those observed in the Moray Firth, Scotland (Culloch, 2004) and in Sarasota Bay, Florida, USA (Barros and Wells, 1998). Re-sighting data in St. Andrew Bay suggests that a small community of dolphins with high site fidelity inhabit the region, but a large number of transient dolphins also frequent the area. These transient dolphins

reveal important movements into and out of the study area. They may come from areas such as St. Joseph Bay, West Bay or East Bay (which are directly connected to St. Andrew Bay) which were not surveyed in this study (Fig. 1).

It is possible that these results may be biased by individual home ranges that extend beyond the limits of the study area and/or by the limited sampling periods occurring during multiple seasons and years. It is unlikely that an individual's home range would coincide exactly with the selected boundaries of the study area. Therefore, such biases may have resulted in an underestimation of the proportion of dolphins inhabiting St. Andrew Bay during the study and thus the estimates of abundance.

The previous estimates of dolphin abundance in this region were based on aerial surveys conducted in 1993 (Blaylock and Hoggard, 1994), thus the effect of UMEs on this population cannot be assessed. Moreover, sources of pollution may be present in this marine ecosystem and may accumulate in the bodies of these dolphins (i.e. heavy metals, organochlorines; Wells *et al.,* 2004) because they are located in a region with intensive human activities. As dolphins are top predators and can concentrate pollutants that accumulate in the environment (Shoham-Frider *et al.,* 2009), they may accumulate high concentrations of anthropogenic chemicals such as PCB and DDT, whose metabolites can be harmful for bottlenose dolphin health (Schwacke *et al.,* 2002). For example, an increased exposure of dolphins to anthropogenic compounds may reduce their immune function (Lahvis *et al.,* 1995) or may impact their reproduction (Wells *et al.,* 2005). These deleterious effects may subsequently result in declining dolphin abundance.

Future mark-recapture surveys should include West Bay and East Bay during each season to improve our understanding of seasonal fluctuations in dolphin abundance in St. Andrew Bay. Moreover, continued year-round monitoring of this dolphin population, (subjected as it is to human and environmental pressures, e.g. tourism, military, fishing, yachting, and harbour activities, red tide and oil spills), is needed to detect possible declines in dolphin abundance (Bejder *et al.,* 2006).

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Review of the Sri Lanka blue whale (*Balaenoptera musculus*) with observations on its distribution in the shipping lane

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ABSTRACT

A population of blue whales is resident off the southern coast of Sri Lanka and has been observed year-round by the crew of a whalewatching vessel, *Raja & the Whales,* a few miles south of Mirissa Harbour. Over the course of three years (1 December 2009 to 30 November 2012), a total of 485 blue whale sightings were reported with an average of 4.56 individuals observed per sighting. This number does not represent the total number of individuals seen because repeat sightings were highly probable. Calves were observed during the northeast monsoon. Sightings were confined to an area of about 200 n.miles that is bisected by a heavily trafficked shipping lane. Much of this area is characterised by submarine canyons and sloping bathymetry, which contributes to monsoonal seasons of high productivity and upwelling suitable for feeding whales. While the numbers of injuries and fatalities due to ship strikes are not known, four dead blue whales were observed along the southern coast over the course of five months (1 January to 31 May 2014). It is of great urgency to understand the identity and size of this population, reduce ship strikes and address all issues threatening this population in order to arrive at possible mitigation measures for its protection.

KEYWORDS: BLUE WHALE; SRI LANKA; NORTHERN INDIAN OCEAN; SHIP STRIKES; BYCATCH; CONSERVATION; WHALEWATCHING; NORTHERN HEMISPHERE; SURVEY-VESSEL; ASIA; SOUTHERN HEMISPHERE

INTRODUCTION

Studies of marine mammal identification, distribution and abundance were carried out in the early 1980s to support the Indian Ocean Marine Mammal Sanctuary initiative (Whitehead, 1983; Alling, 1984; Gordon, 1987). Unfortunately, these offshore research programmes, carried out in Sri Lanka on board the sailing ship *Tulip,* came to a halt in 1985 due to the Singhalese/Tamil civil war. Only a few opportunistic surveys and land-based studies of cetacean strandings and bycatch were permitted (Alling, 1988; Ilangakoon, 1997; Leatherwood and Reeves, 1989). At the end of the war (May 2009), interest in the status of marine mammals off the coast of Sri Lanka returned, as well as understanding the conservation challenges unique to the country. Over this period, a probable subspecies of blue whale (*Balaenoptera musculus*) was sighted year-round in Sri Lankan waters (5–7°N) with observations about feeding along contour lines, aggregations around submarine canyons and in the presence of calves (Alling *et al.*, 1991; Deraniyagala, 1943; de Vos *et al.*, 2012; Ilangakoon, 2012; Martenstyn, 2013). It is this population that is the subject of this paper.

The taxonomic status of this blue whale population is not known but has been proposed to be a sub-species of the blue whale (Yochem and Leatherwood, 1985; Mikhalev, 2000). A Southern Hemisphere subspecies, *B.m. brevicauda,* was first recognised by Ichihara (1966) to be distinct from the polar Antarctic blue whale, *B.m. intermedia*. During the following few decades, studies (e.g. Branch *et al*., 2007b) suggested there are four sub-species of blue whales inhabiting New Zealand, Australia and Indonesia, Madagascar and the Northern Indian Ocean (NIO). These studies have compared and contrasted information about the proportional size of individuals, morphology, geographic distribution and vocalisation repertoires that may be indicative signatures for a mating population. LeDuc *et al.* (2007) analysed blue whale tissue taken from animals in the Antarctic, Chile (Pacific) and the Maldives (NIO) and found them to be highly differentiated from one another in both mitochondrial and nuclear genes, which suggests there may be a fifth sub-species. The identity of the Sri Lanka population is undetermined, but it is likely to be representative of an NIO sub-species classified by Blyth (1989) as *B.m. indica* (Anderson, 2012; Ilangakoon and Sathasivam, 2012).

Although blue whales have been legally protected since 1966, Soviet whaling continued unabated in the NIO and south to the Maldives until the illegal catches ceased in 1973 (e.g. Clapham and Ivashchenko, 2009). The intense clandestine whaling effort severely reduced the NIO humpback whale population; it is classified by the IUCN as endangered. Although there is not enough information about the NIO blue whale identity and size to assess its status today, it is likely that this population is also endangered and thus its protection is of great concern (Branch *et al.,* 2004). Most immediate is the issue of ship strikes because the concentration of these blue whales off the southern coast of Sri Lanka aggregates around one of the busiest shipping lanes in the world (Ilangakoon, 2012; Leaper, 2011). While there is no government or private agency tasked with recording marine mammal ship strikes, the Sri Lanka National Aquatic Resources Agency estimated that up to 20 blue and sperm whales were being killed annually by ships (website: *http://www.LBO.lk* accessed 20 December 2011).

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De Vos *et al.* (2013) reported on two blue whales that had died from ship strikes along the southern coast in a 12 day period during 2012. As comparison, Redfern *et al.* (2013) estimated that 1.8 known blue whales are killed annually along the Californian coast, which exceeds the United States allowable level of anthropogenic impact.

It is therefore urgent to understand the distribution of blue whales in relation to shipping traffic, identify the sub-species, estimate its population size and provide information to implement sound conservation initiatives. In order to understand and compare information with ongoing research on blue whales in the region, the University of Ruhuna (Matara, Sri Lanka) established an Indian Ocean Marine Mammal Research Unit with the Biosphere Foundation to support international and local collaborative research about the Sri Lanka blue whale population. This paper represents our effort to initiate this programme and report on data collected aboard a whalewatching vessel from 2009 to 2012.

METHODS

During a period of three years (from December 2009 through November 2012) data were collected on board *Raja & the Whales*, a vessel berthed in Mirissa Harbour on the southern coast of Sri Lanka. The 225hp vessel is a 13m deep-sea fishing boat converted to whalewatching with a helm on a platform, enabling visual sightings from about 4m above the sea. This is an excellent location from which to spot the high blow of the blue whale, giving the helmsman a sighting distance of about 3–4 n.miles in calm seas.

From December to April of each year, here referred to as the 'high season', the vessel made daily whalewatching trips from Mirissa. During these months the wind and seas are generally calm (Beaufort 3 or lower) and the level of tourism in Mirissa generally ensures reliable business. From May to October the southwest monsoon brings rough weather not conducive to whalewatching and tourism remains low during November. Consequently, during the 'low season' (May to November) the vessel only made trips when advised by fishermen working in the area that whales had been sighted or when specially arranged with visitors.

On whalewatching days the *Raja & the Whales* left Mirissa Harbour at approximately 06:30 and headed offshore until about 11:00. The vessel remained at sea until whales were sighted. If no whales were sighted the vessel returned to the harbour by 15:00 in the afternoon. When one or more whales were sighted, data were collected. Date, time, vessel's latitude and longitude, number of individuals sighted and notes on their behaviour and circumstances were recorded by a crew member trained in whale identification. Only data on blue whales are reported in this paper. If multiple whales were sighted at approximately the same time and location, they were recorded as a single sighting. The vessel operated within a range of approximately 30 n.miles from Mirissa Harbour. This defined the boundary of the area where sightings occurred.

In addition to the sighting data described above, dead blue whale observations made by the primary author (SMR) are reported for the first five months of 2014. These were discovered in the course of whalewatching operations as described above or through local word of mouth.

RESULTS

Summary of observations year-round, December 2009–November 2012

Over the three-year period for which data are presented, a total of 485 blue whale sightings were recorded. These sightings occurred on a total of 390 days with an average of 1.24 sightings per day on days when the crew of was successful in finding blue whales. At least one sighting was reported in every calendar month over this three-year period (Fig. 1).

The number of blue whale sightings associated with a single sighting range from 1–30, with the majority (approximately 96%) of sightings reporting 10 or fewer individuals. A numerical estimate of individuals was not available for a small fraction (8%) of the total sightings, in which the number of individuals was simply recorded as 'many'. For the purpose of this analysis, these sightings were assigned a value of six individuals, which is a conservative yet reasonable assumption. Under this assumption, a total of 2,213 blue whales was observed during the three-year period, yielding an average of 4.56 individuals per sighting. This total likely includes re-sightings of the same individuals.

Field notes taken onboard the vessel during whalewatching trips indicated that whales frequently defecated red faeces before diving, and that calves were

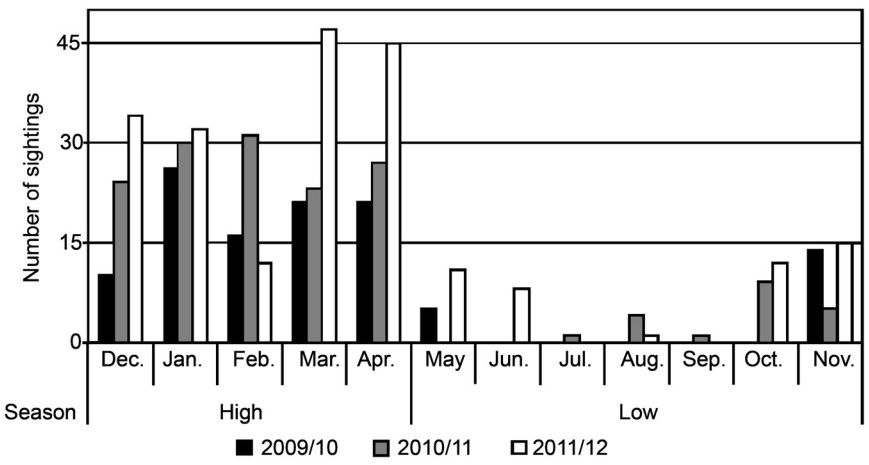

Fig. 1. Number of blue whale sightings by month, indicated as 'high' or 'low' season, from December 2009–November 2012.

observed during the months of January, February, March, October and November.

Comparison of high season (December–April) observations only

Of the total number of sightings, 399 (82%) were reported during the high season (November–April) (Fig. 1). During the three high seasons reported here, blue whales were sighted on 319 out of an estimated 454 days of whalewatching effort giving an average success of 70%. 'Success' here is defined as one or more blue whale sightings on a given day and the success rate was obtained by dividing this by the total number of days of whalewatching effort and converting to a percentage. An estimate of the total whalewatching effort during the low seasons is not available for comparison.

Table 1 summarises the blue whale observations recorded during each of the three high seasons reported: December 2009–April 2010; December 2010–April 2011; and December 2011–April 2012. Across the three high seasons, both the number of sightings and number of individuals sighted increased each season. The average success of sightings increased noticeably from the first to the second season (from 57% to 80%) but changed little from the second to the third season (from 80% to 74%). The fact that success remained relatively constant while the number of sightings grew from the second to the third year resulted in a noticeably higher average rate of sightings per day on successful days: 1.52 during the third season compared to 1.12 during the second. In essence, the crew sighted blue whales on a similar number of days during the second and third high seasons, yet during the third season they achieved more sightings per each successful day. The average number of individuals per sighting fluctuated from season to season; the highest (5.16) was observed during the second season and the lowest (4.47) during the third.

Table 1

	2009/10	2010/11	2011/12
Success (number of days with ≥1 sighting)	86	121	112
Effort (number of whalewatching days)	151	151	152*
(Success/effort × 100)	57%	80%	74%
Sightings (total number)	94	135	170
Average sightings per day (successful days only)	1.09	1.12	1.52
Individuals sighted (total number)	433	697	760
Individuals per sighting	4.61	5.16	4.47

*2012 was a leap year, contributing an extra day to February.

Fig. 2 illustrates the spatial distribution of blue whale sightings for the 2009–10, 2010–11 and 2011–12 high seasons. The mean latitude of sightings remained relatively constant from the first to the second high seasons but shifted northward (closer to shore) approximately 1.8 n.miles from the second to the third year. The sightings became less dispersed with fewer outliers over the time period reported. This is emphasised in Fig. 3, which shows a one standard deviational ellipse (Yuill, 1971) corresponding to each year's distribution of sightings, weighted by the count of individuals observed at each sighting. The concentration of sightings over all three years partially coincides spatially with the traffic separation scheme, which consists of eastbound and westbound shipping lanes separated by a central 'breakdown' lane (Fig. 3). Many of the sightings, particularly those observed during the first two high seasons, occurred within an area of sloping bathymetry, where the seafloor drops from a depth of 200m to 2,000m.

Mortality observations, 1 January–31 May 2014

Four blue whale deaths along the southern coast of Sri Lanka were confirmed during a five-month period in the beginning of 2014 (1 January–31 May) (Fig. 4). Two died from ship-strikes and two washed up on beaches with the cause of death unknown. When it was not possible to measure the whale, 'large' refers to greater than about 20m in length and 'small' is less than about 20m.

(1) From 1–3 February 2014, a large blue whale was observed off Mirissa (05°49'N, 80°28–30'E), unable to dive and seeking shelter along the coast due to a broken dorsal fin and wounds around the blowhole and along the spine to the fluke. After the third day the whale was not seen again. The back injury and broken fin suggested that the whale had been stuck by a ship and it was assumed that it had subsequently died of its injuries.

(2) On 10 March 2014 a small blue whale carcass was found washed ashore in Dickwella, the cause of death is unknown. It was divided into three pieces by a bulldozer and buried within three hours.

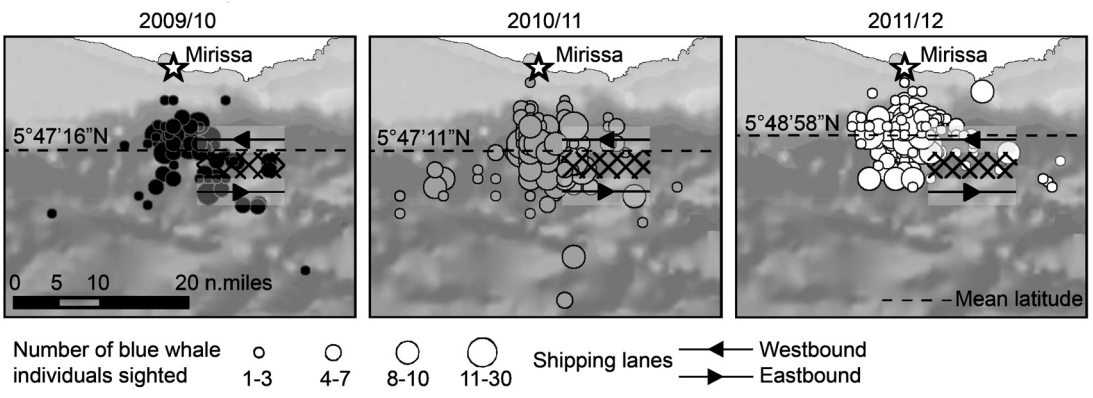

Fig. 2. Spatial distribution of blue whale sightings by yearly high season (December–April). The number of individuals reported at each sighting is indicated by circle size. Also shown is the traffic separation scheme, consisting of eastbound, westbound and central 'break-down' lanes.

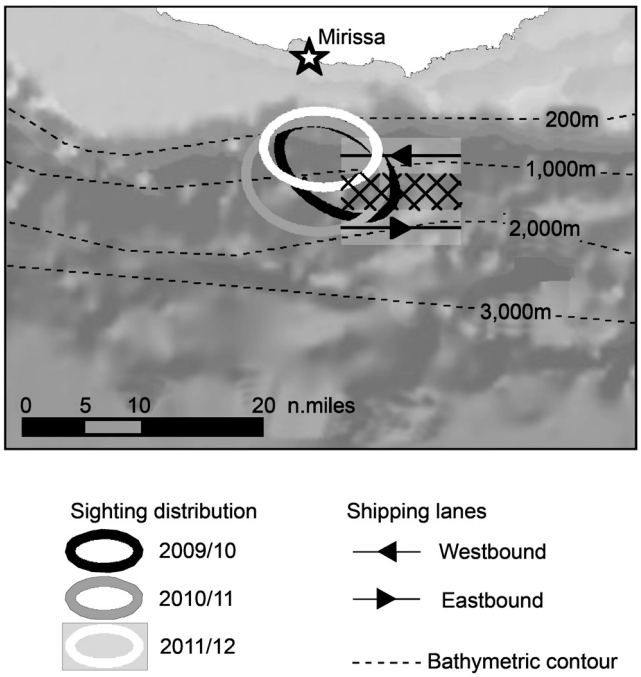

Fig. 3. Distribution of sightings by yearly high season, represented by a one standard deviational ellipse (Yuill, 1971) for each high season. Contour lines illustrate the sloping bathymetry.

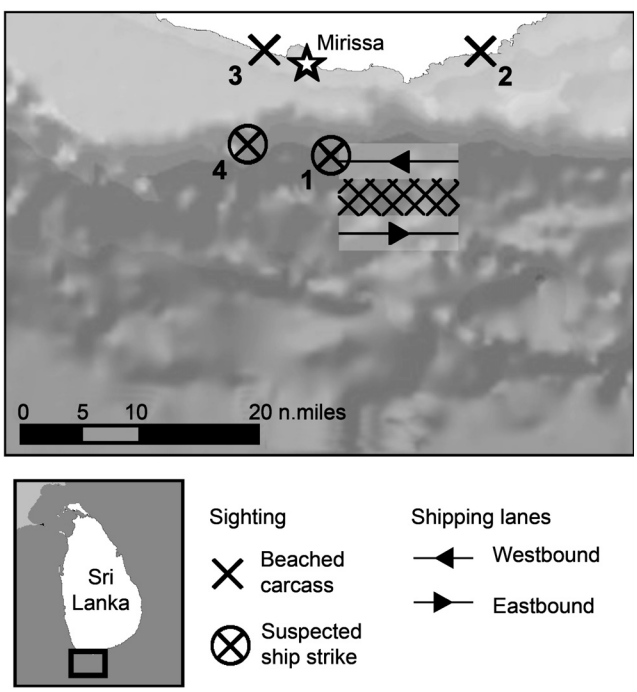

Fig. 4. Locations where injured or dead blue whales were observed between January and May, 2014. Numbers correspond to the numbered descriptions in the text.

(3) On 20 May 2014 a 16m female blue whale carcass was found washed ashore in Midigama Bay after having been seen earlier in the day near Mirissa Harbor. The cause of death is unknown. It had a 3m wound on its left flank, inflicted post mortem by a fisherman looking for ambergris.

(4) On 25 May 2014 a large blue whale was reported dead due to ship strike and floating out to sea in the shipping lane off Mirissa (05°50'N, 80°22'E).

In addition, on 28 April 2014 a large blue whale was reported dead and entangled in 100m of drift net in the Bay of Bengal east of Trincomalee, beyond Sri Lanka's 200 n.mile exclusive economic zone (EEZ). Prior to its death it was observed to be unable to dive due to the buoys attached to the net. The entangled whale had caused so much damage to the drift net that it was beyond repair. The fishermen cut the net and buoys from the carcass and set it loose. This observation was outside of the Sri Lanka EEZ and so has not been included with the number of dead whales observed along the southern coast in 2014. It is mentioned as an example of drift net bycatch of large whales in the wider area near Sri Lanka.

DISCUSSION

A review of the Sri Lanka blue whale

It is known that blue whale feeding behaviour is linked to resource opportunity with regards to the density of euphausiids (Branch *et al.*, 2007b) and feeding locations shift spatially and temporally due to oceanographic conditions (Calambodkis *et al.*, 2009). The monsoonal weather and sloping bathymetry surrounding Sri Lanka supports high productivity during both the northeast and southwest monsoons (Vinayachandran and Mathews, 2003; Vinayachandran *et al.,* 2004). As discussed by Anderson *et al.* (2012), blue whales may remain in the NIO migrating west along the southern coast of Sri Lanka to the Arabian Sea to feed during the southwest monsoon (May–October) and eastwards along the southern coast of Sri Lanka to feed in the Bay of Bengal during the northeast monsoon (November–April). During the northeast monsoon, Alling *et al.* (1991) observed blue whales feeding along the steep slopes separating the continental shelf from the deep ocean basin surrounding the coast of Sri Lanka, and their red faeces were identified as remains of a *Mysidacea spp*. The 2009–2012 data presented here agree with these general feeding observations and movements of whales along the coast of Sri Lanka.

Blue whale vocalisations recorded off the northeast coast of Sri Lanka in 1983–84 (Alling and Payne, 1987) were classified as one of nine different blue whale populations around the world (McDonald *et al.*, 2006). Within the Indian Ocean, the Sri Lanka blue whale vocalisation is distinct from three other sub-species identified as Madagascar, Australia and Antarctic blue whales (Stafford *et al.*, 2004; 2011). The Sri Lanka blue whale has been detected year-round near Diego Garcia; year-round northeast of Amsterdam Island and with some detection in the austral summer (Dec/Jan) southwest of Amsterdam Island and off Crozet Island (46°25'S, 51°40'E), the latter being the farthest south and about 4,000 n.miles from Sri Lanka (Sameran *et al.*, 2010; 2013). The austral summer is also the time that the Sri Lanka blue whale numbers are observed increasing off Sri Lanka on the southern and northeast coasts (Alling *et al.*, 1991; Anderson *et al.* 2012). The sightings of a few whales off the southern coast of Sri Lanka during the southwest monsoon and the two dead whales observed at the end of May suggests that the entire population does not migrate in unison, but rather individuals or groups may roam the Indian Ocean opportunistically following productivity, mating or calving requirements.

Attard *et al.* (2012) found that the Southern Indian Ocean sub-species, *B. m. brevicauda*, is genetically distinct from

the Antarctic *B. m. intermedia*, but there are indications that hybridisation between the two sub-species due to whaling pressures and/or climate change now occurs. In the last few decades, research on the Southern Hemisphere blue whales have revealed that Antarctic blue whales remain south of 60°S during the summer but travel north as far as the equator in both the Indian and Pacific oceans in the winter (Branch *et al.,* 2007a; Branch *et al.*, 2009; Samaran *et al.*, 2010; Stafford *et al.*, 2004). Studies further suggest that Sri Lankan blue whales overlap occasionally with Madagascar or Antarctic whales at three southern locations and all four sub-species (including the Australian sub-species) visit Crozet Island (Samaran *et al.*, 2004; 2013; Stafford *et al.*, 2011). It is possible that these distinct blue whale populations were once geographically or seasonally separated from each other, but now due to unpredictable or scare resources, migration patterns may be shifting, providing new opportunities for mixing between sub-species.

Ship strikes and conservation issues

South of Mirissa the shipping lanes approximately coincide with submarine canyons and deep drop-off regions (Fig. 3) associated with upwelling and high productivity. The recent observations of dead whales in the vicinity suggest that the overlap between the highly productive whale feeding ground and the shipping lanes results in ship strikes. Obtaining an accurate count of ship strike deaths in Sri Lanka is difficult, exacerbated by the fact that dead whales may not make it to shore, and if they do, they are often disposed of within hours, making it impossible for scientists to examine the whale. As blue whales tend to sink when dead, Redfern *et al.* (2013) estimated that the proportion of carcasses detected is less than 17%. Based on the four deaths reported here, if an average rate of 0.8 deaths per month is assumed and 17% of carcasses detected, then the number of blue whale deaths may be as high as 56 per year. The number of deaths attributable to ship strikes versus other causes is still not clear.

In reviewing the available stranding data, Ilangakoon (2006) stated that prior to 1996 (1986–95), no dead whales with noticeable wounds from ship strikes were observed. This may have been the case because fewer people were reporting whale strandings or perhaps the whales were gathering elsewhere to feed. Regardless, the three years of Mirissa whalewatching data reported here show that, in recent years, whales have predictably returned to the southern coastline and the shipping lanes.

Marine mammals are threatened in areas of dense shipping traffic and have been reported as killed in locations around the world such as off the Santa Barbara coast in the United States (Berman-Kowalewski *et al.*, 2010; Clapman *et al.*, 1999). Possible options for mitigation include moving the shipping lane, slowing the traffic in areas of large concentrations of whales or declaring these areas 'no-transit' zones. All three are possible in Sri Lanka, but moving the lanes offshore, south of the 3,000m contour line, would be the most effective and practical way of reducing risk.

An additional dynamic that warrants consideration in this area is a driftnet fishery, active between the shore and the shipping lane and in between the two lanes, along the centre of the traffic separation scheme. Sri Lanka is a bycatch hotspot (Lewiston *et al.*, 2014) and blue whales have been observed entangled in nets, struggling or dead. The drift nets are made of nylon and extend 2–4km along the surface and 100–120m deep. As fishermen must avoid the busy shipping lanes, they often place their nets next to each other, effectively creating one or more continuous lines of nets. Thus, not only is the shipping lane a hazard for the whales but also the sea around the lane due to the nets that may be virtually undetectable to a whale. If the shipping lanes are moved offshore, it is likely that the fishermen will move in to fish the waters previously occupied by the shipping lanes. Thus, an unintended consequence of moving the lanes could be that driftnet fishing increases in the area of whale activity. Similarly, reducing only the speed of the vessels in this area would not change the curtain of nets hanging on all sides of the lanes. Fitting pingers to the fishing gear could discourage whales from becoming entangled in nets but this should be tested experimentally and care must be taken so that this does not drive the whales into the shipping lane. The preferred solution is to move the shipping lanes south and work with the local government to prohibit driftnet fishing but allow non-driftnet methods in the area between the 200m and 2,000m depth contours (Fig. 3), where the whales repeatedly return.

The Sri Lanka blue whale has also been affected by the accelerated increase in coastal development since the civil war ended. The most striking examples of development are the newly constructed maritime port in the natural harbour of Hambantota near to the blue whale feeding grounds and recent seismic activity supporting an emerging oil and gas industry on the west coast of Sri Lanka (NARA, 2009). The increase in tourism in the last years has also supported a growing whalewatching business in several ports around Sri Lanka but most noticeably in Mirissa, which has raised issues of whale harassment (Ilangakoon, 2012).

The slight northward shift in location of blue whale sightings across the three whalewatching high seasons could reflect several things relevant to the above: (1) the locations of blue whale aggregations may have changed from season to season; (2) the locations where the crew of the *Raja & the Whales* searched for whales may have changed; or (3) a combination of both (1) and (2). The first two possibilities cannot be distinguished without data on null sightings (i.e. locations where whales were not sighted), but it is reasonable to assume that a combination of both factors explains the observed data. Most importantly, the data suggest that the whales are following prey movements and are not altering their movements away from vessel activity, either in the shipping lanes or from whalewatching vessels.

While there is still a paucity of information about the number and causes of blue whale deaths, the fact that four dead whales were observed along the southern coast over the course of five months is alarming. If this is indicative of the number of whales that die from anthropogenic causes throughout the year, then understanding the status of the Sri Lanka blue whale population and possible mitigation measures to protect it are of critical importance.

CONCLUSION

The Sri Lanka blue whale is one of four known Indian Ocean populations, but its taxonomic identity, distribution in the

NIO and size of the population remains uncertain. As the location of feeding whales on the southern coast overlaps with shipping lanes, resulting in two or more known ship strikes a year, there is cause for great concern. Additionally, there are other issues impacting the future of this population such as driftnet entanglement, noise pollution (shipping, dynamite and seismic exploration for oil and gas), habitat destruction and climate change, but the aforementioned are the most urgent and alarming because they often result in immediate mortality. Fortunately, there is a growing awareness of this situation and the newly established University of Ruhuna's Indian Ocean Marine Mammal Research Unit provides a centre for international collaborative marine mammal research. The IWC Scientific Committee recognised in 2014 that ship strikes are likely to be having a population level impact on blue whales in the NIO (Priyadarshan *et al.,* 2014). These ongoing initiatives offer new opportunities to conduct research on the taxonomic status of the Sri Lanka blue whale, estimate population size and provide information to guide sound marine mammal conservation.

ACKNOWLEDGEMENTS

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How may an annual removal of humpback whales from Godthaabsfjord, West Greenland, affect the within-fjord sighting rate?

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ABSTRACT

Photo-identifications of humpback whales in the Godthaabsfjord area were collected from 2007 to 2012 and divided into individuals and number of sightings per individual. Monte Carlo simulations were performed on the sighting distributions of individual humpback whales to investigate the potential impact that local removals (e.g. ship strikes, subsistence hunt) could have on the sighting rate of humpback whales in Godthaabsfjord. Half of the sightings were based on the same six individuals during the six year period. Sighting rate was likely to drop regardless of when (spring, summer or autumn) an individual was removed due to the large degree of site fidelity of several humpback whales in Godthaabsfjord. Removals could affect the whalewatching industry in Godthaabsfjord where humpback whales constitute a key species. The least impact may be achieved by conducting the hunt outside the fjord system or minimising summer or autumn hunts within the fjord, as spring removals tend to have the least effect on summer sighting rates.

KEYWORDS: HUMPBACK WHALE; WHALING-ABORIGINAL; WHALEWATCHING; SIGHTING RATE; SITE FIDELITY; WEST GREENLAND

INTRODUCTION

From early spring to late autumn, humpback whales (*Megaptera novaeangliae*) come to West Greenland to feed on prey such as capelin (*Mallotus villosus*), sandlance (*Ammodytes dubius*) and euphausiids (Larsen and Hammond, 2004; Stevick *et al.*, 2006). Large aggregations of whales on the continental shelves of West Greenland have been linked to large densities of krill (Laidre *et al.*, 2010). Furthermore, the humpback whales also target food resources within fjords and bays and a limited number of humpback whales annually arrive to take advantage of the prey availability in Godthaabsfjord (64°11'N, 51°47'W; Fig. 1). Some individuals show a large degree of site fidelity returning to the fjord year after year, while others are seen a single year only. Generally, the whales do not remain in the fjord for the entire feeding period and their residence time seems highly variable (Boye *et al.*, 2010). This is also supported by a study of satellite tagged humpback whales, where individuals remained relatively stationary within an area for a maximum of a month and then moved up to hundreds of kilometres away to a different location, where they remained stationary again (Heide-Jørgensen and Laidre, 2007).

Humpback whales were, up until 1985, an important source of whale meat for the people of West Greenland. Commercial whaling of humpback whales was banned in 1966 but aboriginal hunters from West Greenland and the Lesser Antilles were allowed to continue the hunt (e.g. Martin *et al.*, 1984). In 1981 the abundance of humpback whales in West Greenland was estimated to be only 85–200 animals (Whitehead *et al.*, 1983) and in 1986 the International Whaling Commission (IWC) moratorium reduced the West Greenland quota on humpback whales to zero (IWC, 1986).

Since then, humpback whale abundance has increased rapidly in West Greenland with an estimated rate of 9.4% yr^{-1} and a current abundance estimate between 2,154 (CV = 0.36) and 3,272 (CV = 0.55) (Heide-Jørgensen *et al.*, 2012). This increase has resulted in an agreed quota for subsistence whaling as well as generating ecotourism. The West Greenland humpback whales now constitute a key species for the whalewatching industry. Around Nuuk, whalewatching takes place from smaller vessels within the protected waters of Godthaabsfjord. This is to avoid bad weather conditions or large swells on Fyllas Bank, Davis Strait, where whales are also present. The whalewatching operators in Nuuk are therefore dependent on the humpback whales being within the Godthaabsfjord area.

A recent study on site fidelity in humpback whales within the Godthaabsfjord (Boye *et al.,* 2010) raised the question of what happens to the sighting rate of humpback whales in Godthaabsfjord if individuals are removed from the fjord. Removals are most likely to happen through the subsistence hunt which was reopened in 2009. Since 2010 1–2 humpback whales have been taken yearly in the Godthaabsfjord area. In addition, ships strikes by large vessels are becoming more likely as oil and gas exploration in Greenland waters has resulted in increased shipping both offshore, along the coast and in the outer fjord system. The potential opening of an iron ore mine in the bottom of Godthaabsfjord would lead to an increase in marine traffic within the fjord system of significantly larger vessels than found previously. It is unknown whether the expected increase in noise levels and disturbance from anthropogenic activities could cause humpback whales to leave the Godthaabsfjord and feed in less exposed areas.

Ecotourism has become important in Greenland. This paper examines the possible effects that potential removals

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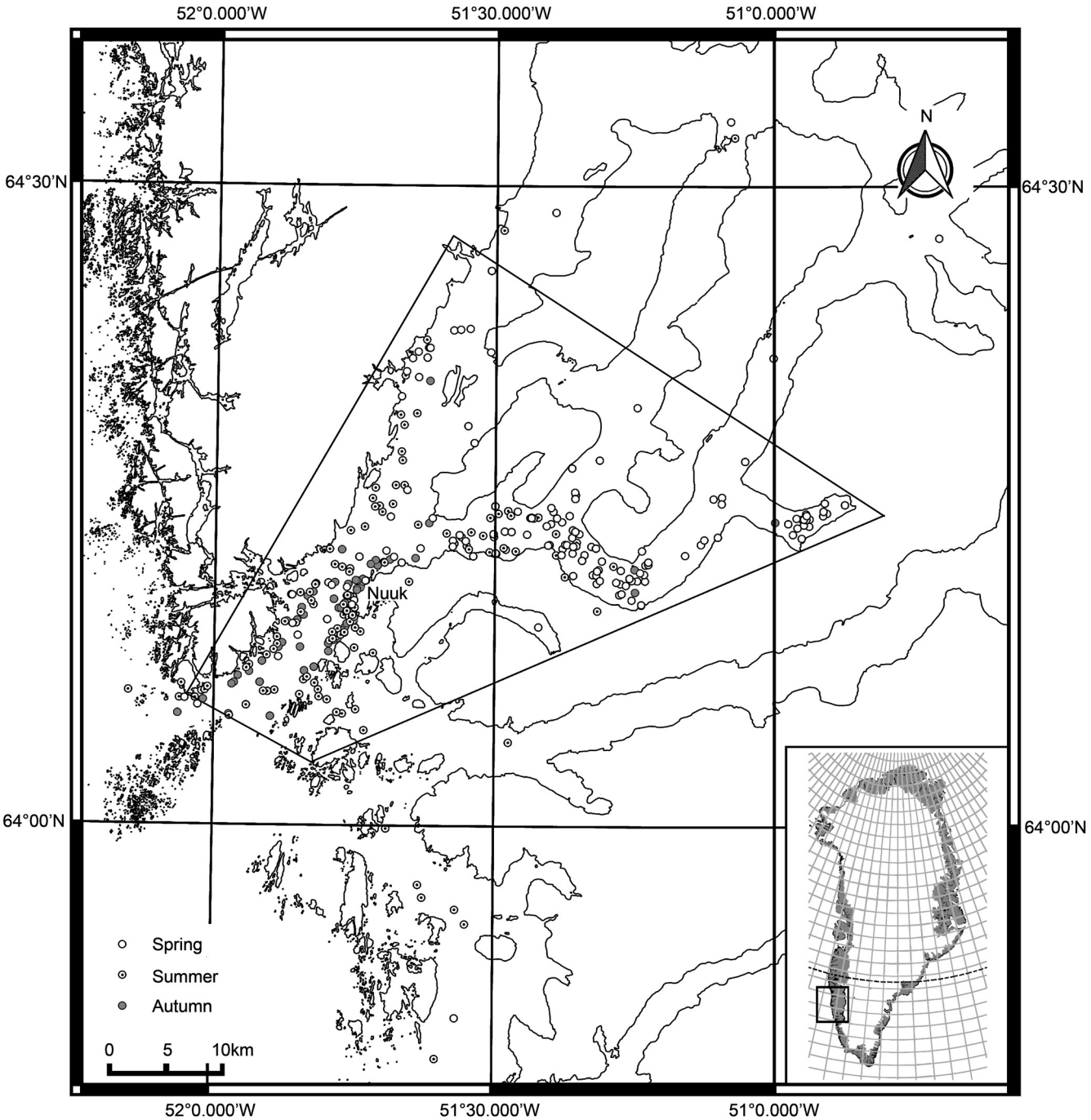

Fig. 1. The black frame indicates the area of effort by the researchers. Pictures from outside the effort zone have been supplied by locals and tourists. Map: Karl Brix Zinglersen, GINR, Coastline: Danish Geodata Agency.

of humpback whales from Godthaabsfjord could have on the sighting rate in the fjord. Assuming that individual whales' likelihood to be removed is proportional to the time they spend in the fjord, the impact on the sighting rate is analysed under the assumption that the number of whales that visit the fjord remains the same. Whilst this is unlikely for large removals, it is not unreasonable for realistic future removals of a single or a few animals per year, should it be from ship strikes or a direct hunt.

MATERIAL AND METHODS

Humpback whale fluke patterns along with the dorsal fin can be used for identification of individual whales (Katona *et al.*, 1979). In the period from 2007–2012 humpback whale identification photos were collected in the Godthaabsfjord area (Fig. 1) by researchers with help from local whalewatching boats. Whalewatching boats aim at areas with a high probability of finding whales, which precludes a quantification of effort. Additional photo-identifications were provided by the public. The researcher's effort on the water was from May to early October but locals and the whalewatching industry continued to provide photos until late October. Date, time and GPS position of the boat was noted for each photo, if available. Some photos only contained information on time and place (Godthaabsfjord). Photographs judged to be of suitable quality (Calambokidis *et al.*, 2000) were compared visually and sorted into individual whales by independent observers with

identification experience. Numbers of encounters of each individual in different years were also noted.

The density of whales was analysed by using the data on the number of whale encounters collected only from the research boat from May to early October and did not include photos from the public or whalewatching industry.

To investigate the potential impact that local removals could have on the sighting rate of humpback whales in Godthaabsfjord, Monte Carlo simulations were performed on the sighting distributions of individual humpback whales. Sightings were divided into the total number of spring (May and June), summer (July and August) and autumn (September and October) sightings per individual whale, with the total number of sightings summed over all individuals in each period giving an estimate of the relative sighting rate. One annual removal in either spring, summer or autumn was then assumed. It was also assumed that a removed whale would be replaced by a new whale drawn at random from the set of whales that had been seen in spring, summer or autumn. The probability that a given whale would be removed was set to be proportional to the relative sighting rate of that whale in the relevant season, so that harvest or potential ship strikes would target predominately the more resident individuals. The relative sighting rate, now given as the total number of sightings summed over the new distribution of individuals, would then decline over time because the distribution of individuals would change towards individuals with fewer sightings, while the total number of whales would remain the same. This made the relative sighting rate change over time, and this removal regime was simulated by 10,000 iterations over 50 years in order to estimate the development in the average of the relative sighting rate.

The estimated future sighting rates may be positively biased if caught individuals are not replaced; yet they might also be negatively biased if for example the integral of the number of whales in the fjord over a year is a function of ecological features, like the availability of food. In addition the estimates do not attempt to include the developments in the population of humpback whales in West Greenland, but attempt only to estimate relative sighting rates as a function of a change in the distribution of individual behaviour.

RESULTS

New individuals arrive in Godthaabsfjord each year (Table 1). However, within the period from 2007 to 2012 between 18.5% and 40% of the whales have been resighted for several years. There is a tendency for the resight rate to drop with time yet some individuals (8%) have been resighted during five to six years of the period and show a strong degree of site fidelity towards the Godthaabsfjord. It is also these individuals that appear to account for 50% of the encounters (Fig. 2). For instance, individuals with strong site fidelity have on average been photographed 4.3 ± 0.7 times (mean ± SE) annually whereas whales seen for a single year on average are photographed 2.1 ± 0.3 times in the given year they are present. The average for the single-year-individuals is drawn towards the higher end by two single individuals which were photographed 12 and 13 times during one year. If these two individuals are excluded, the average would drop to 1.7 ± 0.2 for whales seen for only one year in the fjord.

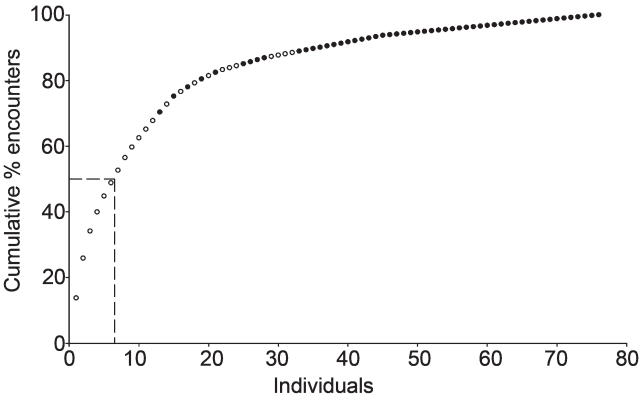

Fig. 2. The sighting rate of each individual. 50% of the encounters have during the past 6 years been based on the same 6 individuals. Open circles are individuals resighted in 2 or more years. Closed circles are individuals sighted for only one year.

May and early June are the months where most whales are seen in the fjord (Fig. 3). Sightings drop during summer and reach a minimum in August. In September, sightings increase again. Whales were also encountered during October and the public and whalewatching industry continued to provide photos during this month.

Fig. 4 illustrates the Monte Carlo simulation of one annual humpback whale removal in Godthaabsfjord. The potential relative sighting rate in spring, summer and autumn (Figs 4a–c) is shown in relation to an annual removal taking place during either spring (Fig. 4a), summer (Fig. 4b) or autumn (Fig. 4c). The potential relative sighting rate during summer is also shown (Fig. 4d) when a whale is taken in one of the seasons. According to the simulation the sighting rate will decline over time no matter what season a whale is removed.

Table 1

Site fidelity of humpback whales in Godthaabsfjord during the past six years. ID = number of whales identified, *N* = number of new individuals. Numbers in brackets are %.

				No. of whales seen in each subsequent year				
Year	No. of photos	ID	*N*	2008	2009	2010	2011	2012
2007	49	20	20	8 (40.0)	6 (40.0)	7 (27.0)	5 (24.0)	5 (18.5)
2008	143	20	12	–	6 (40.0)	10 (38.5)	7 (33.3)	9 (33.3)
2009	38	15	8	–	–	7 (26.7)	6 (28.6)	8 (29.6)
2010	68	26	13	–	–	–	9 (42.9)	9 (33.3)
2011	130	21	10	–	–	–	–	10 (37.0)
2012	85	27	13	–	–	–	–	–
Total	513	129	76	–	–	–	–	–

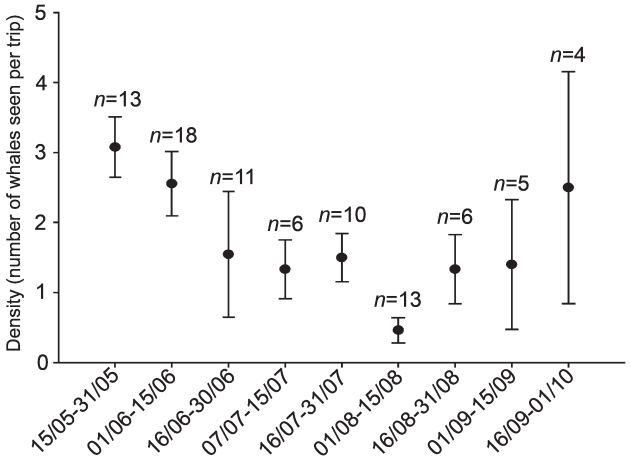

Fig. 3. The density of whales with SE. Most whales are spotted during late spring and early autumn. *n* = effort on the water in days in the given period.

However, there is a large difference in how much the sighting rate may drop. If one whale is removed annually during spring (Fig. 4a), then the sighting rate will gradually drop over a 50 year period and eventually stabilise at a sighting rate of 45% relative to the current spring sighting rate. In addition, the sighting rate during summer and autumn will also be affected by a removal in spring where annual sighting rates may drop to 65% and 55% for summer and autumn respectively relative to their current sighting rate. Autumn removals (Fig. 4c), show more or less the same pattern with the sighting rate dropping to 45% in autumn over a 40 year period and this causes the summer sighting rate to drop to 55% relative to the current sighting rate. Spring sightings will, however, be less affected by autumn removals as sighting rate only drops 20% and stabilises at 80% relative to the current spring sighting rate within a 20 year period. If removals take place only during summer (Fig. 4b) this will have a strong effect on both the summer and autumn sighting rates which may drop to around 40% and 45%, respectively. Again, this will not affect the spring sighting rate as much which drops to around 80% of its current sighting rate.

The main tourist season in Nuuk is during summer and only if whales are removed during spring is the decrease in sighting rate minimised; it stabilises at approximately 65% relative to the current summer sighting rate within a 50 year period (Fig. 4d).

DISCUSSION

The asymptotic sighting rate of the analysis is the same independently of the number of whales removed per year, but higher removals will result in a faster decline toward the asymptotic values. This constancy is obtained because it is assumed that the number of individual whales that visits the fjord will remain constant. While this may only be expected for very small removals, the analysis focuses on the effects caused by an expected change in the distribution of time-periods spend by individual whales in the fjord.

Looking at the density of whales, most encounters are during spring and autumn and fewest encounters during summer. Spring is the time period where the whales arrive from their winter breeding areas and the period corresponds to the spawning of capelin inside the fjords (Friis-Rødel and Kanneworf, 2002). The larger density during spring may therefore reflect an influx of individuals on their northward migration that target spawning capelin in the shallow waters. The higher density during autumn may reflect an influx of whales on their southward migration to the winter breeding areas.

Although new individuals enter the Godthaabsfjord area each year, many of the whales encountered are whales that

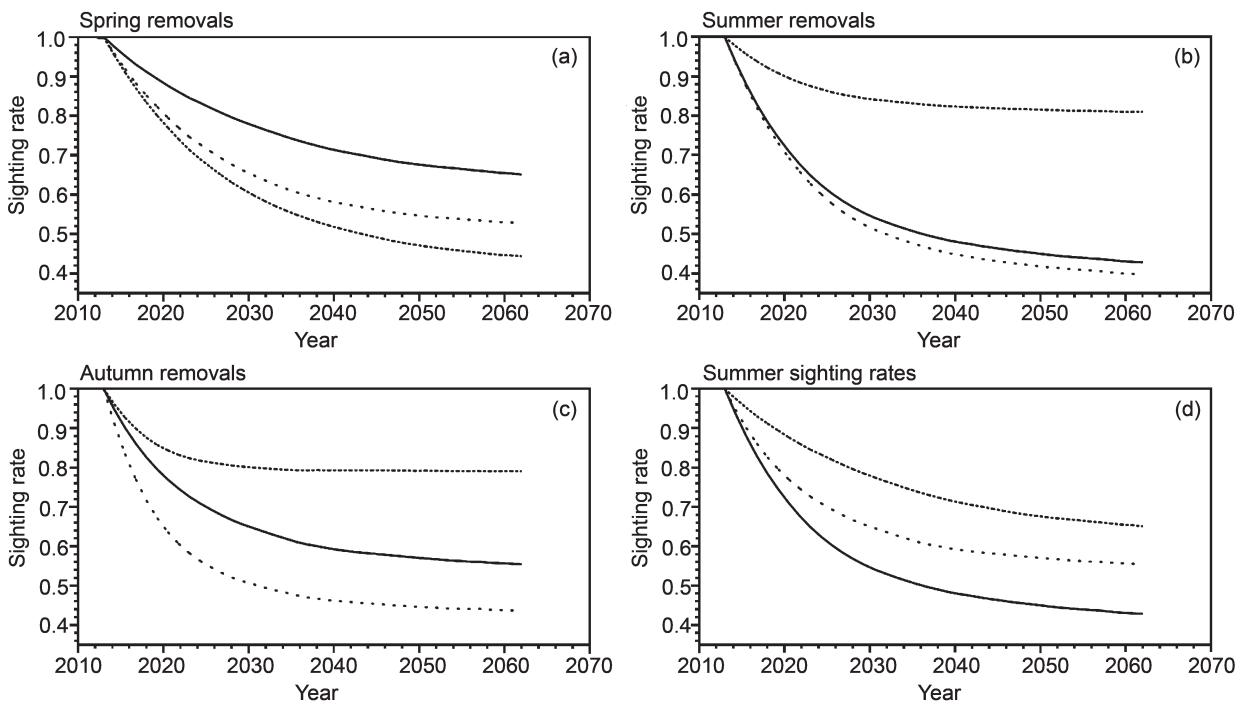

Fig. 4. Illustrates the simulation of removals of humpback whales under three different scenarios (A–C) along with an illustration of how summer sighting rates (D) could appear if whales were removed during different seasons. Spring (dotted line), summer (solid line) or autumn (dashed line). The simulation illustrates the removal of a single whale annually.

have been observed in the fjord in previous years. Whales with the largest site fidelity, i.e. whales that have been seen more or less every year since 2007, are encountered the most. It appears that just six individuals (of the total 76 whales that have been identified in the fjord so far) make up the basis of 50% of the encounters within the six year period. Therefore the most 'site faithful' individuals may be of considerable importance to the whalewatching companies as reflected in all the photos collected.

It is unlikely that photos of every whale entering/leaving the fjord are obtained. The vast majority of the photos collected are from the outer part of the fjord (Fig. 1) which either depict where most whales are present or where most boats are moving about. This means that the photos analysed represent the area used for whalewatching and represent the individuals present in that area.

The reason for the variable site fidelity amongst individuals is unknown but this may be maternally passed on to the calves (Weinrich, 1998). It is therefore a challenge to predict how, when and if new individuals become site faithful with time or if site faithful animals eventually become less site faithful. The simulation made here is based on the situation during the past six years and there is always the possibility that more years of data collection could alter the picture.

According to the simulation, the high site fidelity of individual whales in Godthaabsfjord will result in a decrease in sighting rate over time if humpback whales within the fjord are removed, despite the fact that new individuals arrive annually. If new individuals were encountered just as often as site faithful animals during a single season this would not be the case. But the fact that site faithful individuals are encountered more often and seen over a longer period within the fjord leads to a greater possibility for these animals to be hunted, struck by ships or by other means removed from the fjord. Eventually the yearly sighting rate would then decline over time because the distribution of individuals would change towards individuals that spend less time in the fjord system.

To reduce a decrease in sighting rate over time, several actions could be considered and some are already in use. Hunting of humpback whales most often takes place in spring or autumn when the weather is cold and the chance of destroying the meat in warmer temperatures is smaller. With the reopening of the subsistence hunt on humpback whales in West Greenland there has been an increasing concern and debate on how this might affect the whalewatching industry which relies on the presence of the whales and on the tourists. In Nuuk, whaling takes place within or in the vicinity of Godthaabsfjord as:

(1) the hunters are reliant on being close to the flensing areas to prevent long distance travelling and the risk of the meat being spoiled;

(2) the calmer waters within the fjord facilitates the hunt and reduces the risk of strike and loss; and

(3) long distance travelling would increase the fuel expenses.

However, if whales are not hunted during summer but are taken during the spring this may, according to the results presented here, facilitate a minimum in decrease of sighting rate in Godthaabsfjord. The density of whales within the fjord is larger during this period and the probability of striking a new (rather than site faithful) animal is greater. Furthermore, the whales are not always taken inside the fjord but occasionally just outside the fjord where individuals not associated with Godthaabsfjord may be encountered. According to the results, whaling within the fjord during autumn could have a larger negative impact on the summer sighting rate than hunting during spring. This could be explained by the identification data from spring and autumn which indicate that 41% of encounters during spring are of the six most site faithful individuals compared to 61% during autumn of the same six individuals. However, identification data during October are almost solely based on photos from the public and whale watching boats as very little effort on the water was carried out in October during this study and effort on the water during September was also low. If effort increases during autumn there is a possibility that whale density along with number of individuals encountered will increase further and that catches during autumn will have an equally low impact on the summer sighting rate as spring catches, however, the picture may also remain the same.

Ship strikes and entanglements account for unpredictable removals from the fjord. Entanglements are difficult to prevent and less controllable. Between one and five humpback whales have been entangled annually in West Greenland since 2001 (none in 2007) in fishing gear developed to catch cod or snow crabs (data from the Ministry of Fisheries, Hunting and Agriculture, Greenland Self Rule). In Greenland, the outcome of entanglements is lethal unless the whales are able to get free by themselves. Entanglements have also occurred in Godthaabsfjord.

Traffic from smaller outboard vessels is large within the fjord but has to our knowledge never resulted in any ship strikes fatal for whales or humans, although ship strikes have occurred. In contrast, the larger vessels involved in mineral exploration may pose a threat, as ships larger than 80m according to Laist *et al.* (2001) cause the most severe and lethal injuries. Shipping in relation to oil and gas exploration is already taking place from the mouth of the fjord to Nuuk harbour. Furthermore, the proposed Isua Iron Ore mine in the bottom of Godthaabsfjord may result in approx. 20 return ships trips a month within the fjord, divided into 330m bulk carriers (VLBC), 290m cargo ships, 170m tankers, 135m transport vessels and smaller 31m tug boats (Orbicon, 2013), increasing the possibility of ship strikes. Laist *et al.* (2001) found that most accidents occurred when speed exceeded 14 knots. To reduce the risk of ship strikes, regulations regarding speed of larger vessels entering the fjord could be implemented along with the use of marine mammal observers onboard the boats moving within the fjord. Finally, the risk of ship strikes could be further reduced if studies of humpback whale movements were conducted within the fjord to point out important travelling routes used by the whales or feeding hot spots. Restricted areas for large vessels moving within the fjord could then be established.

In summary, due to the large site fidelity of several individuals in Godthaabsfjord, sighting rate within the fjord is expected to drop over time if one individual is removed from the fjord annually even if the numbers of individuals that visit the fjord remain the same. This is despite a healthy

population of humpback whales along the West Greenland coast and the fact that new individuals enter the fjord every year. These results, however, depend on the assumption that the number of whales that visit the fjord will not increase. Most encounters of humpback whales occur during spring and autumn, corresponding to the influx of whales on their north and southward migration. The simulations of removals of whales from the fjord indicate that removals during spring will have the least effect on the summer sighting rate and hence the least effect on the whalewatching industry. Hunting takes places in either spring or autumn, where autumn hunting may result in a larger decrease in sighting rate than spring hunting. Ship strikes with lethal outcome are a new challenge which may be overcome by lowering speed and establishing restricted areas for heavy traffic within the fjord.

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Upwellings, canyons and whales: An important winter habitat for balaenopterid whales off Mauritania, northwest Africa

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ABSTRACT

The aim of this study was to identify critical habitats for baleen whales in the Mauritanian upwelling zone using data collected from a platform of opportunity: a 60 day geophysical survey approximately 100km southwest of Cap Blanc, Mauritania in winter (2012/13). The bathymetry of the 5,500km^2 study area was complex, including parts of the Cap Timiris Canyon system. Large whales, including sei and blue whales, accounted for 70% of the 238 cetacean sightings. Species identification was often problematic, especially in the case of balaenopterid whales, so data for all whales of this genus were pooled for the estimation of abundance and distribution. Spatial modelling was applied to estimate abundance and to plot a predicted density map of balaenopterid whales. Depth and the chlorophyll-*a* concentration when at its peak (in the previous September) were significant predictors of whale density. Point abundance in the study area was estimated at 272 whales (95% CI 265–279) and density was highest in the depth range 500–2,250m near to the canyon system (6.18 whales/100km^2, 95% CI 6.03–6.51). Steep seabed topography created by canyons running off the shelf edge, together with the strong upwelling system, probably create optimal habitats for the euphausiid prey of sei and blue whales. Sei whales were observed skim-feeding at dawn or dusk on seven occasions; in one sighting an aggregation of 18 skim-feeding sei whales were observed. The high density of these baleen whale species in such a highly productive area and direct observation of feeding behaviour in sei whales, provides evidence of feeding during the winter breeding season, when they have previously been presumed to feed less. This study demonstrates the potential value of collecting further data on seismic survey vessels and would improve understanding of cetacean ecology in remote and under-explored regions.

KEYWORDS: HABITAT; OCEANOGRAPHY; FEEDING GROUNDS; MODELLING; ATLANTIC OCEAN; ABUNDANCE ESTIMATE; SEISMIC SURVEY; SEI WHALE; BLUE WHALE

INTRODUCTION

Upwellings of cold, nutrient-rich ocean water drive high levels of primary productivity, in which zones of high zooplankton density form and provide rich feeding habitats for fish, seabirds and cetaceans (Butler *et al.*, 2002; Croll *et al.*, 2005; Joiris, 2011; Tynan *et al.*, 2005). Off the coast of northwest Africa, the Mauritanian upwelling zone near Cap Blanc is considered exceptionally productive (Hernández-Léon *et al.*, 2007; Peña-Izquierdo *et al.*, 2012; Voituriez and Chuchla, 1978) and of great importance as a feeding ground for both resident and wintering seabirds (Camphuysen and van der Meer, 2005; Wynn and Knefelkamp, 2004; Wynn and Krastel, 2012). Although cetaceans have been recorded during surveys that primarily targeted offshore seabird communities in this region (Camphuysen, 2000; Camphuysen *et al.*, 2012), no dedicated systematic surveys of offshore cetaceans from which density estimates could be obtained have been carried out here to date (Kaschner *et al.*, 2012). The aim of this study is to identify critical habitats for baleen whales off Mauritania using data collected from a platform of opportunity.

The winter distributions of baleen whale species in the northeast Atlantic are poorly understood (Clapham *et al.*, 1999; Prieto *et al.*, 2012a; Reeves *et al.*, 2004; Reilly *et al.*, 2008), largely due to the relatively low levels of offshore survey effort at lower latitudes in the Atlantic. Recent insights have been gained from acoustic monitoring using the SOSUS hydrophone arrays (Charif and Clark, 2009) but logistical difficulties and funding restraints have resulted in limited visual survey effort in offshore waters during the winter months. This paper presents data on cetaceans viewed during a 60 day geophysical survey from November 2012 to January 2013 in a study area of approximately 5,500km^2 straddling the continental shelf edge southwest of Cap Blanc, Mauritania (Fig. 1).

Seismic survey vessels provide a platform of opportunity offering a number of key advantages. Vessels are typically large, with comfortable, high observation platforms. Surveys may last many weeks or months, allowing sustained periods at sea in all seasons of the year, often in remote and relatively unexplored regions of the world that would otherwise be prohibitively expensive to achieve in a vessel dedicated to a cetacean survey. In addition, the systematic survey design, albeit not targeting wildlife, results in the collection of detailed oceanographic data that can potentially provide useful insights into cetacean habitats. However, offshore geophysical surveys use air-guns to produce pulses of low frequency sound, and these have the potential to modify the distribution of cetaceans at the time of the survey and therefore cause bias in the results (Castellote *et al.*, 2012). Issues arising from survey design affect the choice of methods used to analyse the resulting sightings data. Line transect surveys should ideally incorporate some form of random probability sampling, in which transect lines are replicated so that each point within the study area has an equal probability of being sampled (Buckland *et al.*, 2001; Thomas *et al.*, 2007). The systematic design of seismic surveys (see Methods below), which progressively extend coverage across the survey area, give rise to spatio-temporal correlation and can violate the principles of random sampling which are fundamental to conventional analytic methods such as DISTANCE sampling (Buckland *et al.*, 2001).

Spatial modelling provides a statistically robust alternative to conventional line transect analyses and is applicable to

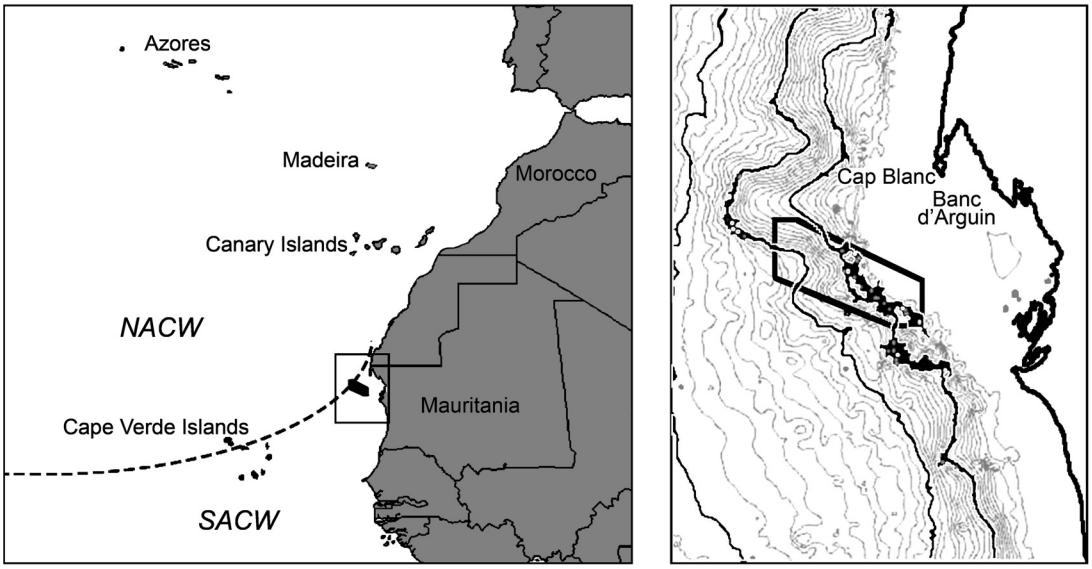

Fig. 1. Map showing the location of the study area off northwest Africa (Fig.1a, left); the dotted line shows the approximate boundary between North Atlantic Central Water (NACW) and South Atlantic Central Water (SACW). The rectangular area off the coast of Mauritania is expanded (Fig.1b, right) to show the location of the polygonal study area in relation to coastal bathymetry. Isobaths are at 100m intervals, with those at 1,000m intervals in bold.

data from platforms of opportunity (Cañadas and Hammond, 2006; Hedley *et al.*, 1999). Model-based abundance estimates have been shown to produce results very similar to those obtained from conventional, design-based line transect data, but with higher precision (Gómez de Segura *et al.*, 2007). There is no requirement to place transect lines randomly, providing coverage is representative of habitats within the region of interest, which is achieved by the comprehensive coverage of a geophysical survey. Spatial models were therefore applied to estimate the abundance and distribution of whales in relation to the undersea topography and oceanography of this highly productive area, and demonstrate that this area supports high densities of baleen whales.

METHODS

Survey design

The survey was designed as a 3D seismic survey, in which closely spaced parallel transect lines were surveyed in a systematic, progressive pattern through the study area (IAGC, 2011), with seismic operations carried out continuously. The survey vessel towed a set of 12 evenly-spaced parallel streamers of 7km in length. The need to maintain the geometry of this configuration required a wide radius when turning. The most efficient survey plan follows a so-called racetrack, in which the survey is conducted in swathes, as illustrated in Fig. 2. However, this survey design results in spatio-temporal correlation as effort moves slowly across the study area. Seismic source activity is confined largely to the straight lines and is turned off through the first part of the turns, with a gradual ramp-up of energy and a so-called soft start being initiated in the final section of each turn, so source activity is spatially correlated. There may also be uneven coverage during daylight hours, depending on the phase relationship between the racetrack and diel cycles; in the survey reported on here, each pair of survey lines took approximately 24 hours to complete, so some contiguous sections of lines were transited at night. The distribution of effort in the turns was also uneven as they were concentrated towards the centre of the swathe at the outer parts of the turns (Fig. 2). Vessel speed averaged approximately four knots, which was slow compared with typical dedicated cetacean surveys, e.g. 10 knots for SCANS surveys (Hammond *et al.*, 2002).

Data collection

Two teams, each of two experienced marine mammal observers (MMOs), took part in the survey changing over approximately at the half-way point. In the first team, Richard Woodcock had 12 years of experience and Peter Tuffy 5 years of experience as MMOs on seismic surveys, and in the second team (the authors) both had 11 years of experience. All four observers had previous experience either as fisheries observers or of cetacean research. Observations were carried out continuously through daylight hours, from a platform with an eye height of 21.5m. Protocols developed by the UK's Joint Nature Conservation Committee (JNCC) specifically for data collection by MMOs on seismic surveys (JNCC, 2010) were followed for data collection and recording. JNCC protocols require a set of environmental variables including sea state, wind force and direction, swell height, glare, visibility and depth to be recorded whenever one of the variables changes, or at least every hour during effort periods. Species identity and group size were recorded for each sighting event, together with an estimate of the bearing and range of the sighting. The closest distances between the animals and the seismic source (whether active or not) and their behaviour during sighting events were also recorded.

Whales were encountered as single individuals, pairs or small coherent groups, or as loose aggregations. When whales were seen in close proximity to one another (the separation criterion was not strictly defined but was approximately <1km), they were considered a single sighting event and the count of whales present in that sighting was estimated by tracking the location and pattern of blows and

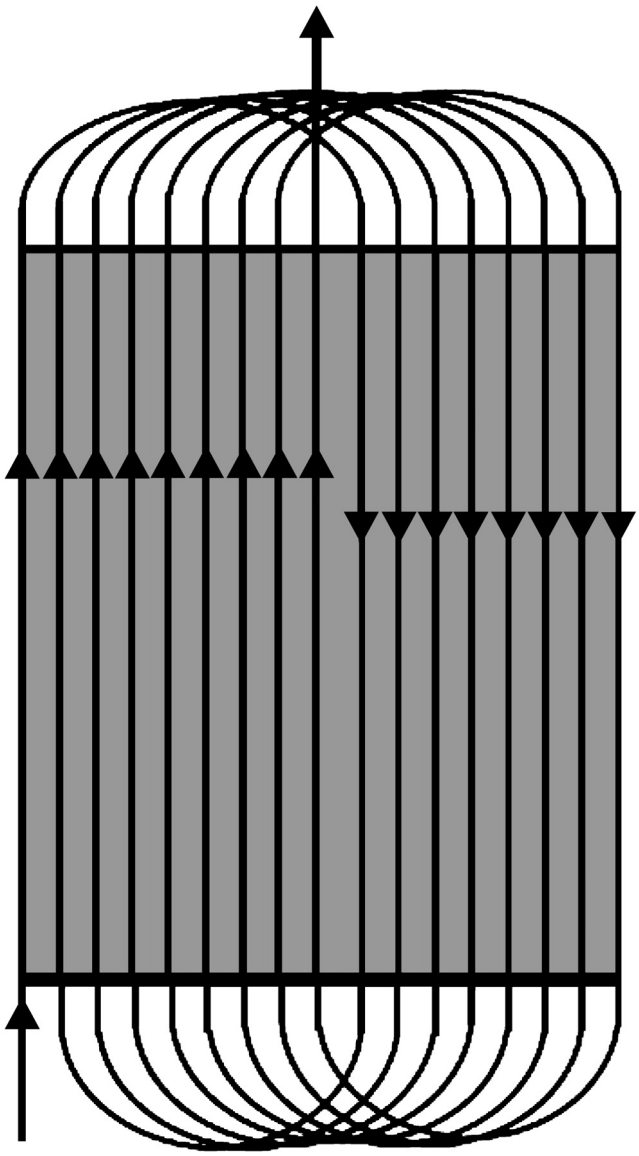

Fig. 2. Diagram showing an idealised racetrack design for a seismic survey. A single swathe is shown, although larger surveys are typically acquired in multiple swathes. Note that as observer effort is maintained through the turns, the area covered by the sighting survey is greater than the geophysical survey area (shaded).

surfacing cues. When higher densities of whales were encountered and it became difficult to track individuals or small groups, counts of all animals in view at one time were recorded as a single sighting.

Without the option to approach a sighting, species identification was often problematic, particularly in the case of balaenopterid whales, when only blows and/or dorsal fins were seen. In order to maximise the data set available for modelling, data for all balaenopterid whales were pooled.

Bathymetry data

A geographical information system (GIS) bathymetry raster layer was developed using the open source software package System for Automated Geoscientific Analyses (SAGA, 2013). Echo-sounder data collected at 25m intervals along survey lines spaced 500m apart were combined with depths recorded by the MMOs during line turns and effort outside the core geophysical survey area. The combined data set was interpolated into a raster grid with cell size of 0.02° latitude and longitude (approximately 2.1 × 2.2km). Inverse distance weighting was used for interpolation because the set of input points was dense enough to capture the extent of variation, and both maximum and minimum values would be retained in a continuous layer, with a smoothed gradation between input points. Approximate positions for sightings were calculated using the range and bearing from the observer's position, depths for sighting positions were then extracted from the bathymetry raster layer and these were used to calculate mean depths for each species or species group.

Analysis of baleen whale data

The initial analysis of the sightings data was carried out using DISTANCE Version 6 (Thomas *et al.*, 2009). Detection probabilities for balaenopterid whales were modelled as smoothed functions of perpendicular distance using both conventional distance sampling (CDS) and multiple covariate distance sampling (MCDS) methods, with sea state, swell height and visibility as potential covariates in the case of MCDS. The Akaike information criterion (AIC) (Akaike, 1973) and coefficient of variation were used to select the best fitting models (Buckland *et al.*, 2001) and to determine which covariates to include. It was assumed that all whales on the trackline were detected, i.e. the probability of detection at 0 distance from the trackline, $g(0) = 1$ (Buckland *et al.*, 2001) and, given the high platform height and slow speed of the vessel, together with the prominent characteristics of whales blows, any change to this assumption was likely to have been minimal. Although the best fitting models were obtained by truncating the data, truncation was not considered desirable in order to maximise the data set available for spatial modelling. Detection functions from half-normal models without truncation were extracted for each of the two observer teams for incorporation in models; a separate detection function was generated for each of the two observer teams in order to account for any potential differences between the two. A table of model selection parameters is provided in the supplementary data file.

Abundance and distribution were estimated using generalised additive models (GAMs) (Hastie and Tibshirani, 1990; Wood, 2006). A single data set was compiled comprising effort and associated sightings. The mean length of each effort record made in the field was 3.7km (SD = 1.3), a length found to perform well in studies using similar methods (Williams *et al.*, 2006). No further partitioning of the data was therefore necessary and the field records were used as the effort segments for input to the modelling process. In the case of effort segments when the vessel was turning, segment length was calculated from the duration of the segment and vessel speed, and not from the straight-line distance between start and end points.

The response variable associated with each effort segment was the count of balaenopterid whales first seen in that segment (Baleen count) rather than the count of groups, in order to account for the different way in which groups were defined in high and low density situations. Modelling counts as the response variable has been found to be highly robust to variation in segment length (Hedley, 2000); unequal segment length was accounted for by including segment length in model offset terms. A set of potential explanatory

variables was generated for each segment, comprising the latitude (*Lat*) and longitude (*Lon*) of the mid-point, sea state (*Sea*), wind speed (*Wind*), swell height (*Swell*) and visibility (*Viz*). The mean depths (*Depth*) for each segment were extracted from the GIS bathymetry layer. The depth range within each cell (*Range*) was calculated by creating raster layers for maximum and minimum depth and subtracting one from the other. Seismic source activity (*SSA*) was converted to a Boolean variable (on or off). Observer or observer team identity was considered as a potential variable, but its incorporation in models was rejected due to spatio-temporal correlation; potential differences between the two teams were addressed by incorporating separate detection functions in the model offset term. Sea state and wind speed are strongly correlated, so only one of these terms was used. Sea state was recorded as one of four categories in the JNCC protocol (glassy, slight, choppy, and rough) and assignment to a category was often a matter of subjective judgement, while wind speed was measured on the ship's instruments, so sea state was dropped in favour of wind speed.

Sea surface temperature (SST) and chlorophyll-*a* concentration (mg/m^3) (CHL) were obtained from the NOAA Ocean Color website (NOAA, 2014) as monthly composite data at a resolution of 4km. Chlorophyll-*a* provides a measure of primary productivity, but as balaenopterid whales feed on zooplankton or small schooling fish, a time lag might be expected between the time of peak primary production and the peak time of prey availability for whales. Chlorophyll-*a* concentrations within the study area were therefore summed for each month in the six month period August 2012 to January 2013 using the formula:

$$CHL_{total} = \sum_{n} \left(\frac{CHL_n \, \mathrm{A}_n}{10^9} \right)$$

Where CHL_{total} is the total estimated weight of chlorophyll-*a* in metric tons, CHL_n is the chlorophyll-*a* concentration in the nth cell and A_n is the area of the cell in m^2. The results were plotted (Fig. 3) to determine the month of peak primary production, and values from that month (September) were extracted as a potential explanatory variable (CHL_{peak}) in addition to the chlorophyll-*a* values for the concurrent month (*CHL*).

Animal density can be expressed as counts per unit area, so counts can be modelled, providing that an offset term representing the area effectively searched is included, and the fitted model may then be used to predict density (Hedley *et al.*, 1999). The offset term representing the estimated area surveyed in each effort segment was calculated as:

$$Offset = \log\left(\frac{2l_i}{f(0)} \right)$$

Where l_i is the length of the segment and $f(0)$ is the estimated probability density function evaluated at zero perpendicular distance. The general structure of the model incorporating the offset term was:

$$\widehat{N}_i = \exp\left[\log\left(\frac{2l_i}{f(0)} \right) + \theta_0 + \sum_k f_k\left(z_{ik}\right) \right]$$

where θ_0 is the intercept, f_k represents smoothed functions of explanatory covariates, and z_{ik} is the kth covariate in i^{th} the effort segment.

Whale sightings tended to be clustered rather than randomly distributed, so a Poisson error distribution was inappropriate due to over-dispersion, and a quasi-likelihood error distribution was assumed, in which variance is proportional to the mean. A GAM was developed using the mgcv package in program R (Wood, 2006), with a 'quasipoisson' family and log link. The model fitting process was guided by minimising the GCV score, maximising the deviance explained, examination of residual plots, and comparison of predicted density with plots of actual sighting positions.

Explanatory variables in a GAM can be multi-dimensional, and models with Lat and Lon as one-dimensional variables were compared with models in which these were combined as a two-dimensional variable [Lat, Lon]. The flexibility of a smooth term in the GAM is determined by the number of knots in the thin-plate regression spline, which for a one-dimensional variable is set by default to 10. If the degrees of freedom of a variable approached nine, the number of knots for that variable were increased. Non-significant terms were dropped unless it increased the GCV score. The argument *gamma = 1.4* was passed to the model as an *ad hoc* method of avoiding overfitting (Wood, 2006).

A data frame was then constructed based on a raster grid with a cell size of 0.02 minutes latitude and longitude, and the mgcv *predict.gam* function applied to estimate the predicted count of whales per cell. The values for each cell were summed to obtain an overall abundance estimate and the values plotted as a GIS raster layer of predicted whale density.

Variance was estimated using a jackknife method, which has been shown to perform well with spatially modelled estimates (Hedley, 2000). Survey day was used as the resampling unit. The data from three randomly selected days were removed and an abundance estimate generated from the GAM. This was repeated using a function written in *R* to produce a set of 300 estimates. The distribution of abundance estimates cannot include negative values and is positively skewed, so a log-normal distribution was assumed for the calculation of 95% confidence intervals using a modified version of the Cox method (Zhou and Gao, 1997).

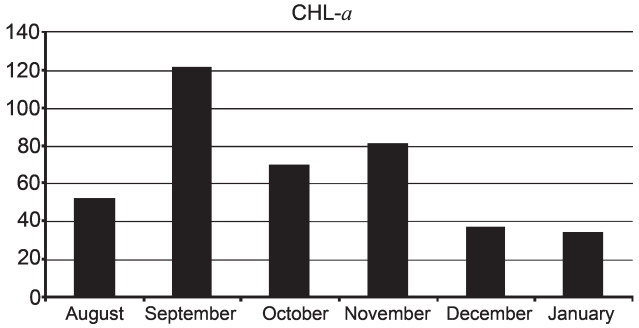

Fig. 3. Estimated monthly quantities (metric tons) of chlorophyll-*a* in the study area from August 2012 to January 2013.

RESULTS

Bathymetry

The bathymetry of the study area is illustrated in Fig. 4 as a three-dimensional image, as an aid to the interpretation of

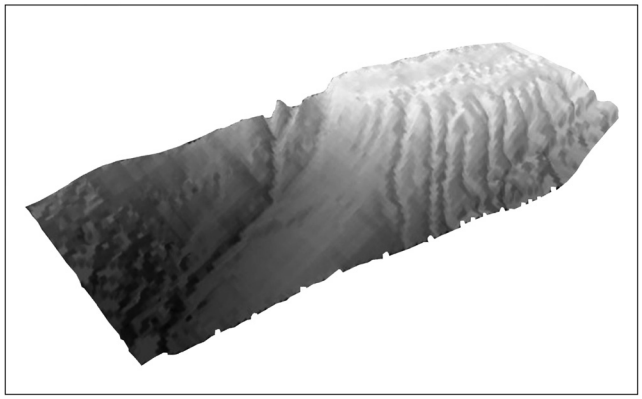

Fig. 4. Bathymetry of the study area displayed as a 3D shaded relief plot with a view-point from the southwest. A series of deeply incised channels run down the southwest face of the continental shelf and a canyon extends from approximately the mid-point of the north side to the southwest corner of the study area.

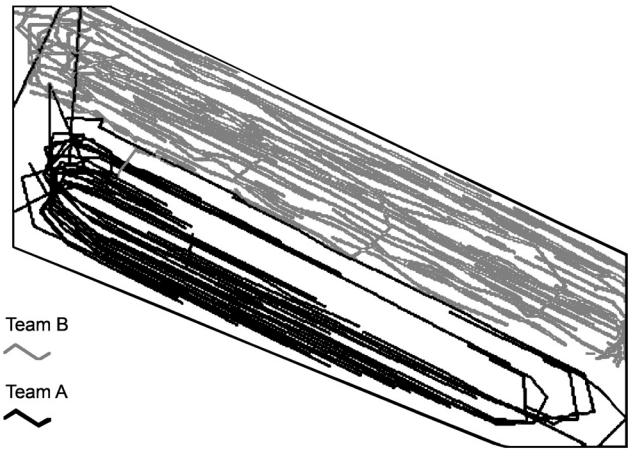

Fig. 5. Plot showing the distribution of realised effort lines within the study area. The gaps in coverage represent areas surveyed at night when no observations could be carried out. Note that effort during turns between transect lines are represented by straight lines connecting points at which an effort record was made, whereas in fact the vessel track followed smooth curves. Effort by the two teams is depicted in different line weights.

the two-dimensional plots. Sea bed topography was both varied and complex. The continental shelf extended into the northeast of the study area as a level plain with a depth of less than 100m. Along its southern and southwestern face, the shelf edge was dissected by a series of incised, dendritic channels. A canyon feature ran down the northwest face of the shelf edge, then turned westwards extending across to the south-western border of the study area at a depth of a little over 2,000m. In its upper reaches, the canyon was divided into three main tributary canyons, separated by ridges and terraces.

Upwellings and primary productivity

The extent of the northwest African upwelling system through an annual cycle from June 2012 to May 2013 is illustrated in a set of plots of monthly composite SST values provided in the supplementary data file. The upwellings appeared throughout the year as regions of cooler water extending from Mauritania through Western Sahara to the middle latitudes of Morocco. The area of upwelling reached its greatest extent in northern Mauritania and southern Western Sahara between December 2012 and February 2013, coinciding with the period of the survey. The supplementary file also includes higher resolution plots of SST values in the near vicinity of the study area for the three months of the survey, and chlorophyll-*a* concentrations for the six months (August 2012 to January 2013).

Survey effort

In some 680 hours of observation between 15 November 2012 and 14 January 2013, a total of 2,838km of effort was recorded, which is equivalent to an overall mean of 0.52km of transect effort for each km^2 of the study area. Note however, that observer effort was not evenly distributed through the study area (Fig. 5), in part because some sets of adjacent transect lines were surveyed at night. The division of the survey into two swathes is also apparent in this figure, with the change in observer teams coinciding with the swathe change.

Viewing conditions varied predominantly due to the prevailing northeasterly winds. Wind speeds were Beaufort force 4 or less for 56% of the total effort time and swells were classed as moderate (2–4m) for 61% of the time. There was no fog or precipitation, but wind-blown sand reduced visibility to moderate (1–5km) or poor (<1km) for 12% of effort time.

Sightings

A total of 236 cetacean sighting events were recorded and 15 species identified (see supplementary data file for a summary of all sightings). Large whales accounted for 70% of sightings, although short-beaked common dolphins (*Delphinus delphis*) were more abundant, being encountered in groups of up to an estimated 500 individuals. Sightings of balaenopterid whales are summarised in Table 1.

The identification to species level of whales of the genus Balaenoptera was frequently impossible, so a conservative approach was taken for species identification. When blows were the only feature seen and they could be distinguished from the blows of sperm whales (*Physeter macrocephalus*), sightings were recorded as unidentified baleen whales. When dorsal fins and the backs of surfacing whales could be seen, it was frequently only possible to assign sightings to a two-species category, Bryde's whale (*Balaenoptera edeni*) or sei whale (*B. borealis*). On seven occasions, all at dawn or dusk, medium-sized balaenopterids were observed and photographed skim-feeding, with their rostra held raised above the surface of the sea for extended periods; their smooth rostra which lacked lateral ridges and had distinctive down-curved tips, positively identified these animals as sei whales. The largest single aggregation of skim feeding sei whales encountered was a count of 18 at dusk on 4 January 2013, when whales appeared to converge on the survey vessel from both sides as darkness fell. Some of these animals came to within a few metres of the ship, despite the fact that the seismic source was active. On no occasion was the potentially sympatric Bryde's whale specifically identified. A z-test found no significant difference between the mean depths at which positively identified sei whales (1,233m), sei/Bryde's whales (1,373m, $p = 0.62$), and unidentified baleen whales (1,255m, $p = 0.94$) were recorded.

Table 1
Summary of balaenopterid sightings.

Species	Sightings (*n*)	Group size			Depth (m)		
		Mean	Min	Max	Mean	Min	Max
Blue whale	8	1.25	1	2	772	45	1,556
Fin whale	1	2	2	2	856	856	856
Sei whale	7	5.3	1	18	1,233	43	2,123
Sei/Bryde's whale	51	2.3	1	25	1,373	43	2,220
Unidentified balaenopterid	75	2.4	1	25	1,260	47	2,245

Blue whales (*B. musculus*) were identified on eight occasions, with a total count of ten animals. At least two of the unidentified baleen whale sightings had blow characteristics suggesting the likelihood that they were also of this species, but only those sightings in which the characteristic small dorsal fin and body colour could be distinguished were recorded as blue whales. Fin whales (*B. physalus*) were identified on one occasion, when two individuals were seen together.

The question of whether sightings of whales were affected by source activity was initially addressed by comparing sighting rates when the source was and was not active. There were 32 sightings of balaenopterids during 204 hours of observation while the source was inactive (0.16/hour), and 106 sightings in 436 hours when the source was active (0.24/hour). A chi^2 test with Yates' correction indicated that the higher sighting rate while the source was active was statistically significant ($chi^2 = 18.35$, $df = 1$, $P < 0.01$). However, this result reflects the spatial bias in source activity, as the region in which most balaenopterid sightings were made coincided with the area over which the source was always active. A second approach was therefore taken, by comparing the closest distance that animals came to the seismic source, with the null hypothesis being that if their distribution was not changed by an avoidance reaction when the source was active, there would be no significant difference in the closest range to an active or inactive source. In fact, the mean approach distance was closer when the source was active (1,931m) compared to when it was inactive (2,233m), although a t-test indicated that this difference was not significant ($t = 1.02$, $P = 0.31$).

Model predictions

The best fitting GAM, in which the deviance explained was 43%, took the form:

$$Baleen_count \sim offset(Offset) + s(Lat, Lon) + s(Depth) + s(CHL_{peak}) + Month + Wind + Viz$$

In which Lat and Lon were combined as a two-dimensional variable, and Month, Wind and Viz were included as linear terms. The most significant environmental predictors of whale density were Lat, Lon ($p < 0.01$), CHL_{peak} ($p < 0.01$) and Depth ($p = 0.02$).

Balaenopterid sightings were made throughout the study area (Fig. 6), but the largest aggregations were to the north of the canyon, and 93% of sightings were encountered at depths of between 500 and 2,250m. The density of baleen whales predicted by the GAM in the study area as a whole was 4.97 whales/100km^2 (95% CI 4.84–5.09), but the density in the depth band 500–2,250m was 6.18 whales/100km^2 (95% CI 6.03–6.51). The point estimate of balaenopterid abundance in the study area was 272 individuals (95% CI 265–279). The plot of predicted density for January 2013 (Fig. 7) shows the main concentration of whales located close to the north side of the main canyon's upper reaches and extending from there to the northwest.

Observations of dead whales

During the course of the survey, dead whales were observed floating on the surface on two occasions. These were both of mysticete whales, one of which could not be identified, the other being a medium-sized balaenopterid, probably a sei/Bryde's whale. The latter had suffered massive traumatic injuries consistent with the possibility of ship strike, although it could not be ascertained whether these had been inflicted pre or post mortem. Both whales were observed in deeper water in the vicinity of the main north–south shipping lane.

DISCUSSION

Factors affecting the reliability of estimates

The high density of effort in this survey resulted in a relatively high degree of precision in the model-based abundance estimate. However, the systematic design and slow progress of the survey resulted in spatial and temporal correlation of effort. The survey was divided into two swathes, with the swathe change coinciding with crew change. Count rates of whales were 3.6 times higher in the second, more northerly swathe ($n = 284$, rate = 0.18 whales/km) compared with the earlier surveyed southern section ($n = 65$, rate = 0.05 whales/km). Because there was no overlap in space or time, it was not possible to determine whether this difference in sighting rates was due to there being more suitable habitat in the area covered by the second swathe, or an influx of animals part way through the survey, or perhaps both these factors. There may also have been differences in observer efficiency between the two teams, although separate detection functions for the two teams were applied in an effort to account for this.

It is possible that some whales reacted to the survey by moving away before being visually detected. It should therefore be borne in mind that the estimates presented here represent the abundance and distribution of whales during the operation of a seismic survey, which may conceivably differ from results that might have been obtained had there not been such a survey in progress at the time. Behavioural responses, such as changes in direction, were observed on some occasions when animals came close (<1km) to the

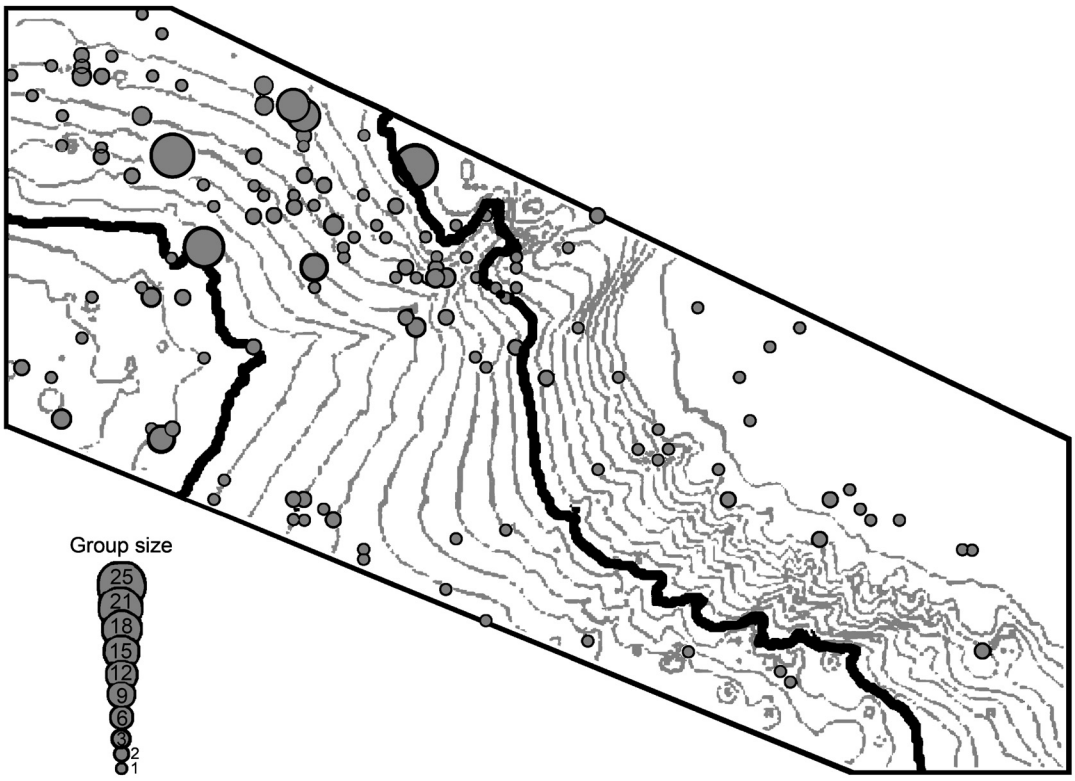

Fig. 6. Balaenopterid sighting positions. Isobaths are at 100m intervals, with those at 1,000m intervals in bold.

active source, but no evidence of avoidance reactions by whales was found within the data.

Potential errors in the estimation of group size were not addressed and this may have led to errors in density estimates that were not taken into account. Counts of small groups were probably less prone to error than counts when larger numbers of whales were in view at one time, although there were occasions when two animals swam together in such close proximity that the presence of a second animal was only discovered when photographs were later examined. There was greater scope for error when high densities of whales were encountered and it became difficult to track individual animals. However, a conservative approach to group size estimation was adopted, so any errors are likely to have resulted in an underestimate of abundance.

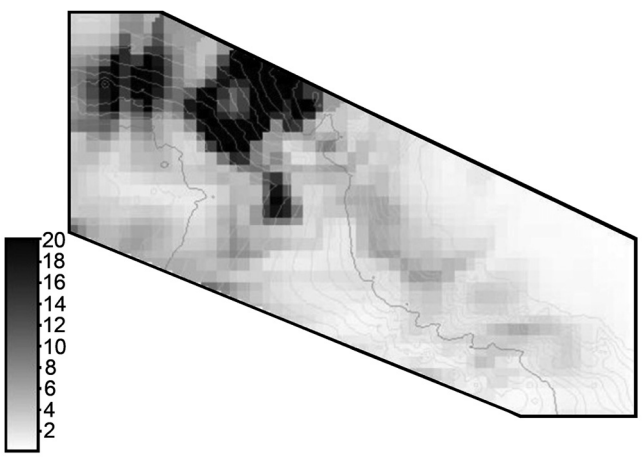

Fig. 7. Plot of the predicted density of balaenopterid whales (count/100km^2) for January 2013.

There was typically only one observer on watch at any one time during the survey, with a maximum of two for short periods of time, and this may have resulted in reduced observer efficiency. Each of the factors discussed above and the assumption that g(0) = 1, had the potential to bias abundance estimates downwards, so the results given here are probably conservative and should be regarded as minimum values.

Oceanographic characteristics of the study area

The Mauritanian upwellings occur where the southward flow of North Atlantic Central Water meets the northward flowing, less saline and nutrient-rich South Atlantic Central Water, over which strong northeasterly winds drive warmer surface waters (Peña-Izquierdo *et al.*, 2012). The upwellings off Cap Blanc are persistent throughout the year, but are strongest from November to February (Mittelstaedt, 1991) and show considerable inter-annual variability (Demarcq, 1998). In the period 1987–2006, the upwelling system off northwest Africa has intensified, and upwelled waters off Cap Blanc have increased their offshore spreading (Marcello *et al.*, 2011). The mixing of nutrient-rich cold water with the warmer surface water in the presence of strong sunlight creates optimal conditions for the primary production of phytoplankton and thence the secondary production of zooplankton. The cetacean data presented here were collected during the main upwelling season between November and January, which coincides with the time of year when northeast Atlantic populations of those balaenopterid species that feed predominantly on zooplankton, i.e. blue and sei whales, are thought to have migrated southwards. This is the whales' breeding season when they have been presumed to feed little, but their high density in this very productive area, and direct observation

of feeding in the case of sei whales, suggests that they aggregate here in order to take advantage of a locally abundant food supply.

Submarine canyons worldwide have been shown to create attractive habitats for a range of cetacean species, in the case of baleen whales this is thought to be by a process of enrichment and concentration of prey (Moors-Murphy, 2014). The canyon feature running through the study area and the series of channels incised into the shelf edge appear to form part of the recently discovered Cap Timiris Canyon system (Krastel *et al.*, 2006). The canyon is thought to have been created originally by a major terrestrial river system during an era when glaciation had reduced sea levels (Antobreh and Krastel, 2006). The region is now extremely arid and there are no significant fluvial inputs from the Sahara Desert. Although sediment transport from rivers has now ceased, the predominantly northeasterly Harmattan winds carry large quantities of aeolian sand that precipitates into the sea. This was a prominent feature during the survey, as fine sand was continuously deposited on the open decks of the ship. The appearance of the canyon, which has a V-shaped cross-section and a sparse pattern of sedimentation, indicates that it remains active; this activity is thought to be caused by the erosive action of ocean currents carrying sediments through the canyon in the reverse direction to the original fluvial currents (Antobreh and Krastel, 2006; Krastel *et al.*, 2006). The complex bathymetry formed by the various canyon features of the Cap Timiris system creates a diversity of habitats and shapes local patterns of current flow and upwellings, contributing to the creation of hot-spots of primary productivity and biodiversity.

Sei whale

The winter distribution of sei whales in the northeast Atlantic is poorly understood. Few sightings have been reported from northwest Africa and there are no historic estimates of abundance that can be compared with those reported here. Until now, the best indication of the winter distribution of sei whales has come from records kept by whalers, although these data are bedevilled by confusion between sei and Bryde's whales (Horwood, 1987; Prieto *et al.*, 2012a). In the period 1976–79, the unregulated whaling boat *Sierra*, together with associated vessels, tended to hunt in the region 18–22°N, 20–25°W from November to May, targeting balaenopterids, including sei whales (Best, 1992).

Relatively high levels of survey effort have been carried out in the Canary Islands, but sei whales have only occasionally been reported, with small numbers seen between autumn and early spring, which is during their migration (Carrillo *et al.*, 2010). A survey conducted by the International Fund for Animal Welfare (IFAW) in April 2005 between the latitudes of 20°N and 37°N, found only one sei whale in off-shelf waters (Boisseau *et al.*, 2010), while a survey of coastal waters of southern Morocco in 1996 failed to find any live whales, although a newborn Bryde's whale was found stranded (Notarbartolo di Sciara *et al.*, 1998). A sighting of a single whale during a seabird and cetacean survey off Mauritania for an environmental impact assessment of the Chinguetti oilfield in March 2003 was recorded as a sei whale (Anon, 2003), although no details were given to positively distinguish the sighting from the sympatric Bryde's whale. In April 2001, at least two sei whales were sighted off Mauritania by a touristic expedition vessel, the species identification was confirmed by Prieto *et al.* (2012a). While balaenopterid whales have been recorded during seabird surveys off Mauritania (Camphuysen, 2000; Camphuysen *et al.*, 2012) sei whales have not been specifically identified. Sightings of sei whales further south in the Gulf of Guinea appear to be extremely rare (Weir, 2010).

A total of 33 sei whales were identified in seven sighting events during the survey reported on here. Based on their observed behaviour and blow characteristics, together with the localisation of sightings within a similar depth range, the opinion of the observers was that a high proportion of the medium sized rorquals encountered during this survey and not identified to species level, were probably also sei whales.

The paucity of sei whale sightings previously reported from the wider region highlights the significance of the results presented here for the identification of important areas for this species in winter. The main concentration of whales was found immediately north of the canyon feature, off the outer edge of the continental slope in waters of 500–2,250m depth. Similar habitats in terms of circulation patterns, upwellings and canyon features occur along the entire outer shelf edge of Mauritania (Krastel *et al.*, 2006; Peña-Izquierdo *et al.*, 2012), an area that has recently been found to be of prime importance for both resident and wintering seabirds (Camphuysen and van der Meer, 2005; Wynn and Knefelkamp, 2004; Wynn and Krastel, 2012). It is therefore possible that an area of importance for sei whales in winter may extend throughout the entire outer shelf region of Mauritania, and may perhaps include much of offshore Western Sahara into which the upwelling system extends.

Sei whales that summer in the northeast Atlantic off Scotland, Norway and Iceland are thought to move south to winter somewhere to the south of the Iberian peninsula or off northwest Africa. However, recent studies using satellite tags (Prieto *et al.*, 2012b) have shown that sei whales seen on migration off the Azores in spring, move to summer feeding grounds in the Labrador Sea, while a single animal tagged in autumn moved southeast from the Azores and was last recorded between Madeira and the Canary Islands. This raises the possibility that sei whales wintering off Mauritania may belong to either or both northwest and northeast Atlantic 'stocks'.

North Atlantic sei whales appear to be stenophagous, feeding exclusively on copepods and euphausiids, typically by skim-feeding at the surface (Brodie and Vikingsson, 2009; Prieto *et al.*, 2012a). The concentration of sei whales in such a productive area, together with direct observations of skim-feeding behaviour, provides evidence of feeding during the winter breeding season, when feeding was thought to be uncommon. The sensory systems used by balaenopterids to detect their prey are not well understood. There is no evidence to suggest they detect prey acoustically, in the manner of echo-locating odontocetes. Indeed, sei whale vocalisations show a diel pattern, with increased rates of vocalisation during the day, perhaps in a social context, and reduced rates during the night when they mainly feed (Baumgartner and Fratantoni, 2008). Right whales may use sensory hairs to detect zooplankton density (Kenney *et al.*,

2001), but it appears most likely that sei whales use available light to visually locate high-density patches of zooplankton. This could explain the circumstances of the sighting made at dusk on 4 January 2013 when an estimated 18 skim-feeding sei whales appeared to be attracted to the survey vessel, approaching to within a few metres of the ship from either side. The vessel was well lit at night, with floodlights illuminating the working areas on the back deck and spotlights directed at the towed equipment. It seems likely that either their prey was attracted by the vessel's lights, or the whales were attracted by the lights which assisted their location of zooplankton swarms, or both.

Bryde's whale

The taxonomy of Bryde's whales remains unresolved and there may be more than one species in the African Atlantic; in southern Africa a smaller inshore type found in neritic habitats has been distinguished from the 'ordinary' type found further offshore (Best, 1977; Best, 2001). Little is known about the Bryde's whales of the northeast Atlantic, and we assume that any occurring within the present study area belong to the offshore type, *Balaenoptera edeni*.

In contrast to the stenophagous behaviour of sei whales, Bryde's whales tend to be more catholic, targeting a range of prey species including small schooling fish, squid and euphasiids (Pauly *et al.*, 1998; Tershy *et al.*, 1993). Analysis of stomach contents recorded by whaling vessels off southern Africa showed a seasonal variation in prey type, with 'shrimps', presumed to be *euphausiids*, being unimportant in the (austral) autumn and winter, becoming increasingly important in spring and predominating in summer (Best, 2001). However, this may simply reflect seasonal changes in prey availability rather than any seasonal change in dietary preference.

A marked seasonal change in the distribution of the southern African offshore Bryde's whales has been reported on the basis of whaling records and a single marked individual, the whales moving north towards equatorial waters in winter, when they were absent from the southwest African whaling grounds (Best, 2001). A similar movement towards equatorial waters in winter has been reported for northwest Pacific Bryde's whales (Kishiro, 1996). By analogy, it might be expected that equivalent movements take place in the northeast Atlantic, in which case they would likely be absent from the more northern parts of their range in winter, when this survey was carried out. However, the distribution and seasonal movements of this species in the northeast Atlantic remain unclear. Whaling records cite catches of Bryde's whales off southern Spain in the 20th century (Sanpera and Aguilar, 1992), but the species identification was probably unreliable due to confusion between Bryde's and sei whales. A juvenile Bryde's whale was found stranded near Dakar, Senegal, in late March 1955 and sightings have been reported recently from the Azores in summer (Silva *et al.*, 2014; Steiner *et al.*, 2007). Mauritania therefore lies within the range of this species, but the seasonality of their occurrence here remains obscure.

The identification of Bryde's whales at sea depends on seeing the diagnostic lateral ridges on the rostrum, and this is problematic without a close approach in good viewing conditions (Gendron and Rosales, 1996). So although this species was not positively identified during the survey, its presence among those sightings recorded as Bryde's/Sei whales cannot be discounted.

Blue whale

Blue whales are stenophagous, feeding almost entirely on euphausiids, and populations that summer in higher latitudes are thought to migrate to lower latitudes in winter when their prey becomes unavailable (Clapham *et al.*, 1999). However, the population structure of blue whales is complex and it is possible that not all animals make seasonal migrations. There is evidence of year-round occurrence in some tropical waters, e.g. in the eastern tropical Pacific (Reilly and Thayer, 1990), and of some whales remaining at higher latitudes at least in the early part of winter (Charif and Clark, 2009). Migratory behaviour may also vary with sex and age class. Knowledge of blue whale ecology and status remains limited and the winter distribution of blue whales in the North Atlantic is poorly understood (Clapham *et al.*, 1999; Reeves *et al.*, 2004; Reilly *et al.*, 2008). Surveys at different times of year would be needed to establish the seasonality of blue whale presence in Mauritania, but from the geographic location alone, it would appear possible that these whales belong to the same population that migrates west of the British Isles and inhabits Icelandic and Norwegian waters in summer. Further evidence in support of this link comes from photo-identification studies: a blue whale encountered off Mauritania in March 2005 was matched with photographs of the same individual taken off Iceland in July of both 1997 and 1999 (Sears *et al.*, 2005).

Blue whales are the largest animal ever to have existed and their energetic demands and therefore prey requirements are correspondingly large (Rice, 1978). The conventional view that blue whales feed primarily in their high latitude summer habitats and that they fast in their low latitude calving areas has been modified in the light of subsequent studies (Reilly and Thayer, 1990). Blue whales have been found feeding in highly productive, lower latitude upwelling zones during the winter in several regions of the Pacific, e.g. in Chile (Hucke-Gaete *et al.*, 2004), Monterey Bay, California (Fiedler *et al.*, 1998), Australia (Gill, 2002) and New Zealand (Torres, 2013). In Monterey Bay, the distribution of blue whales has been found to be closely associated with the edges of a submarine canyon in an area of upwelling (Croll *et al.*, 2005; Schoenherr, 1991), a habitat with similar oceanographic characteristics to our study area in Mauritania. Euphausiids and copepods undertake a diel vertical migration to avoid visual predation by day (Lampert, 1993), feeding at night on phytoplankton in the upper water column. Optimal habitats for these zooplankton species are therefore found in upwelling zones with high primary productivity, over deep bathymetry that facilitates predator avoidance. Croll *et al.* (2005) suggest that topographic breaks created by the Monterey Submarine Canyon edge form just such optimal habitats for euphausiids by providing water depths of 1,000m or more, close to highly productive, recently upwelled, near-shore waters. A similar situation occurs in Mauritania, where canyon features close to the shelf edge are associated with a highly productive upwelling zone, and these topographic features may form an important contributory factor in creating optimal habitats for zooplankton, that in turn attract both blue and sei whales.

CONCLUSIONS

This study highlights the potential value of data collected by trained and experienced observers on seismic survey vessels in furthering our understanding of cetacean ecology in remote and under-explored regions. The importance of Mauritania's offshore habitats for wintering seabirds has become recognised in recent years; the findings presented here suggest the area is also important for balaenopterid whales, particularly sei and blue whales. The winter distribution of both sei and blue whales in the northeast Atlantic has so far been shrouded in mystery, and both species are classified as endangered in the IUCN Red List of Threatened Species (Reilly *et al.*, 2008). Relatively high densities of whales were recorded in the outer margins of the continental shelf edge, but the extent of this high density area and the regularity and seasonality of its use needs to be established by further research in order to inform management of potential impacts, particularly in the light of the nascent offshore hydrocarbon industry in the region.

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A characterisation of common bottlenose dolphin (*Tursiops truncatus*) interactions with the commercial shrimp trawl fishery of South Carolina, USA

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ABSTRACT

In the United States, interactions between the shrimp trawl fishery and bottlenose dolphins are known to exist; however, the level of mortality is largely unknown, and has not been studied in South Carolina, USA. The current study attempted to determine if interactions between bottlenose dolphins and the South Carolina commercial shrimp trawl fishery pose a significant threat to dolphin populations and if fishery related mortality is underreported. Onboard observations were made during a 25 day (August–December 2010) field study. No dolphin takes occurred during the observational period. These observations focused on direct physical interactions with the gear and depredation behaviours. Additionally, a sub-sample of the shrimp fishery in South Carolina was asked to participate in a mailed survey. The survey included questions related to gear, dolphin observations, and the status of the shrimp fishery. This paper also examines historical dolphin stranding data from the NOAA/CCEHBR MMIS database for signs of shrimp fishery interactions. A three-tiered flow diagram was developed to characterise each stranding case according to the likelihood that mortality resulted from trawler interaction. Field results point to significant dolphin presence around commercial trawlers ($x^2 = 23.406$, $p < 0.001$). Survey results showed 12 unreported incidents of shrimp trawl fishery mortality of dolphins. Finally, stranding records revealed several more cases with signs of possible trawler interaction. The current US National Marine Fisheries Service (NOAA) designation of the fishery as a Category II fishery is correct. Increased observer coverage and improved communication with the fishery on the importance of reporting takes is warranted.

KEYWORDS: COMMON BOTTLENOSE DOLPHIN; FISHERIES; INCIDENTAL CATCHES; TRAWLS; STRANDINGS; CONSERVATION; MANAGEMENT PROCEDURE

INTRODUCTION

Although not previously studied in South Carolina, interactions between bottlenose dolphins (*Tursiops truncatus*) and trawl fisheries are well documented in other parts of the United States and around the world (Fertl and Leatherwood, 1997; Zollett, 2005). Previous research has focused on social structure (e.g. Chilvers and Corkeron, 2001; Fleming, 2004; Scheinin, 2010), feeding behaviours (e.g. Broadhurst, 1998; Corkeron *et al.*, 1990; Gonzalvo *et al.*, 2008; Svane, 2005), and mortality from bycatch (e.g. Dans *et al.*, 2003; Fortuna *et al.*, 2010; Zeeberg *et al.*, 2006). The current study investigated all of these topics to characterise the interaction between trawl fisheries and bottlenose dolphins in South Carolina.

Previous stranding record studies have shown that the crab pot fishery is the most common source of fishery related mortality of dolphins in South Carolina (Burdett *et al.*, 2007; Burdett and McFee, 2004; McFee and Hopkins-Murphy, 2002; McFee and Lipscomb, 2009; Sturgeon, 2010). Burdett and McFee (2004) noted that many dolphins stranded dead without gear attached to the body but still exhibited line wounds. Some of these animals, however, presented wounds that were larger in diameter than crab pot line wounds, raising the suspicion that they were caused by some other source, potentially the shrimp trawl fishery. In addition to direct signs of fishery interaction (e.g. rope or net marks and gear attachment), stranding records can reveal other signs of fishery related mortality. For instance, dolphins that die as a result of entanglement often appear to be robust and otherwise healthy at their time of death, but necropsies can reveal sub-dermal haemorrhaging, froth in the lungs and bronchi, and undigested fish and shrimp in the stomach. Dolphins that die from chronic illness or disease often have difficulty feeding and as a result usually have relatively empty stomachs (Pate and McFee, 2012).

The US shrimp harvest in 2010 exceeded 250 million pounds (about 114,000 tonnes) and yielded over 400 million US dollars in revenue (NMFS, 2011). Although the South Carolina shrimp harvest contributes only a small portion (approximately 0.8% or 2 million pounds per year) of the total US domestic shrimp production, it is the largest and most economically valuable commercial fishery in South Carolina. It averages just over 400 trawl licenses per year, about two-thirds of which are held by residents of South Carolina (Julia Byrd, SCDNR, pers. comm.; SCDNR, 2007). The exact opening and closing dates for this fishery are decided annually by the South Carolina Department of Natural Resources (SCDNR), but the season generally runs from May/June to December/early January. Trawling is restricted to daylight hours and to oceanic and lower sound and bay areas. Most trawling occurs at depths of 5–15m (SCDNR, 2007), but may vary depending on the bottom structure and where shrimp are being found.

Although they range in size and shape, the basic bottom-trawl shrimping set up used in South Carolina involves 1–4 nets towed along the seafloor (Fig. 1). The mouth of each net is stretched apart by two ‘doors’, one attached to either side of the net. In four-net configurations, each side (port and

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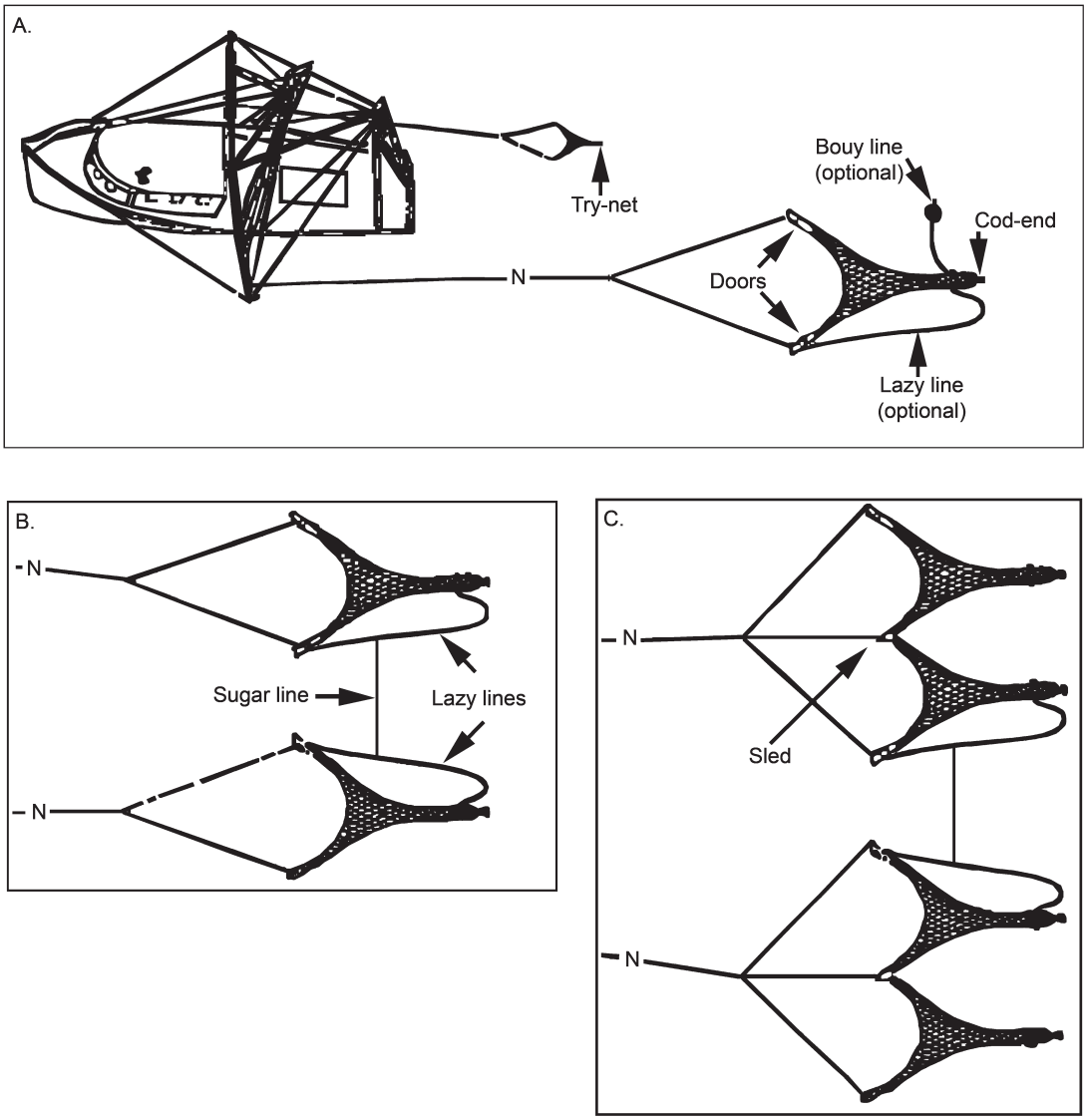

Fig. 1. Three common trawl net configurations. A: Single Net; B: Two-Net; C: Four Net. Modified from: US Bureau of Commercial Fisheries (Kristjonsson, 1967). [Available at: *www.fao.org/docrep/005/ac740t/AC740T05.htm*].

starboard) has two nets. Each pair of nets is connected by a steel 'sled' which is attached between the two nets. A float-line on the top of the net's mouth keeps the net from collapsing vertically. A weighted bottom line keeps the net close to the bottom, while a tickler chain acts to disturb the sediment and force organisms into the net and ultimately to the posterior, or 'cod-end', of the net. Some vessels attach additional mesh and/or chafing gear around the posterior end of the net to protect the cod-end from wear. Attached to most nets is a 'lazy' line which is connected to the door lines and aids in pulling in the nets. When a vessel has more than one lazy line, it may use a 'sugar' line to connect the two lazy lines, allowing both lines to be retrieved at once. Some smaller vessels may also attach an optional buoy line to the net to aid in retrieval. In addition, some trawlers drag a small 'try-net' during the normal tow and retrieve it frequently to assess the shrimp catch.

Each year, in accordance with the US Marine Mammal Protection Act (MMPA) of 1972, the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NMFS) produces its annual List of Fisheries (LOF), which classifies the level of incidental serious injury and mortality of marine mammals occurring in each of the nation's fisheries (NOAA, 2011). Classifications are determined using the Potential Biological Removal (PBR) approach, which is used to estimate the number of individuals that may be removed (i.e. serious injury or mortality) from a stock without adversely affecting the optimum sustainable 'population' (OSP) (NOAA, 2011). The concept of OSP is such that it represents a population size that maximises reproductive potential while staying within the constraints of an area's carrying capacity (NOAA, 2011). NOAA currently uses three classes to describe US fisheries based on the percent of PBR a fishery is responsible for taking. Fisheries that are responsible for taking a significant percentage (i.e. >1% of PBR per year over a consecutive five year period) are classified as either Category I (≥50% of PBR) or Category II (between 1% and 50% of PBR). Due to the relatively high incidence of marine mammal mortality, fisheries in these two categories are subject to several regulations meant to monitor and mitigate the likelihood of fishery interactions. In addition, these fisheries are required to accommodate a marine mammal observer onboard their vessel, if NMFS requests one.

Category I and II fisheries are also required to follow any applicable take reduction plans developed by NMFS.

If a fishery is responsible for removing less than 1% of PBR per year over a given five year period, it is classified as a Category III fishery. These fisheries are estimated not to pose a major threat to marine mammal populations and are therefore subject to little regulation. Up until 2010, the Southeastern US Atlantic and Gulf of Mexico shrimp trawl fishery, of which the South Carolina fishery is a member, was classified as a Category III fishery. The 2011 LOF however, reclassified the fishery as a Category II fishery, in part due to two reported shrimp trawl fishery entanglement cases from South Carolina, one that was entangled in a buoy-line attached to the cod end of a net in 2002 and one that was brought up dead in a trawl net in 1998 (NOAA, 2010). In addition, from 2006–2012, the SCDNR research vessel '*Lady Lisa*' caught three dolphins (two in SC, one in North Carolina) in their net during scientific trawling operations.

In South Carolina, coastal dolphins are managed as the South Carolina/Georgia Coastal Stock (SCGCS), (Waring *et al.,* 2012). This stock inhabits the same waters commonly used by shrimp trawlers; therefore it is believed that this stock is the most impacted by the shrimp trawl fishery. The current minimum population estimate for the SCGCS is about 6,300 individuals and it has a PBR of 64 (Waring *et al.*, 2012). Thus, 1% PBR would be 0.64 dolphins and 50% PBR would be 32 dolphins. Therefore, in order to be classified as Category II, the shrimp fishery would have been expected to take a total of between 3.2 and 160 dolphins over a given five year period. South Carolina also experiences seasonal influxes of coastal dolphins from the Southern Migratory Coastal Stock (SMCS) during the spring and fall months. While travelling to and from their coastal fishing grounds, trawlers are also likely to encounter the Charleston Estuarine System Stock (CESS) and the Northern Georgia/Southern South Carolina Estuarine System Stock (NGSSCES).

The overall objective of this study was to characterise and quantify physical gear interactions between dolphins and trawl gear and to determine the impacts of these interactions on bottlenose dolphins in South Carolina. This study sought to: (1) determine if gear configuration and fishing method have a significant effect on dolphin presence, abundance, and behaviour around shrimping vessels; and (2) investigate if commercial shrimp trawl takes in South Carolina are underreported and if mortality has exceeded 1% of PBR per year for any given five-year period.

METHODS

Onboard observations

Onboard observations were conducted aboard four South Carolina commercial shrimp trawl vessels. One based out of Beaufort, one from McClellanville, and two vessels from Charleston, one that primarily trawled north of Charleston Harbor and one that trawled south of the harbor (Fig. 2). Observations were conducted over 25 days from August to December 2010; 16 days were out of Charleston, six out of McClellanville, and three from Beaufort.

Dolphin observations were recorded during each gear-deployment and gear-retrieval as well as every 10 minutes during the tow. Using the 'one-zero' sampling method, the presence or absence of dolphins, mother/calf pairs (M/C), direct physical gear interaction behaviours (Fertl and

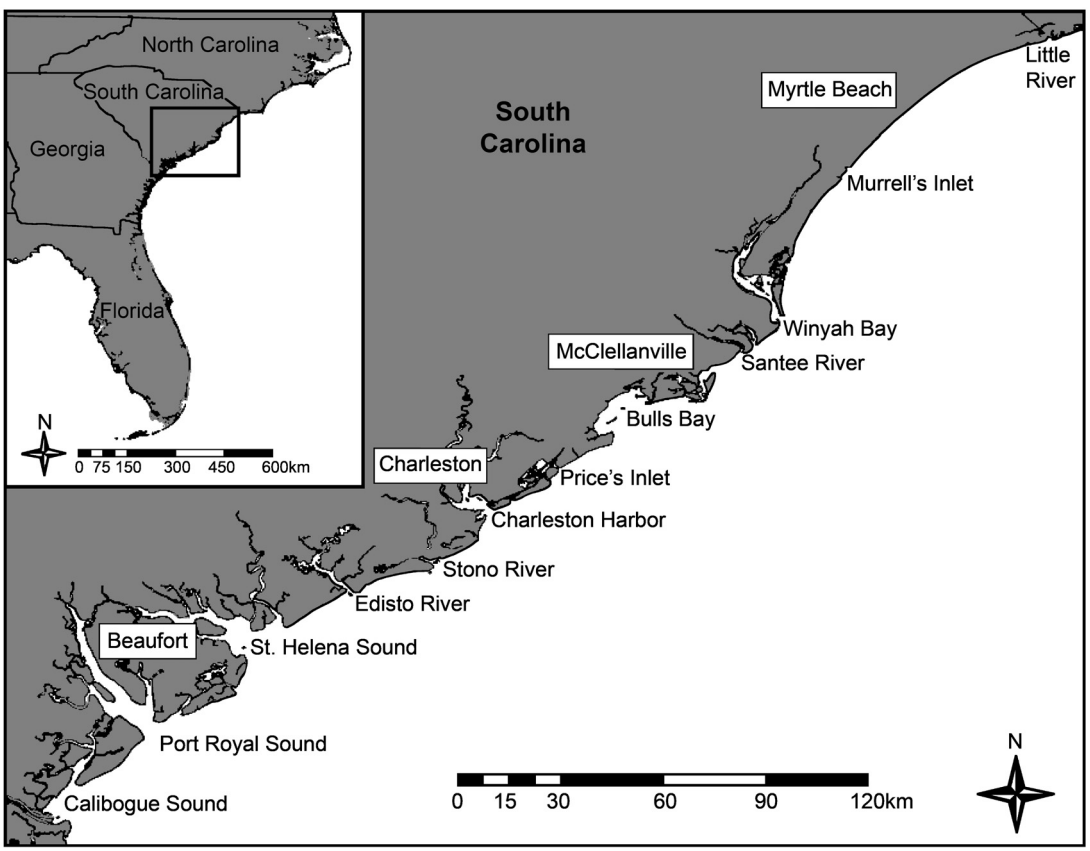

Fig. 2. Map of the study area.

Leatherwood, 1997; Zollett, 2005) and the presence of other trawlers was recorded at each interval (Mann, 1999). All dolphins seen within 100m of the stern of the vessel were considered to be 'present'. The number of dolphins and mother/calf pairs (M/C) present at each interval was estimated. Calves were defined as swimming in echelon position and being 2/3 or less the size of the adult dolphin or those with visible fetal folds (Shane, 1990). Feeding behaviours such as net depredation and eating discards (Fertl and Leatherwood, 1997) were recorded using the *ad libitum* sampling method and therefore the data on these behaviours was anecdotal (Mann, 1999).

The time and locations of each tow were determined using a *Garmin* GPSmap 76 handheld GPS unit (Olathe, Kansas, USA). Photo identification was conducted using a *Canon* EOS-1 Ds Mark II digital camera (Ōta, Tokyo, Japan) with a *Canon* 100–400mm telephoto lens. Photographs of each dolphin's dorsal fin and any direct physical interactions were then entered into *FinBase*, a *Microsoft Access* database, to create a catalog of 'Shrimp Boat Dolphins' (Adams *et al.*, 2006). This database will be used in future research to determine if the dolphins photographed are known individuals of a particular stock and how often individual dolphins engage in trawler interactions.

Shrimp trawler survey

In order to enhance knowledge of dolphin/shrimp trawl fishery interactions, a mail survey questionnaire was created and distributed to a subset (n = 157) of the fishery who had maintained a South Carolina commercial trawler license for at least the last five years consecutively (2007–2011). The survey questionnaire was organised into three sections: Status of the Fishery; Shrimping Logistics; and Bottlenose Dolphin Observations. Information was obtained using the SCDNR shrimp trawl licensing database. Each fisher was mailed a survey packet that included a cover page, the survey questionnaire, and an empty, postage-paid, pre-addressed envelope to facilitate in the return of the completed survey. In order to protect anonymity, no return address was listed on this empty envelope.

Stranding record data

Bottlenose dolphin stranding records were accessed via the National Ocean Service (NOS), Center for Coastal Environmental Health and Biomolecular Research (CCEHBR), Marine Mammal Information System (MMIS) Database. Using this Microsoft Access database, a query was run for Human Interaction (HI) data. In the database, these records are separated into 'Yes HI', 'No HI', 'Cannot Be Determined' (CBD-HI), or 'Not Available' (N/A). Stranding records that were 'No HI' or 'N/A' were excluded from the dataset. Further, only 'Fishery Interaction' (FI) cases of the 'Yes HI' records were used. Cases in which 'Crab Pot' or 'Monofilament' gear could be identified were removed from the dataset. In addition, only strandings that occurred during the commercial shrimp trawl season for that year were included in the final dataset. All remaining records categorised as 'Yes HI' were included in the final dataset, including four confirmed trawler takes. Any CBD-HI cases which mentioned suspicion of human interaction were also included in the final dataset.

Information gathered from the four confirmed stranding cases, the onboard observation study and the mail survey were used to create a Dolphin/Trawl Fishery Interaction Flow Chart (Fig. 3). The purpose of the flow chart is to provide a tool for marine mammal researchers to use when determining if a dolphin's mortality likely resulted from a shrimp trawl fishery interaction. The chart is divided into three levels: 'Level 1: Gear Attachment', 'Level 2: Gear Wounds', 'Level 3: Post-Mortem Exam'.

In Level 1 if gear attachment is present, researchers are offered a choice of gear type and gear size. Gear size ranges were determined from field measurements, the fisher survey, and data from a previous crab fishery gear tension test (Burdett *et al.*, 2007; Burdett and McFee, 2004). The 16mm to 4mm range provided for line width represents the overlap between the gear types used in the trawl fishery and other South Carolina fisheries, particularly the crabpot fishery. Based on the answers provided by researchers, categories are assigned: 'Confirmed', 'Unconfirmed/Probable', 'Unconfirmed/Possible', 'Cannot Be Determined' (CBD), and 'Other'. A full description of each category can be found in Table 1. Level 2 is focused on gear wounds and is structured almost identically to Level 1, but 'Confirmed' and 'Other' are not included in the list of potential classifications since without the presence of gear, it is impossible to confirm whether or not mortality resulted from interactions with a given fishery. Level 3 focuses on gross pathology data obtained during necropsies, including external observations of body condition and internal examinations of the respiratory system, digestive tract and musculature. This level is meant to be read from left to right and takes an 'all or nothing' approach. If the body condition is robust, researchers continue across the chart until they answer 'No' to one of the options. Only if all of the answers are 'Yes', Unconfirmed/Probable is the potential classification.

Statistical analysis

Statistical analysis was conducted using IBM SPSS statistical software (Armonk, NY, USA). Dolphin presence and gear interaction data collected during onboard observations and all data collected from the survey were categorical. These categorical data were tested using cross tabulation and the Pearson chi-square (x^2) test to determine the statistical significance of the observations. Effects on mean dolphin group size, mean number of M/C pairs, and the mean number of nearby trawlers were analysed using an ANOVA test. For both tests, a 95% confidence interval was used and thus p-values < 0.05 were considered to be statistically significant.

RESULTS

Direct onboard observations

Bottlenose dolphin mortality

No bottlenose dolphin mortality was observed during 25 days of onboard observations. However, physical interactions with the fishery were noted. Rubbing and biting of the lines was seen only during haul-back. These line interactions occurred on 6% (n = 4) of haul-backs. Net interactions were seen on 1% (n = 1) of set-outs and 14% (n = 10) of haul-backs. Since physical gear interactions could

Table 1

Criteria used to classify trawl fishery interaction in South Carolina.

Classification	Criteria
Confirmed trawl fishery interaction	Stranded with gear, reported sighting with gear, freed from gear.
Unconfirmed, probable	Wounds and body condition very similar to confirmed cases (i.e. rope and/or net abrasions, stomach full of common fishery bycatch fish remains, robust body condition, froth in lungs and bronchi).
Unconfirmed, possible	Wounds and body condition similar to confirmed cases. Wounds may have resulted from other fishing practices and may not be characteristic of trawl gear (i.e. puncture wounds, lacerations, rope marks that may be post mortem).
CBD, mutilation	Interaction with trawl fishery could not be determined. Animals showed signs of fishery interaction, but carcass was too heavily mutilated or appendages were lost, preventing complete wound analysis.
Other fishery	Interaction with a fishery other than the trawl fishery. Dolphins stranded with gear attached or evidence of entanglement not congruent with trawl gear (i.e. crab pot gear, monofilament lacerations).

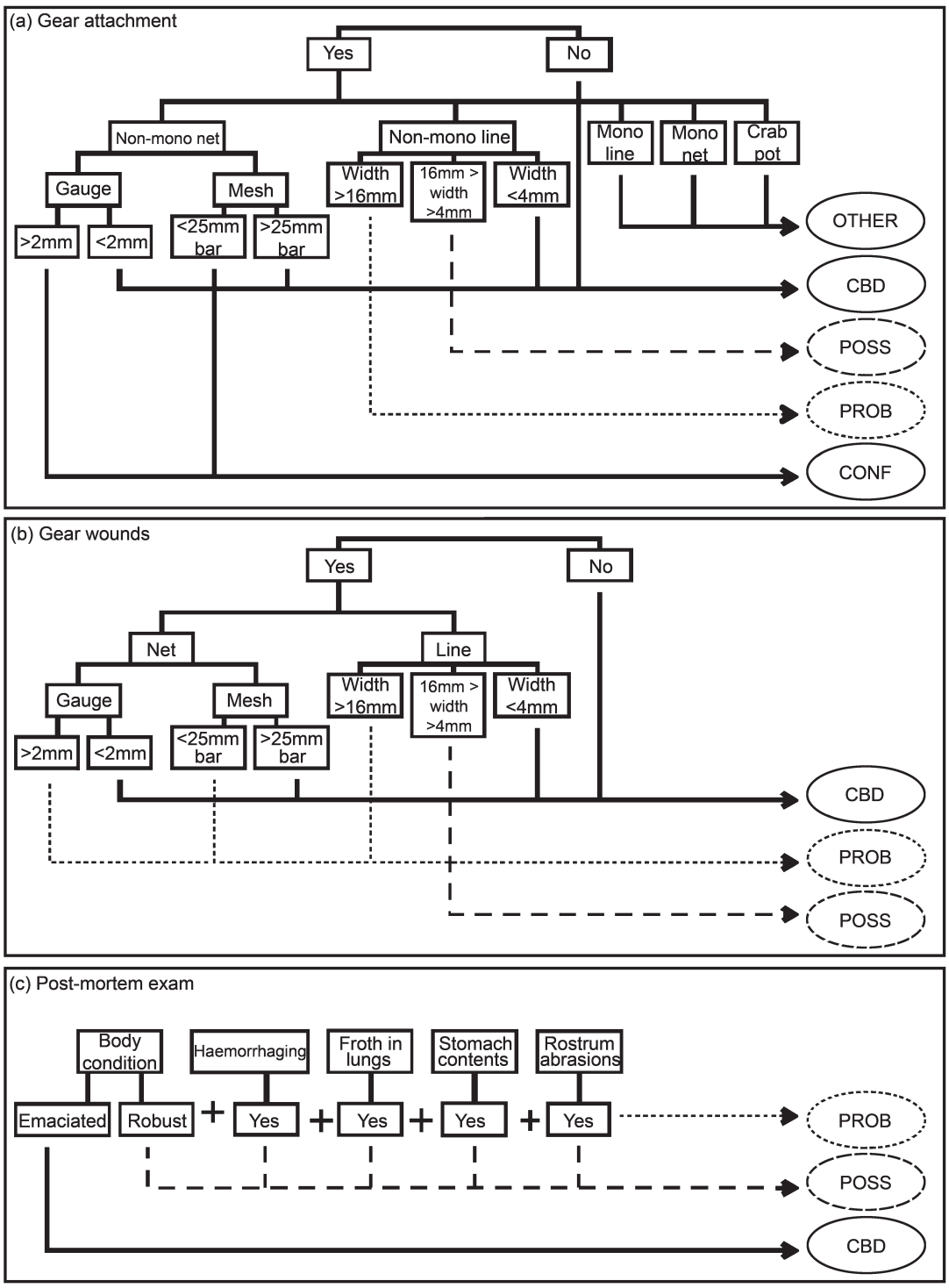

Fig. 3. Dolphin/Trawl Fishery Interaction Flow Chart.

not be observed during towing, this stage was removed from further analysis of gear interactions. Vessels towing four nets (Charleston Harbour North and Charleston Harbour South) had significantly more net interactions than the two-net commercial vessels ($x^2 = 4.394$; $p = 0.036$). When the two Charleston based vessels (Charleston Harbour North and Charleston Harbour South) were compared over their overlapping range, no significant differences in physical gear interactions were observed.

Bottlenose dolphin presence and abundance

From August to December 2010, 1,176 observations were made, including 71 at set-out, 1,034 during towing and 71 at haul-back. Dolphins were present in 69% ($n = 810$) of the total observations. Dolphins were observed significantly more often during towing and at haul-back ($x^2 = 68.613$; $p < 0.001$) than at set-out. When analysed with and without the observations made during the towing stage, Charleston Harbour and Beaufort had significantly higher dolphin presence than the other vessels ($x^2 = 39.630$; $p < 0.001$; $x^2 = 10.281$; $p = 0.016$). The group size over all vessels and all stages ranged from 1 to 40 individuals with a mean of 6.72 ± 5.88 dolphins. When other commercial trawl vessels were seen in nearby waters, dolphin group size had a slightly smaller mean of 5.91 ± 4.98 dolphins. When group size was analysed based on location, Charleston had a mean of 8.38 ± 6.70, which was significantly higher than in Beaufort (5.44 ± 4.805) or McClellanville (4.29 ± 3.148) ($F = 45.835$, $p < 0.001$).

Mother-calf (M/C) pairs were seen in 35% ($n = 281$) of the observations. This includes 28% ($n = 5$) of set-outs, 34% ($n = 250$) during towing, and 46% ($n = 26$) of haul-backs. M/C pairs were seen significantly more often on the vessels towing four nets, both of which were Charleston (Charleston Harbour South and Charleston Harbour North) based vessels ($x^2 = 4.841$; $p < 0.028$). However, when compared over their overlapping range, no significant differences in dolphin presence or M/C presence were seen between these two Charleston based vessels. When M/C pairs were observed, total group size ranged from 2–25, with a mean of 10.19 ± 6.07 dolphins, including a mean of 1.30 ± 0.46 M/C pairs per event.

Indirect observations

Shrimp fishery survey: Gear types

Of the 157 surveys mailed, there were 44 (28%) complete responses. Although respondents were asked a variety of shrimp fishery related questions, only the gear type and dolphin interaction data will be presented here. More than half of the respondents said that they only use a single net. The rest were split between two nets and four nets with some reporting that they have used both two and four net configurations. A majority of respondents (>70%) said they use a lazy-line. Twisted polypropylene and twisted polyester were the most common types of line used, with line widths ranging from 0.5–1 inch. Sugar-line use was less common (57%), but for those that use one, twisted polypropylene and twisted polyester were the most common type of line used and they ranged in width from 0.25–0.75 of an inch. The mesh sizes of nets were much more varied; body-mesh width ranged from 1–2 inches stretched, while bag-mesh size ranged from 0.75–1.75 inches stretched.

The low level of sugar-line use, along with the answers to several of the shrimping logistics questions, suggests that about half of the respondents run small-scale shrimping operations with small trawlers and single, hand-pulled nets. However, when SCDNR licensing data were queried, these small, single net trawlers only made up about 25% of the total fishery (George Steele, SCDNR, pers. comm.). It appears that the demographics of the survey respondents may be skewed towards small-scale and 'recreational' shrimping operations. In contrast, the vessels used in the onboard observations were larger, two to four net, winch-pulled operations.

Shrimp fishery survey: Dolphin interactions

A majority of the respondents said that they saw dolphins eating discarded bycatch on most or every trip. Discarded flounder (*Paralichthys spp*.), cutlass fish (*Trichiurus lepturus*) and Spanish mackerel (*Scomberomorus maculatus*) were specifically mentioned as 'favourites' of the dolphins. Most, (>60%) said that they rarely or never saw dolphins biting, tugging, or rubbing their nets or lines, while the rest reported that they had witnessed dolphins depredating fish or shrimp from their nets and several reported that dolphins have caused damage to their gear.

When asked about incidental takes of bottlenose dolphins, five respondents (11%) said that they had caught a dolphin in their net, including one respondent who caught more than one. In addition, four other respondents said that while they had never caught a dolphin, they had heard of someone catching one. Six respondents (14%), including two that reported net takes, said that they had entangled a dolphin in the lazy line; none more than once. In addition, two respondents said that while they had never entangled a dolphin, they had heard of someone else entangling one in their lazy line. None of the respondents said that they had entangled a dolphin in their sugar line or had ever heard of someone entangling one in their sugar line. A total of nine respondents admitted to dolphin takes in at least one gear type, with several having more than one; the survey revealed at least 12 dolphin takes.

A description of the take was provided in 10 of the 12 cases. In one case the dolphin freed itself from the gear, in four cases the shrimper freed the dolphin from the gear, whilst in five cases the dolphin was dead. Two respondents of the latter commented that the dolphin was decaying and one said that the dolphin died from drowning. Of note is that the net, lazy line and chaffing gear were all implicated in at least one of the dolphin takes. Only two (5%) of the respondents said that they had ever contacted the SCDNR or Marine Mammal Stranding Network (MMSN) about a dolphin take and 10 (26%) said that they had never even heard of the MMSN. There was no significant difference between number of nets a trawler used and whether or not they reported having ever caught a dolphin in their net or lazy line. However, all six line entanglements were reported by shrimpers with home ports in South Carolina.

Stranding record review

An initial database query of bottlenose dolphins that stranded in South Carolina yielded 1,024 total records spanning from

1992–2011. When this dataset was queried for signs of human interaction (HI), it resulted in 105 cases that were determined to be HI, 438 cases in which HI could not be determined (CBD-HI) and 481 cases with no signs of HI. Of the 105 HI cases, 70 had signs of fishery interaction (FI), 15 showed characteristics of a boat strike, 10 had evidence of mutilation and 10 had other signs of HI (e.g. marine debris, died during capture, multiple compounding sources). All HI reports were reviewed to confirm their classification and to look for signs of trawler interactions (TI). In addition, 17 CBD-HI cases with specific comments about HI suspicions were also reviewed. Thus, 122 standings were used for this part of the stranding analysis.

Based on the Dolphin/Trawl Fishery Interaction Flowchart, as described in the Methods, four cases were confirmed as TI, of which two dolphins were taken in the SCDNR SEAMAP scientific survey. In addition, three cases were determined to be Unconfirmed/Probable TI and five cases were determined to be Unconfirmed/Possible TI. A description of the 12 TI confirmed, probable, or possible cases is shown in Table 2. Forty-eight of the remaining cases were attributed to other sources such as boat strike, other fisheries, mutilation and marine debris. However, for over half (n = 64) of the cases reviewed, interactions with the trawl fishery could not be determined.

The 12 confirmed, probable, and possible TI cases were assigned age classes based on McFee and Hopkins-Murphy (2002). None of the TI animals were classified as neonates. However, five of the animals, including one confirmed case and four possible cases were <184 cm and classified as young of the year calves. Two of the confirmed cases, two of the probable cases and one of the possible cases were classified as immature (201–240cm). One probable case was classified as mature (>240cm), while the total length of the last confirmed case was unknown.

DISCUSSION

Direct observations

Bottlenose dolphin mortality

While no bottlenose dolphin takes were observed during onboard observations, dolphins were observed rubbing and biting the nets and using their foreheads and rostrums to manipulate the mesh to gain access to the fish inside (Fig. 4). This type of gear interaction is consistent with previous studies (Broadhurst, 1998; Svane, 2005) and could place them at risk for entanglement. This behaviour was also reported by several of the mail survey respondents who claimed that dolphins damaged their gear by biting holes in the nets. However, it is also suggested that the source of much of this gear damage is from sharks which also feed behind shrimp trawlers (Fertl and Leatherwood, 1997; Zollett, 2005).

The small mesh size used in commercial shrimping makes it unlikely that a dolphin would get its fins or flukes caught in the net. Yet, while picking fish out of the net, it is possible that a dolphin could get its teeth or entire rostrum stuck in the mesh (Fertl, 1994). Broadhurst (1998) theorised that this behaviour does not result in direct bycatch of the dolphins and that the use of chaffing gear could deter dolphins from manipulating the net. However, one respondent in the mail survey reported a dolphin take in which the animal was actually stuck in the chaffing gear.

It is also believed that dolphins can be caught when they enter the mouth of the net to feed (Waring *et al.*, 2012; Zollett, 2005). Changes in speed or direction of a vessel can alter the shape of the mouth and body of the net, reducing or eliminating a dolphin's ability to escape (Zollett, 2005). At the beginning of set-out, the net is relatively shapeless and slow-moving and at haul-back, trawler speed decreases significantly which causes the mouth of the net to collapse (Waring *et al.*, 1990).

It is possible that some of the dolphins trapped during set-out and haul-back are alive when they are caught in the net,

Table 2

Date, location, sex, length, and classification of confirmed, probable, and possible shrimp trawl fishery mortalities in South Carolina (1992–2013).

Field no.	Date	Location	Sex	Length	Classification	Criteria for classification
SC1236	02/08/12	Georgetown Co.	Male	223	Confirmed	SCDNR trawler take.
SC0630	28/07/06	Beaufort Co.	Male	236	Confirmed	SCDNR trawler take.
SC0224	23/08/02	Beaufort Co.	Female	152	Confirmed	Commercial trawler take in float line.
SC9827	28/05/98	Beaufort Co.	–	–	Confirmed	Commercial trawler take in net.
SC0842	10/12/08	Beaufort Co.	Female	185+	Probable	Flukes cut off, stomach full of shrimp and fish, foam in bronchus, rostral abrasions, hatch marks.
SC0236	11/12/02	Charleston Co.	Female	229	Probable	Hatch marks on flippers, foam in bronchi.
SC9835	04/07/98	Charleston Co.	Male	248	Probable	Line marks circumventing body, froth in bronchi, fish in esophagus and stomach, wound to upper right tooth row.
SC1052	28/08/10	Charleston Co.	Male	135	Possible	5mm line wounds through mouth causing dislocation of jaws, also constricting wraps around both pectoral fins and the thoracic region, haemorhagging on head and jaw.
SC0952	25/11/09	Charleston Co.	Male	221	Possible	Wounds consistent with rope entanglement.
SC9826	28/05/98	Charleston Co.	Female	176	Possible	X-marks on left flipper, left fluke cut off, left side of body with line marks running from flipper back, other line marks on body.
SC9726	01/06/97	Charleston Co.	Male	145	Possible	Line marks on right side, abraded rostrum, bloody mouth, partially digested fish in stomach. A leatherback turtle found mutilated, no head or appendages on the same day ~½ mile south of the dolphin stranding.
SC9725	18/05/97	Charleston Co.	Female	113	Possible	Dorsal fin crosshatches, line marks on rostrum 6cm, flukes and peduncle, bruise right ear 7 × 6cm, partially digested fish and shrimp were observed in the forestomach.

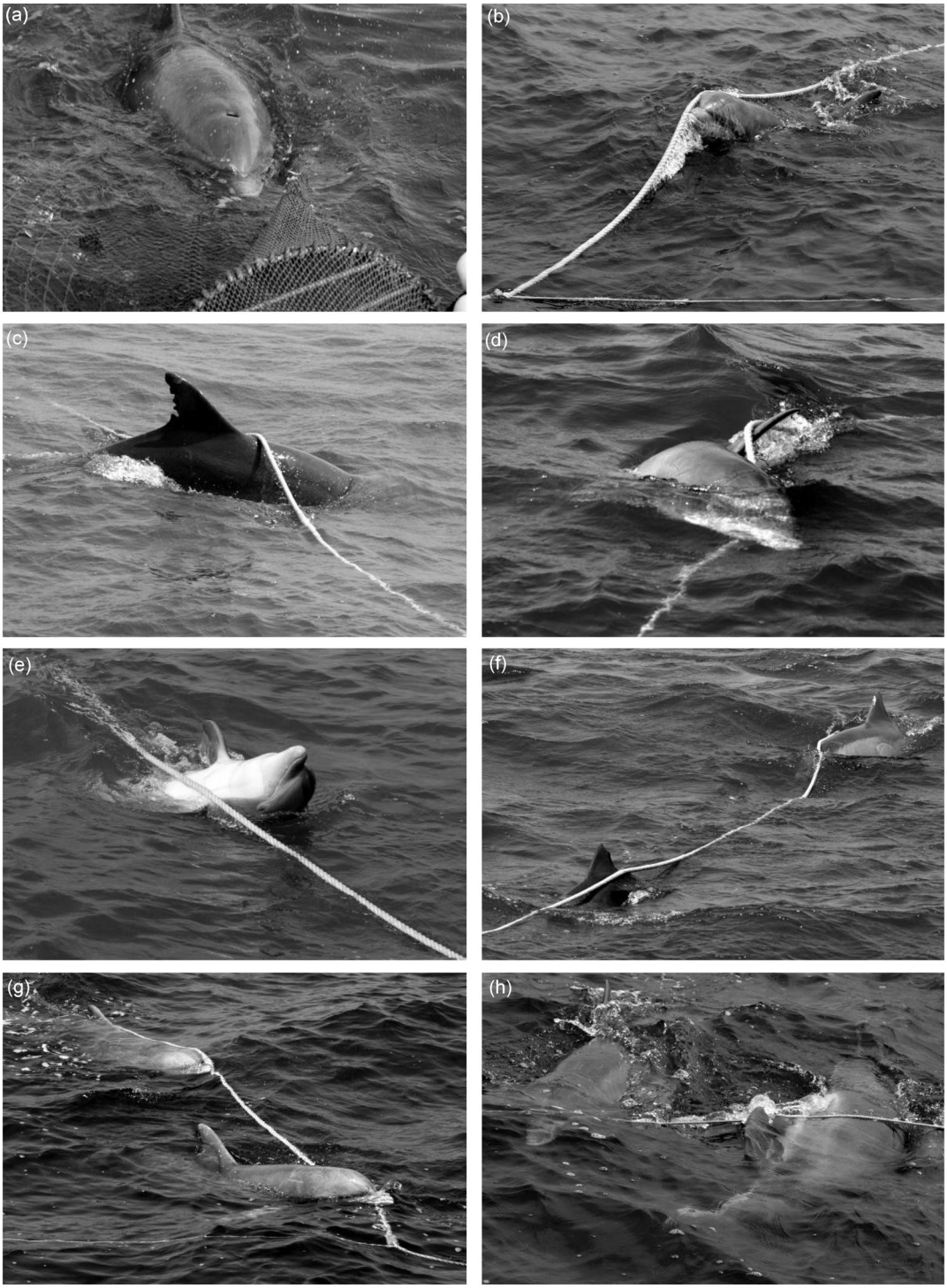

Fig. 4. Individual (a,b,c,d,e) and multiple (f,g,h) dolphins engaging in physical gear interactions with trawl net (a), lazy line (b,c,d,e,f,g), and sugar line (h). Photos by J. Greenman.

but die since tow times can last for multiple hours (Fertl and Leatherwood, 1997). Several necropsies of dolphins caught by trawlers in other areas indicated that the animals had drowned, and that they had experienced traumatic muscle and ligament injuries while struggling to free themselves from the underwater entrapment (Lipscomb, 1996; Northridge, 2003). It is also believed that dolphins found in the nets are rarely alive when caught, but rather that they are dead or dying when they are scooped up in the net (Fertl and Leatherwood, 1997). Mail survey respondents reported that the dolphins they caught were 'long dead' and decaying. In this survey, as seen in previous ones (Fertl, 1994), many respondents insisted that dolphins were too quick or smart to be caught in the net. While this may be true for healthy and experienced adults, sick or injured animals as well as calves and neonates may not be strong enough to swim out of the net. This may account for why calves made up 50% (n = 6) of the TI cases.

During both set-out and haul-back, there is a period of time when the lines and nets are sitting slack on the surface of the water making them more likely to entangle. Several studies reported that bottlenose dolphins can drown when they are entangled around the tail stock by hanging lines (Fertl, 1994; McFee *et al.*, 2007). Those animals that do

manage to free themselves may still have a serious injury. In rough seas, these lines can move in even more unexpected ways, perhaps increasing the likelihood of entanglement.

During onboard observations, dolphins were observed rubbing and biting the lazy line and sometimes the sugar line (Fig. 4). It appears that dolphins use the line as a 'scratching post'. Dolphins are tactile animals and it is believed that touching plays a large role in dolphin social structure (Dudzinski, 1998). In several cases, multiple dolphins were rubbing on the same line at the same time (Fig. 4). 'Playing' with the lines during haul-back was also reported by Fertl and Leatherwood (1997). While the lazy line is a relatively thick and stiff line, the sugar line is often similar to lines used on crab pots. A study on the movement of this type of line suggests strong currents can cause this line to move in erratic ways, making it more likely to cause entanglement (McFee *et al.*, 2007). In addition to currents, water churned up by the trawler's propeller or by dolphins splashing and engaging in social behaviours could have a similar effect on the lines.

Line types and widths can vary depending on the vessel, especially when individuals make modifications to their gear. One such modification was actually implicated in a South Carolina bottlenose dolphin entanglement in 2002. A small-scale shrimp fisher had attached a 20ft line and buoy to the top of the cod-end to aid in grappling the net. This 9mm diameter line became wrapped twice around the mouth, body and peduncle of the animal. This gear modification may be quite common, since a similar line-buoy modification was observed on two of the commercial vessels in the current study although no direct interaction with this gear was observed. These modifications create difficulties for researchers using gear attachment and gear wound width as a method for identifying trawler interactions, since some of the lines are of the same type and size as those used in the crab pot fishery. If the take had not been reported and instead the buoy line cut, the animal could have washed up on the beach with what would have appeared to be textbook characteristics of a crab pot fishery interaction. This could result in the crab pot fishery being falsely implicated as a possible cause of death.

Several factors have been suggested as having a significant effect on rate of marine mammal fishery interactions and bycatch, including the prevalence of other marine mammals in the fishing area, time of day, tow duration, level of tow in water column, size of net opening, haul-back speed and gear design (Waring *et al.*, 1990). In the present study, both line and net interactions were seen significantly more often during haul-back. In addition, significantly more net interactions were observed on vessels towing four nets than those towing just two nets. This seems logical, since four nets provide more surface area for dolphin interaction than two nets.

Presence and abundance

Bottlenose dolphins, including M/C pairs, were observed associating with trawl vessels along the entire study area and during all stages of trawling. However, dolphins were present at the haul-back more frequently and in larger group sizes than at set-out. Dolphins were also observed following the cod-end during haul-back and depredating on fish protruding from the mesh and other fish that had fallen out of the net. These findings are consistent with the results from several other studies which frequently observed dolphins congregating around the cod-ends at haul-back (Broadhurst, 1998; Corkeron *et al.*, 1990; Fertl, 1994; Svane, 2005). There are several factors that may explain this occurrence. At haul-back the gear and the catch are at the surface, making them more visible to observers than during the tow. Additionally, the haul-back process can be noisy and the sound of the engine and winch may alert nearby dolphins to the food source (Fertl and Leatherwood, 1997; Zollett, 2005). In addition to picking fish out of the net, dolphins fed on catch that washed out of the net during the haul-back process and bycatch discarded during culling. Fertl (1994) also suggested that in addition to foraging, social and sexual interactions between dolphins may play an important role in dolphin movements around shrimp trawlers.

Onboard observations revealed that there were significant differences in dolphin presence based on observation vessel. The Charleston Harbour-North and Beaufort vessels had significantly higher dolphin presence than the other vessels. This is an interesting result, since the Charleston Harbour-North and Beaufort vessels differ not only in where they shrimp but also in how many nets they use. Charleston Harbour-North used four nets and primarily trawled north of Charleston Harbour, while Beaufort used two nets and trawled in St. Helena Sound. Therefore, number of nets and shrimping location do not appear to be good predictors of overall dolphin presence, but M/C pairs were seen significantly more often on both of the four-net, Charleston-based vessels. It is possible that M/C pairs are attracted to four net trawlers because they provide more cod-ends to feed from or because they catch more per tow and thus have more discards. However, it may also be that M/C pairs are drawn to the habitats around Charleston Harbor. Charleston observations also showed a significantly higher mean group size than in McClellanville or Beaufort. Yet, the mean group size for Charleston (8.38 ± 6.70) is much smaller than the mean groups size of 15 observed near shrimp trawlers during previous photo-id studies in Charleston (Speakman *et al.*, 2006). It is possible that this discrepancy is a result of differences in the study methods and sampling season. While the current study was conducted aboard commercial trawlers during the months of August to December and included a large number of observations (n = 810), Speakman *et al.* (2006) used a small motorboat during the months of June to November and had a smaller number (n = 47) of trawler associated observations.

Indirect observations

The mail survey results clearly showed that dolphin takes in the South Carolina shrimp trawl fishery are underreported. Three of the takes reported in the survey were by fishers that have been trawling for 11–20 years suggesting at least three takes since 1992. The other nine were by fishers with over 20 years of experience. In addition, the 44 respondents of this survey only represent about 10% of the fishery, which has averaged about 433 licenses per year over the last five years. Therefore, it is possible that the total number of dolphins taken in this fishery is much higher.

As stated earlier, it is believed that the South Carolina/Georgia Coastal Stock (SCGCS) has the most overlap with the shrimp trawl fishery. Using this SCGCS

assessment (PBR = 64), the two known commercial dolphin takes that occurred in 1998 and 2002 are not enough to meet the NMFS criteria for classification as a Category II fishery (1% PBR <50% PBR). However, the SCGCS also includes the entire Georgia coast and a recent study found that dolphins frequently associated with shrimp trawlers near Savannah, GA (Kovacs and Cox, 2014). If dolphin takes in Georgia occur at a similar rate as in South Carolina, it may provide enough data to confirm its Category II designation. Given that the small subset (n = 44) of shrimper survey respondents admitted to an additional 12 takes, it is still likely that the fishery as a whole has exceeded 1% PBR.

Using the Dolphin/Trawl Fishery Interaction Flowchart (see Methods), the four known takes (two SCDNR and two commercial) were confirmed as trawler interaction (TI) cases. In addition, the flow chart revealed three cases of Unconfirmed/Probable TI and five cases of Unconfirmed/ Possible TI. Even if just the probable cases are included, the shrimp trawl fishery has met the Category II criteria for any given five year period from 1994–2012.

SUMMARY

No dolphin takes occurred during the direct onboard observations though it is clear that dolphins increase the likelihood of entanglement by rubbing on lines and nets. The four-net vessels (Charleston Harbour South and Charleston Harbour North) had significantly more net interactions and higher M/C presence. However, these were also the only two vessels based out of Charleston and therefore location may also be a factor in these direct physical gear interactions. Line type and number of lines were too similar to compare between vessels. Fishing method differed very little between the vessels, but was variable depending on the presence of shrimp. When shrimp catch is good, commercial trawlers tend to circle around a specific area while trawling, allowing dolphins more time to interact with the vessel. Tow time was not a significant factor, but the longer the gear sat at the surface between tows, the more likely dolphins were to be observed interacting with it. In conclusion, while gear configuration and fishing method appear to play a role in dolphin presence, abundance, and behaviour around shrimping vessels, these results were not statistically significant.

Only two commercial shrimp fishery dolphin takes were reported to NMFS, SCNDR, or SCMMSN from 1998–2002, yet 12 dolphin takes were reported in the shrimp fisher survey. In addition, the flow chart revealed three cases of Unconfirmed/Probable TI and five cases of Unconfirmed/ Possible TI. Based on these data, shrimp trawl related bottlenose dolphin mortality is clearly underreported. Mortality exceeded 1% of the Potential Biological Removal (PBR) annual average for the five-year period of 1998–2002; therefore, in conclusion, the current status of the fishery as Category II is warranted.

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A summary history of the application of statistical catch-at-age analysis (SCAA) to Antarctic minke whales

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ABSTRACT

Various forms of SCAA methods have been applied to data for Antarctic minke whales since this method was first presented to the Scientific Committee of the International Whaling Commission by Punt and Polacheck (2005). A brief overview is provided of the historical use of methods which use catch-at-age data to draw inferences regarding trends in abundance for Antarctic minke whales. The original version of the SCAA and how this method has been modified over time to more adequately mimic the available data on length, conditional age-at-length and indices of abundance from IDCR/SOWER and JARPA/JARPAII is described. The paper also lists the specifications for the reference case analyses in each paper presented to the Scientific Committee. The focus is on methodology, with only limited comment on the results from each subsequent analysis.

KEYWORDS: CATCH-AT-AGE; ANTARCTIC MINKE WHALE; POPULATION MODEL; SOUTHERN HEMISPHERE

INTRODUCTION

Several catch-at-age methods have been applied to data for Antarctic minke whales. The range of questions which have motivated the analyses using these methods have increased over time in response to the needs and priorities of the International Whaling Commission (IWC) and its Scientific Committee. This paper reviews the application of catch-at-age methods to data for Antarctic minke whales. The first section provides some of the early history, including how catch curve methods, and subsequently virtual population analysis (VPA)-based approaches, were applied. However, the focus of the paper is on the statistical catch-at-age (SCAA) method which has been presented to the Scientific Committee since 2005. The purpose is to outline how this method has been developed in response to input from the Scientific Committee, and to summarise the current state of the method and the key issues which need to be addressed. Table 1 provides a summary of the main topics which have been discussed by the Scientific Committee in regard to the SCAA for Antarctic minke whales.

THE PRE-SCAA YEARS

Debates over the reliability of inferences that might be drawn from catch-at-age information for Antarctic minke whales have a long history in the IWC Scientific Committee. In the early 1980s, the Committee's recommendations on catch limits for minke whales followed from its acceptance that Antarctic minke whales had been increasing, prior to being exploited to a substantial extent. This increase was postulated to be a response to the substantial exploitation of other baleen whale species and hence to the creation of a 'krill surplus' (IWC, 1980). The evidence that points towards these conclusions (until these came under question in 1983; IWC, 1984a), involves estimates of the slope of the descending limb of minke whale catch curves (Ohsumi, 1979). Catch limit recommendations in that period (e.g. IWC, 1983; 1984b; 1985) were based on estimates of replacement yield (RY), where the catch levels were intended to stabilise the increasing populations[1]. The methods used to estimate RY in turn depended critically on the catch-at-age data and the value of natural mortality, M, and included taking the difference between the catch curve slope (Z) and M, and later the multi-cohort method (Sakuramoto and Tanaka, 1985; 1986). However, reservations (e.g. Chapman, 1983; Cooke, 1985; de la Mare, 1985a; 1985b) that came to be expressed over that period concerning the reliability of the resultant estimates included concerns of confounding, with the possibility that M increased at larger ages and also that an age-independent value for M was not well determined (note the sensitivity of population trend estimates to the value of M as illustrated in Fig. 1). As the justification for these reservations came to be more widely appreciated, by the mid-1980s the Scientific Committee found itself in the position of being unable to reach consensus on catch limit recommendations for Antarctic minke whales.

The Japanese Whale Research Programme under Special Permit in the Antarctic (JARPA) stated that its primary objective was to estimate the age-specific natural mortality coefficient for minke whales in response to this situation (Government of Japan, 1987), although this was later changed to estimation of average (over age) natural mortality (Government of Japan, 1992). This objective was planned to be achieved by obtaining representative samples of the age structure of the population through random sampling, combined with systematic sighting surveys. However, several members of the Scientific Committee (e.g. de la Mare, 1990) argued that JARPA would not provide estimates of natural mortality with sufficient precision to determine the historical recruitment trend and refine sustainable yield predictions even if catch-at-age data in addition to survey estimates of abundance were available with a CV of 0.15 for 30 years. Butterworth and Punt (1990) showed that future catch-at-age data from JARPA could, in principle, resolve

[1]The IWC's 'New Management Procedure' was not designed to address cases where a population was increasing above its unexploited population size, e.g. Allen (1980).

Table 1
Major issues considered during the development of the SCAA and their current status.

Issue	Current status
Model structure	
Stock structure	Stock I (Indian) is found in Areas III–E, IV and V–W; Stock P (Pacific) is found in Areas V–E and VI–W.
Can the model fit the Japanese length-at-age data	• Allowing for time-varying growth and selection addressed most of the bias. • Diagnostics reported by Punt *et al*. (2014) suggest adequate fits. • The time-trajectory of the growth rate parameter κ may be biologically unrealistic.
How does *M* change with age	• Changes piecewise linearly at ages 3, 10, 30, 35. • Sensitivity is explored to a Siler function in Punt *et al*. (2014).
How does carrying capacity change with year	• Changes as an autoregressive function of time.
Vulnerability	(1) JARPA/JARPA II: Logistic function of length. (2) Japan commercial: Dome-shaped function of length, with the length of maximum selectivity time-varying. (3) Soviet Union commercial: As for Japan commercial.
Extent of process error	Results are generally insensitive to the values for the parameters which determine variation in selectivity, recruitment, growth and spatial distribution.
Calves can exceed mature females	Resolved by adding a penalty term and re-parameterizing how recruitment is modelled.
Likelihood function	
Indexes	
IDCR/SOWER indices agreed	Punt *et al*. (2014) used the estimates by Okamura and Kitakado (2012).
Use of JARPA indices	Punt *et al*. (2014) used the estimates in Hakamada *et al*. (2013).
Why are the results insensitive to ignoring the JARPA indices	Still be to be resolved: Punt *et al.* (2014) found the results from the SCAA were sensitive to ignoring the JARPA age and length-composition data, but not the JARPA abundance indices.
Composition data	
How should the composition data be included in the assessment	• The Soviet Union length data have been dropped from the assessment owing to concerns about misreporting. • The Japanese data (both commercial and JARPA data) are included in the assessment as length-frequency data and conditional age-at-length data.
Inclusion of age-reading error matrix	The most recent estimates of age-reading error matrices as developed by Kitakado *et al.* (2013) are included in the latest version of the SCAA.
Data weighting	
Abundance index data	No additional variance assumed; 'process error' accounted for by allowing the proportion of each stock in each area to vary over time.
Compositional data	• Selected using the method of McAllister and Ianelli (1997). • Results are generally insensitive to how the data are weighted (e.g. Punt *et al*., 2014).
Quantification of uncertainty	
Sensitivity analyses	All assessments have reported results in which assumptions have been changed.
Variance estimation	Asymptotic variances are computed for all model outputs; attempts to apply MCMC have not been successful given the complexity of the model (i.e. the time to compute a single evaluation of the likelihood function).
Simulation testing	Limited simulation testing has been undertaken – a full evaluation of the method would require very considerable computing resources.

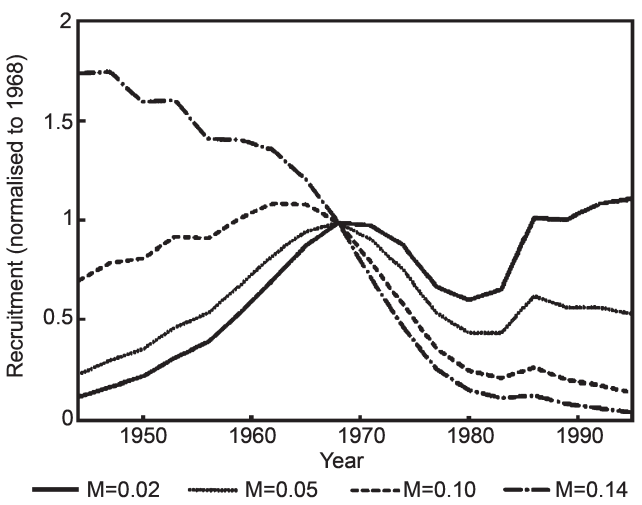

Fig. 1. Estimates from ADAPT-VPA of time-trajectories of age-2 abundance for minke whales in Antarctic Area IV for fixed values for age-independent natural mortality, M = 0.0,5 0.05, 0.10, and 0.14yr^{-1}. Each series is normalised to its 1968 level (reproduced from Butterworth *et al*., 1999).

whether or not abundance was increasing historically given temporal invariance of selectivity-at-age above a certain age and knowledge of natural mortality-at-age. However, they also showed that a simple VPA-like method was unable to discriminate an annual rate of increase of 4% from zero even after 25 years of data. Bergh *et al.* (1991a; 1991b) refined the VPA method, which improved the precision of the estimates of the rate of increase.

Butterworth *et al.* (1996) introduced the use of ADAPT-VPA (Gavaris, 1988) to the Scientific Committee. This method, in common with other VPA-like procedures, assumes that the catches-at-age are measured with negligible error compared to other model inputs such as survey estimates of abundance. Unlike most fishery assessments, the ADAPT-VPA developed by Butterworth *et al.* (1996) was based on grouping and analysing the catch-at-age data on a 3-age-3-year basis to overcome small sample size problems for the statistical distribution underlying the estimator used at that stage. This variant of ADAPT-VPA, however, performed poorly in terms of retrospective analyses (Butterworth and

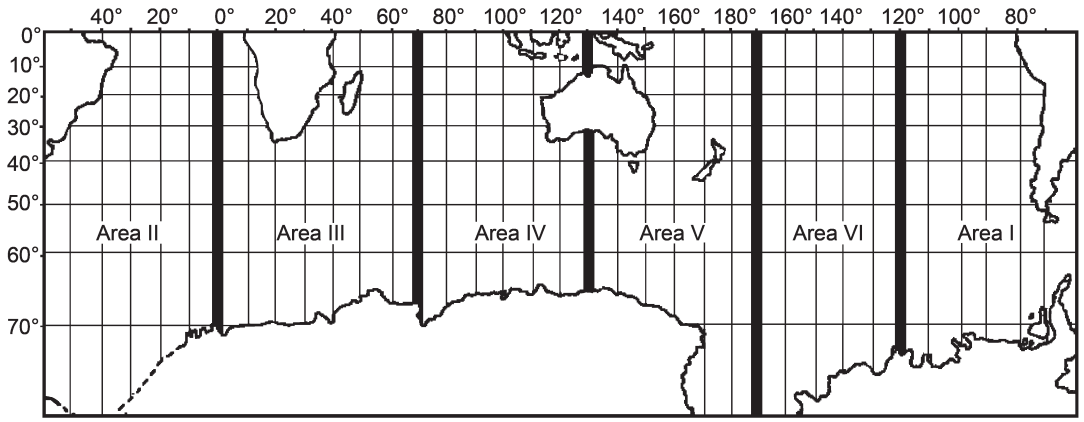

Fig. 2. Map of the Southern Hemisphere showing the locations of the areas referred to in this paper.

Punt, 1996). Butterworth *et al.* (1999) extended the ADAPT-VPA framework by making the separability assumption for the commercial (catches of Antarctic minke whales were taken by Japan and the USSR in the Antarctic and by Brazil and South Africa to the north, prior to the ban on commercial whaling that came into force in 1986) as well as JARPA catches and by taking JARPA as well as IDCR/SOWER estimates of abundance into account for parameter estimation purposes. Butterworth *et al.* (1999) estimated the precision of the results from the ADAPT-VPA using a bootstrap procedure and evaluated the performance of the method using simulations with a focus upon IWC Management Areas IV and V (see Donovan, 1991 and Fig. 2). They estimated a historical rate of increase for Area IV (Fig. 2) of 0.055yr^{-1} (90% CI 0.014–0.091) over the period 1947–68 (Fig. 3). The estimate of the rate of increase for Area V was positive, but less precise. Age-independent natural mortality for Area IV was estimated to be 0.057y^{-1}. A notable feature of the Area IV assessment in Butterworth *et al.* (1999), which was confirmed by further analyses by Butterworth *et al.* (2002) and all subsequent analyses, was the marked drop in recruitment from 1970 to the mid-1980s (Fig. 3)[2].

Butterworth *et al.* (1999) identified several hypotheses for the decline in recruitment including 'super-compensation', increased competition from other krill predators, poor environmental conditions and bias in the estimation method. IWC (2002; 2003) identified further hypotheses which could address the reasons for the decline, expressing these in terms of the change in abundance estimates from CPII and CPIII, along with sources of information and analysis methods. IWC (2005) noted that population modelling could provide a way to address the plausibility of the hypothesis that decline in recruitment is related to competition and other population dynamic-related factors. It considered that a SCAA modelling approach would provide the most appropriate way to address the population dynamics-related issues because a SCAA could allow *inter alia* for errors in catch-at-age data, more than a single stock, environmental covariates, fleet-specific vulnerabilities (IWC, 2005)[3] and

[2]The wide confidence intervals in Fig. 3 are due in no small part of uncertainty in the estimate of M.

[3]Often also referred to as 'selectivities' by the Scientific Committee. Vulnerability combines the effect of age (or length) – specific selectivity by the whalers with the relative probability of whalers encountering a whale of a given age or length given the spatial and temporal distribution of the whaling effort.

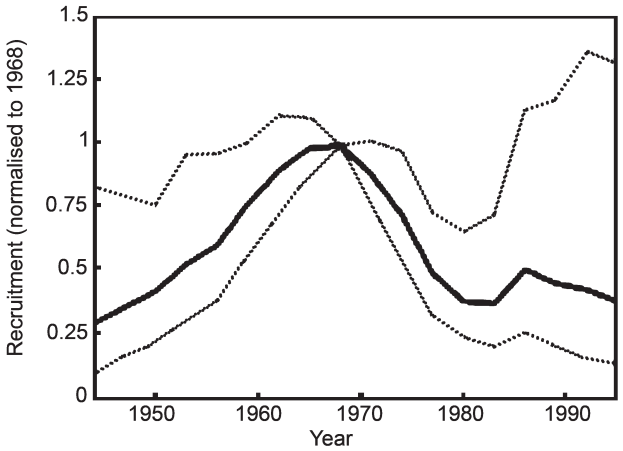

Fig. 3. Bootstrap estimates of medians (solid lines), and 5%- and 95%-iles (dotted lines), for recruitment at age-2 (relative to its estimated 1968 level) for Area IV for the ADAPT-VPA base-case estimator (reproduced from Butterworth *et al.*, 1999).

changes over time in vulnerabilities to be addressed and explored within a single model framework. IWC (2005) noted that there were also other tasks which needed completion to address the issues:

(1) development of a set of stock structure hypotheses for the animals found in Areas IV and V;

(2) compilation of time series of abundance estimates to use, including both from IDCR/SOWER and JARPA cruises, as well as estimates of variances and co-variances; and

(3) compilation of a set of relevant environmental covariates.

ENTER THE SCAA

Punt and Polacheck (2005) noted that there were several potential concerns with the ADAPT-VPA approach as implemented at that time that could be addressed within the context of SCAA as described below.

(1) The catch age-composition data are assumed to be known exactly when constructing the numbers-at-age matrix. This assumption may be invalid due to the impact of ageing error, sampling error associated with construction of age-length-keys, and because age-length keys[4] are available only for the Japanese fleets and need

[4]Also referred to as conditional age-at-length data.

to be applied to construct the age-composition of the Soviet catches.

(2) It is not possible to estimate the numbers-at-age for some of the oldest ages in the earliest years for which commercial age-composition data are available directly using back-projection. Butterworth *et al.* (1999) provided only an *ad hoc* means to specify these.

(3) One of the key objectives of these past assessments of minke whales in Areas IV and V was to estimate the Maximum Sustainable Yield Rate (*MSYR*), whether carrying capacity has changed (and in what way) and whether inter-annual variation in recruitment can be partly explained by environmental covariates. Butterworth and Punt (1999) addressed this issue by fitting the Baleen II model (de la Mare, 1989; Punt, 1999) to the estimates of recruitment from the ADAPT-VPA. While this approach was sufficient to enable estimates of *MSYR*, changes in carrying capacity, etc. to be obtained, Punt and Polacheck (2005) argued that this approach was questionable as it involved fitting a model to the output from another model rather than to raw (or appropriately summarised) data.

SCAA (Fournier and Archibald, 1982) involves developing a population dynamics model and fitting it by maximising an objective function (which under some circumstances can be interpreted as a likelihood function). Two key differences between the original ADAPT-VPA approach (for example, Butterworth *et al.*, 1999) and SCAA analysis are that the latter does not assume that the age-composition data are known exactly (although it often makes fairly strong assumptions regarding age- or length-specific vulnerability and how it changes over time) and can calculate numbers-at-age for years for which catch age-composition data are not available. Punt and Polacheck (2005) noted that this shows that it is possible to estimate numbers-at-age and *MSYR*/carrying capacity simultaneously[5].

The original SCAA method of Punt and Polacheck (2005) allowed for errors in the catch-at-age data, more than a single stock, environmental covariates on recruitment, fleet-specific vulnerabilities, age-specific natural mortality and changes over time in vulnerability. This method included two ways to include the catch-at-age data in the objective function minimised: (a) including the commercial age-composition data (by fleet: Japan/Soviet Union) as information on the age-structure of the commercial catches; and (b) including the age-length keys (available for the catches by Japan only) and the length-frequency information (available for both Japan and the Soviet Union) separately. The latter was preferred by Punt and Polacheck (2005) because it reflects the way the data were collected[6]. The catch data were assumed to be log-normally distributed, but with a CV small enough (0.05) that the model closely mimicked the observed data almost perfectly. The JARPA and IDCR/SOWER estimates of abundance were also assumed to be log-normally distributed. Two types of error associated with the catch-at-age data were considered: age-reading error (readings assumed to be correct on average, but with non-zero random ageing error) and sampling error. The extent of sampling error was related to the number of animals aged (adjusted by an overdispersion factor), but the parameters determining the age-reading error matrix were guesses in the absence of information to parameterise an age-reading error matrix for Antarctic minke whales. The lack of information on age-reading error was addressed following an age-reading experiment conducted under the auspices of the Scientific Committee in 2010 (see below).

The SCAA method of Punt and Polacheck (2005) allowed natural mortality to change in a piecewise linear manner with age and carrying capacity to change in a piecewise linear manner with the year. Vulnerability was allowed to be uniform over all ages (for JARPA)[7], logistic or dome-shaped. Time-dependence in vulnerability was modelled by allowing the length-at-50%-vulnerability to change from one year to the next when vulnerability was assumed to be governed by a logistic curve, i.e. the shape of the vulnerability curve was the same each year, but the length at which vulnerability reached 50% changed over time[8]. Growth was assumed to be governed by a time-invariant von Bertalanffy growth curve.

Punt and Polacheck (2005) noted that there were substantial differences between growth curves estimated within the assessment and those estimated externally to the assessment, which led them to conclude that 'there is clearly some inconsistency between the JARPA length-at-age data and the remaining data sources'. During discussion of this issue at the 2005 meeting of the Scientific Committee, Hatanaka commented that growth rate may have changed over time, as suggested by analyses by Kato (1987). Hatanaka also noted that the commercial catches were closer to the ice edge, which may have influenced relative vulnerability. Polacheck and Punt (2006) extended the SCAA to allow for time-varying growth and found that a large part of the apparent inconsistency between the lengths-at-age for the commercial and JARPA catches could be explained by changes over time in vulnerability and growth. However, Polacheck and Punt (2006) noted that the time-changes in growth and vulnerability may be artefacts because: (a) the model generally estimates that smaller animals were either similarly or more vulnerable during the period of the commercial catches than during JARPA; (b) a large change in growth rates is estimated to have occurred coincidentally with the change from commercial harvesting to JARPA; and (c) residual systematic lack of fit still existed.

The original version of the SCAA (in common with the original ADAPT-VPA analyses) was applied to data for Areas IV and V, treating the populations in those areas as separate

[5]Subsequent development of the ADAPT-VPA approach (e.g. Mori *et al.*, 2007) estimated the stock-recruitment relationship, allowed for age-reading errors, allowed for time-varying proportions of the assessed stock in multiple areas, and considered the possibility of changes over time in the age-at-sexual-maturity.

[6]This is also a preferred way to include age-length key and length-frequency data in many fisheries assessments, particularly when the length-frequency includes sizes for which age data are not available.

[7]This assessment assumed that vulnerability was uniform across all ages; subsequent assessments estimated a specific vulnerability parameter for age 1 owing to poor fits to the abundance of age-1 animals in the JARPA samples when vulnerability was assumed to uniform. Sensitivity was also explored to assuming that the vulnerability for JARPA was logistic or dome-shaped.

[8]The length at maximum vulnerability was assumed to change over time when vulnerability was assumed to be dome-shaped.

stocks. Punt and Polacheck (2005) outlined how multiple stocks which mix could be modelled within the context of a SCAA. Punt and Polacheck (2006) developed a number of scenarios for the minke whales in Antarctic Areas III–E to VI–W in terms of number of stocks (one or two) and whether Area V–W was an area of mixing. Punt and Polacheck (2006) also extended the SCAA to include time-varying proportions of stocks in each spatial stratum considered in the analysis. This allowed the model to mimic the abundance estimates without the need to estimate an 'additional variance' parameter. Estimating an additional variance parameter postulates that the sampling CVs for the abundance estimates are too small so discrepancies between model predictions and data are due to additional error whose cause is not necessarily identified. In contrast, modelling time-varying proportions of the stocks spatially assumes that the sampling CVs are approximately correct, but that the proportion of each stock in each area changes over time. IWC (2007) noted that the SCAA method of Punt and Polacheck (2006) could lead to the number of calves produced approaching or exceeding the available number of sexually mature females. In response to this, later analyses included a penalty term to avoid this behaviour.

Punt and Polacheck (2007) further modified their reference case analysis by fitting the length-frequency and conditional age-at-length data for JARPA separately; previous analyses had fitted to the age-composition data for JARPA, obtained by multiplying the length-frequencies by the age-length keys. The change was made so that it was possible to estimate the extent to which the growth rate had changed over time. They provided the first SCAA-based estimates of $MSYR_{1+}$[9]. However, in common with subsequent attempts to estimate $MSYR_{1+}$, the estimates were sensitive to the assumptions on which the analysis was based, with some estimates of 0% (although those cases often corresponded to poor fits to the data and/or model runs in which it was not possible to obtain a positive definite Hessian matrix).

Some of the results in Punt and Polacheck (2007), such as the estimated rates of natural mortality for age-0 animals, were biologically unrealistic. IWC (2008) therefore recommended that consideration be given to estimating common values for some parameters for the W (Areas III–E, IV, and V–W) and E (Areas V–E and VI–W) stocks[10,11]. This is because by pooling the data across stocks, the estimates of some of these parameters would be less noisy and hence the model fitting process would be less likely to 'chase noise in the data'. Punt and Polacheck (2008) therefore conducted analyses in which some of the parameters of the model (those related to carrying capacity, resilience, growth and natural mortality) were assumed to be the same for the I- and P- stocks. This pooling was clearly supported by model selection methods, and subsequent analyses assumed that the age-specific pattern of natural mortality is the same for the I- and P-stocks, but that the average value for natural mortality differs between stocks. They found the results from the SCAA were sensitive to large (random) age-reading errors. They also tried to evaluate the precision of the estimates from the SCAA by applying a Markov chain Monte Carlo (MCMC) method to sample parameter vectors from the posterior distribution, but this algorithm failed to converge. In addition, they conducted some preliminary simulation tests.

IWC (2009) noted that the SCAA indicated that the JARPA abundance estimates were uninformative, particularly with respect to the variance associated with mortality rate estimates. It was suggested that the general lack of sensitivity to ignoring the JARPA abundance estimates may be due to some structural constraints of the model (i.e. the stock-recruitment relationship and/or the vulnerability functions). As such, within the then-current model structure, the JARPA abundance estimates might provide little additional information. IWC (2009) recommended that this be explored further. Punt (2009a) conducted additional sensitivity tests using the same reference model as Punt and Polacheck (2008). It was found that while the results were insensitive to ignoring the JARPA indices, the results were sensitive to ignoring the JARPA length-frequency and conditional age-at-length data. The issue of which data sources are informative regarding which model outputs remains a topic for analysis (see below).

IWC (2009) agreed that resolution of questions concerning ageing of Antarctic minke whales was the highest priority task for the catch-at-age modelling work at that time and proposed a workplan to address the issue. Punt (2009b) used simulations to assess the implications of different levels of ageing bias on the performance of the SCAA method of Punt and Polacheck (2008). Simulations based on deterministic data suggested that a 20% under-estimate of age in 1970 which changes linearly to zero in 1986 would lead to estimated time trajectories of historical increases in carrying capacity which match those from actual applications of the SCAA method when the true carrying capacity is time-invariant. Allowing for observation error made the results more variable. IWC (2010) noted that these results highlighted the need for 'appropriate' error models for use in the modelling.

An experiment to evaluate age-reading error was conducted during 2010 (Lockyer, 2010). This involved an experienced age-reader (Lockyer) reading 250 earplugs which were collected between 1974/75 and 2005/06 and using the resulting age-estimates to obtain estimates of ageing bias and random age-reading error for three of the readers who read earplugs during the period of commercial whaling as well as during JARPA[12]. This experiment essentially confirmed that the commercial ageing data were reliable (IWC, 2011). Kitakado and Punt (2010) applied the methods of Punt *et al.* (2008) to results from the experiment to develop age-reading error matrices for use in the SCAA. Punt (2010) included the new ageing error matrices in the SCAA, but there was evidence for non-convergence of the minimisation algorithm.

After exploring the reasons for the lack of convergence in Punt (2010), the SCAA was modified (Punt, 2011) by changing the mathematical form of the penalty that prevents

[9]The ratio of MSY to the number of animals aged 1+ and over when exploitation is uniform over ages 1 and older.
[10]See IWC (2007) for the rationale for this option for stocks.
[11]Thereafter referred to as the 'I' (Indian) and 'P' (Pacific) stocks.

[12]The analyses have subsequently been updated to include a fourth age-reader (Kitakado *et al.*, 2013).

the number of calves exceeding the number of mature animals and by assuming that the age-specific pattern of natural mortality is independent of stock (but the average value for natural mortality differs between stocks). The attempt to fit the length-composition data was dropped for the Soviet Union catches, given the information on possible misreporting of catch length distributions by the fleet (IWC, 2011). Rather than estimate vulnerability patterns for the Soviet Union fleet, the vulnerability patterns for the Soviet Union were assumed to be the same as those for Japan. Punt (2011) also explored whether the SCAA, along with its estimated vulnerability patterns, could account satisfactorily for the different length-at-age distributions for younger animals using diagnostics statistics from the r4ss package (Taylor *et al.*, 2014), and found the fits to be adequate.

Punt *et al.* (2013) provided revised SCAA results based on the recommendations from the 2012 Committee meeting (IWC, 2013). This version differs from the 2012 (and 2011) versions of the SCAA in terms of the assumed extent of over-dispersion, as well as the value of the assumed variance of the parameters that defines the proportion of stock, by area and year. It also used revised age-reading error matrices developed by Kitakado *et al.* (2013).

Punt (2014) provides the most recent version of the SCAA based on the recommendations from the 2013 Scientific Committee meeting (IWC, 2014). This assessment is based on the data in Table 2. Rather than forcing the changes in carrying capacity to follow a piecewise linear function, Punt (2014) modelled changes in carrying capacity as an autoregressive function of time and changed the ages at which natural mortality changes using the results of an analysis in which natural mortality was allowed to be an autoregressive function of age. Punt (2014) also revised the approach used to weight data sources by basing the weights for the length-frequency and conditional age-at-length data on the method of Francis (2011) rather than that of McAllister and Ianelli (1997) which will overweigh composition data when the residuals are not independent of year and age. The plus and minus groups for length and age were revised in Punt (2014).

REFERENCE ANALYSES AND SENSITIVITY TESTS

Table 3 lists the specifications for the reference case analyses and Table 4 lists the specifications of all of the sensitivity tests conducted since 2005. It is noteworthy that the early analyses included more sensitivity tests related to the shape of the vulnerability functions. However, recent assessments have not considered many sensitivity tests along these lines, perhaps because the assessment now includes a fairly complicated model for vulnerability, and the length data for the Soviet Union have been removed from the assessment (Table 1). Thus, the current reference case analysis includes many of the options considered as more complex variants of the earlier reference cases (such as that the JARPA selectivity function is a logistic function of length) as part of the reference case analysis.

SUMMARY AND GENERAL CONCLUSIONS

A variety of diagnostic statistics and plots have been developed to evaluate model fit. In general, the model has been able to mimic the estimates of absolute and relative abundance given the estimated changes in abundance, as well as inter-annual variation in the proportion of each stock in each area (for example, figs 5 and 6 of Punt, 2014). The confidence intervals for the abundance estimates have generally intersected the population trajectory, indicating that the extent of process error in the proportion of each stock in each area is sufficient to capture additional variance. The model has also been able to fit the length-frequency and conditional age-at-length data adequately (Punt *et al.*, 2013). One key reason for being able to fit the conditional age-at-length data is time-varying growth. The reasonableness of the inferred changes in growth rate was, however, questioned during the 2013 Annual Meeting of the Scientific Committee (IWC, 2014).

Virtually all of the applications of the SCAA have indicated that recruitment increased substantially between 1930 and 1960–70 and declined thereafter (Fig. 4). The estimated changes in recruitment mimic those inferred from carrying capacity, which is robustly estimated to have increased from 1930 and then declined (Fig. 4). However, the extent of increase and decline in carrying capacity is sensitive to the assumptions of the analysis (see Table 5 for a recent summary of the conclusions from the SCAA).

Natural mortality is estimated to increase with age after about age 30 (Fig. 4). The most recent applications of the SCAA have inferred that natural mortality for younger animals is higher than for older animals, but this has not always been an outcome of the SCAA (e.g. Punt and Polacheck, 2005).

The assumption that vulnerability was constant during the period of commercial harvesting is rejected based on the quality of the fit to the data. Similarly, the earlier SCAA

Table 2

Summary of the data used in the most recent applications of SCAA to data for Southern Hemisphere minke whales in Antarctic Areas III–E, IV, V–W, V–E and VI–W. The range of years denotes the years over which the data concerned are available. In general, the data types concerned are not available for all years in the range.

	Region				
	Area III–E	Area IV	Area V–W	Area V–E	Area VI–W
Catches	1953/54–2009/10	1955/56–2009/90	1955/56–2011/12	1955/56–2011/12	1953/54–2011/12
Length-frequency	1971/72–2009/10	1971/72–2009/10	1974/75–2011/12	1977/78–2011/12	1973/74–2011/12
Age-length keys	1971/72–2009/10	1971/72–2009/10	1974/75–2011/12	1977/78–2011/12	1973/74–2011/12
IDCR estimates	1987/88–1994/95	1988/89–1998/99	1985/86–2001/02	1985/86–2003/04	1990/91–1995/96
JARPA/JARPA II indices	1995/96–2007/08	1989/90–2007/08	1990/91–2008/09	1990/91–2008/09	1996/97–2008/09

Table 3
Summary of the specifications of the reference case SCAAs.

Feature	Assessment year						
	2005 Punt and Polacheck (2005)	2006 Punt and Polacheck (2006)	2007 Punt and Polacheck (2007)	2008/09 Punt and Polacheck (2008); Punt (2009)	2011/12 Punt *et al.* (2012)	2013 Punt *et al.* (2013)	2014 Punt *et al*. (2011)
Population dynamics assumptions							
Spatial strata	IV, V	III–E – VI–W	III–E – VI–W	III–E – VI–W	III–E – VI–W	III–E – VI–W	III–E – VI–W
Ages natural mortality changes	3, 10, 30, 35	3, 10, 30, 35	3, 10, 30, 35	3, 10, 30, 35	3, 10, 30, 35	3, 10, 30, 35	3, 10, 20, 40
Years carrying capacity changes	1960, 1980	1960, 1980	1960, 1980	1960, 1980	1960, 1980	1960, 1980	Autoregressive (σ_K=0.05)
Vulnerability							
JARPA	Uniform	Uniform	Uniform	Logistic	Logistic	Logistic	Logistic
Japan commercial catches	Logistic-length	Logistic-length	Logistic-length	Domed-length[1]	Domed-length[1]	Domed-length[1]	Domed-length[1]
Soviet commercial catches	Logistic-length	Logistic-length	Logistic-length	Domed-length[1]	As for Japan	As for Japan	As for Japan
Age-1 selectivity estimates	No	Yes	Yes	Yes	Yes	Yes	Yes
Likelihood function assumptions							
Plus-group for age data	45	45	45	45	45	45	45
Commercial length data minus and plus lengths	22ft, 32ft (F) 22ft, 31ft (M)	22ft, 32ft (F) 22ft, 31ft (M)	22ft, 32ft (F) 22ft, 31ft (M)	22ft, 32ft (F) 22ft, 31ft (M)	22ft, 32ft (F) 22ft, 31ft (M)	22ft, 32ft (F) 22ft, 31ft (M)	25ft, 32ft (F) 22ft, 31ft (M)
JARPA length data minus and plus lengths	N/A	N/A	17ft, 32ft (F) 17ft, 31ft (M)	17ft, 32ft (F) 17ft, 31ft (M)	17ft, 32ft (F) 17ft, 31ft (M)	17ft, 32ft (F) 17ft, 31ft (M)	25ft, 32ft (F) 17ft, 31ft (M)
Survey abundance indices							
IDCR/SOWER bias	None	None	None	None	None	None	None
JARPA bias	Estimated	Estimated	Estimated	Estimated	Estimated	Estimated	Estimate
Additional variance	No	No	No	No	No	No	No
Age-reading error							
Bias	0	0	0	0	From Kitakado and Punt (2010)	From Kitakado *et al*. (2013)	From Kitakado *et al*. (2013)
Standard error	0.1	0.1	0.1	0.1			
Overdispersion parameters							
JARPA age data	0.5	0.65	N/A	N/A	N/A	N/A	N/A
Length data[2]	0.65	0.8	0.65	0.65	0.65	0.7	1 commercial 0.15 JARPA
Conditional age-at-length data	0.75	0.75	0.8	0.8	0.8	0.8	0.5 commercial 1 JARPA
Extent of variation in births, σ_e	0.2	0.2	0.2	0.2	0.2	0.2	0.3
Extent of variation in vulnerability, σ_s	10	10	10	10	10	10	10
Extent of variation in the proportion of the population by area, σ_P	N/A	0.2	0.2	0.2	0.2	0.3	0.3
Extent of variation in growth rate, σ_k	N/A	0	0.1	0.1	0.1	0.1	0.02

[1]The length at which vulnerability is 50% is time-varying for logistic selectivity. [2]Commercial only before 2008; commercial and JARPA thereafter.

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Table 4a

Summary of the sensitivity tests conducted. 'RC' indicates that the factor concerned was part of the reference case analysis. The symbols used relate to those used in the actual assessments. For example '2,8,27,28' on the line 'Logistic for JARPA/JARPA II' means that sensitivity tests 2, 8, 27 and 28 in Punt and Polacheck (2005) made the assumption that selectivity for JARPA/JARPA II was logistic.

	Assessment year					
Factor	2005 Punt and Polacheck (2005)	2006 Punt and Polacheck (2006)	2007 Punt and Polacheck (2007)	2009 Punt (2009)	2013 Punt *et al.* (2009)	2014 Punt *et al.* (2011)
(a) Sensitivity tests related to the population dynamics model						
Length-specific vulnerability	–	–	–	–	–	–
Uniform for JARPA/JARPA II	RC	RC	RC	–	S3, S4	B1, B2
Logistic for JARPA/JARPA II	2,8, 27, 28	4	B[1]	RC	RC	RC
Dome-shaped for JARPA/JARPA II	3, 21, 23	–	C,D[1]	–	–	–
Separate logistic selectivity for JARPA and JARPA II	–	–	–	–	S10	B7
Time-varying logistic for JARPA	–	–	–	Yes	–	–
Logistic for Japan commercial catches	RC	RC	RC	–	–	–
Dome-shaped for Japan commercial catches	27,28	5	D	RC	RC	B8
Logistic for Soviet Union commercial catches	RC	RC	RC	–	–	–
Dome-shaped for Soviet Union commercial catches	27,28	5	D	RC	–	–
Extent to which selectivity is time-varying	17	–	–	–	D3, D4	B6, C1, C2
Time-varying logistic between 1988 and 1999	23	–	–	–	–	–
Age-specific vulnerability						
Uniform for JARPA/JARPA II	13	1	A	–	–	–
Logistic for JARPA/JARPA II	14	–	B[1]	–	S1	–
Dome-shaped for JARPA/JARPA II	25	–	C,D[1]	–	–	–
Logistic for Japan commercial catches	13,14,15.24	1	A	–	–	–
Dome-shaped for Japan commercial catches	25	–	B,C,D	–	S1	–
Logistic for Soviet Union commercial catches	13.14,15,24	1	A	–	–	–
Dome-shaped for Soviet Union commercial catches	25	–	B,C,D	–	–	–
Carrying capacity						
Changes piecewise	RC	–	–	–	–	–
Changes in 1960 and 1980; 1960, 1980 and 2002	29, 30	–	–	–	P7	–
Constant carrying capacity	4,8, 23, 24	–	–	–	P5, S4	A5, B1
Carrying capacity as auto-regressive function of time	5	–	–	–	P6	RC
Extent of variation in changes in carrying capacity		–	–	–	–	C3, C4
Growth curve (estimated within the assessment unless specified otherwise)						
Time-invariant von Bertalanffy with constant variance in LAA	BC	6	–	–	P3	A4
Flat topped time-invariant von Bertalanffy[2]	9	–	–	–	–	–
Growth parameters set based on auxiliary information	16, 21, 28	–	–	–	–	–
Constant CV for LAA	17	–	–	–	–	–
Extent of time-varying growth	–	–	–	–	D9, D10	C7, C8
Other						
Density-dependent natural mortality	–	–	Yes	–	–	–
Alternative density-dependence function	–	–	–	–	P1	–
Siler natural mortality	–	–	–	–	–	A1
Autoregressive natural mortality	–	–	–	–	–	A2
Natural mortality is the same for all stocks	–	–	–	–	P4	–

[1]Analyses were conducted with the length/age at modal selection pre-specified instead of being estimated. [2]Length assumed to be constant from age-20. [3]The random deviation about the stock-recruitment relationship is applied to the density-dependent component rather than to the expected number of calves.

analyses consistently found that the vulnerability pattern for the Japanese and Soviet Union commercial fleets were dome-shaped. However, the length data for the Soviet Union are no longer included in the analysis owing to concerns regarding misreporting of catches. The vulnerability pattern for JARPA was initially assumed to be uniform with respect to length or age, but model selection suggested that vulnerability increases with age/length at low values of these quantities, which has led to vulnerability for JARPA (and JARPA II) being assumed to be a logistic function of age/length, consistent with general understanding that the youngest minke whales do not all migrate to the Antarctic in the austral summer.

The results from the SCAA have consistently been found to be insensitive to the weights assigned to the data sources and even when the abundance indices from JARPA/JARPAII are ignored, although why this latter results occurs is the subject of ongoing research because *a priori* the results of the SCAA would be expected to depend on the use of these JARPA/JARPA II data. Punt (2014) found that changing the JAPRA/JARPAII indices so they exhibited a trend changed the results from the SCAA and concluded that the reason that the results of the SCAA are insensitive to ignoring the actual JARPA/JARPAII indices is because these indices are consistent with the other data included in the assessment.

Although the sensitivity of the results from the SCAA to changes to its assumptions has been explored thoroughly (Table 3), the ability to quantify 'estimation error' has remained somewhat elusive. Recent assessments have reported asymptotic variance estimates for key model outputs such as natural mortality as a function of age, as well as for the time-trajectories of 1+ abundance and recruitment (Fig. 4). However, attempts to use MCMC methods or bootstrapping to quantify estimation uncertainty have been

Table 4b

Factor	Assessment year						
	2005 Punt and Polacheck (2005)	2006 Punt and Polacheck (2006)	2008 Punt and Polacheck (2008)	2009 Punt (2009)	2011 Punt (2011)	2013 Punt *et al.* (2013)	2014 Punt *et al.* (2011)
(b) Sensitivity tests related to the likelihood function and data weighting							
JARPA/JARPA II abundance indices	–	–	–	–	–	–	–
JARPA/JARPA II indices ignored	12, 30	–	Yes	Yes	–	S7	Fig. 11
JARPA II indices ignored	–	–	–	–	–	D1	Fig. 11
Indices relate to 1+ abundance[1]	–	–	–	–	–	P8	–
JARPA/JARPA II indices are absolute	–	–	–	–	–	–	B3
IDCR/SOWER abundance indices	–	–	–	–	–	–	–
Not unbiased	10,11	–	Yes	–	–	S5, S6	B4, B5
Composition data	–	–	–	–	–	–	–
Robust likelihood for proportions[2]	6	–	–	–	–	–	–
Ignore JARPA age data	–	–	–	Yes	–	–	–
Ignore JARPA length data	–	–	–	Yes	–	–	–
Downweight early commercial LF data	7	–	–	–	–	S2	C17
No ageing error	26	–	–	–	–	D2	A6
Linear trends in bias	–	–	Yes	–	–	–	–
High rate of age-reading error	–	–	Yes	–	–	–	–
Bias and random error in age-reading	–	–	–	–	Yes	–	–
Ignore JARPA II composition data	–	–	–	–	–	D1	Fig. 11
Weight on the length-composition data	–	–	–	–	–	D11, D12	C11, C12, C15
Weight on the conditional age-at-length data	–	–	–	–	–	D13, D14	C13, C14, C15
Change length cut-off	–	–	–	–	–	–	C16
Spatial variation in the population distribution							
None	RC	–	–	–	–	P2	A3
Extent of variation in distribution	–	2, 3	–	–	–	D7, D8	C5, C6
Recruitment	–	–	–	–	–	–	–
Extent of temporal variation in recruitment changed	19,20	–	–	–	–	D5, D6	C9, C10

[1]And vulnerability is flat for ages 1+. [2]See Fournier *et al.* (1990) for details.

unsuccessful. This is partially attributable to the complexity of the model (>1,000 parameters, many of which relate to exploitation rates).

Overall, the SCAA has progressed to the point at which most, but not all, of the key issues have been addressed (Table 1). The application of SCAA to Antarctic minke whales is now as sophisticated (or more sophisticated) than applications of this general modelling framework for fisheries management (e.g. Methot and Wetzell, 2013). IWC (2014) evaluated the status of the SCAA (based on the results in Punt *et al.*, 2013). This evaluation highlighted that several of the outcomes of the SCAA were consistent and robust to changes to the assumptions of the analysis (such as that the populations increased prior to 1970 and declined thereafter). It also highlighted that estimates of MSYR were not robust to such changes. This is likely a result of lack of contrast in population size relative to carrying capacity (Punt, 2014). It is, however, not uncommon that estimation of the shape of the stock-recruitment relationship and hence MSYR is poor even when data on stock and recruitment are available which cover a range of levels of relative stock size (Conn *et al.*, 2010; Lee *et al.*, 2012). In addition, the CVs for the estimates of natural mortality seemed very low and that the estimated growth curves may not be reliable.

The amount of data available for Southern Hemisphere minke whales is amongst the most for any marine species. The assessments conducted of this species have been able to estimate trends and absolute population size but it remains impossible to estimate MSYR with much precision. The next steps in this work remain to better understand stock structure for Antarctic minke whales (and hence whether boundaries for the I and W stocks are indeed at the western ends of Areas III–E and IV–W and to allow for mixing of the I and W stocks perhaps using the results from analyses of genetic and non-genetic data (e.g. Kitakado *et al.*, 2014) as priors for the associated mixing parameters.

The assessments developed for Southern Hemisphere minke whales have advanced approaches for conducting stock assessments for marine species in several ways. In particular, the assessments were amongst the first to include multiple stocks within the same model to allow the values of parameters (such as those which determine how natural mortality changes with age) to be shared amongst stocks to improve precision, to include age-composition data in form of conditional age-at-length so that growth can be estimated within the assessment rather than being pre-specified, and to allow for age-reading error to differ among readers. The approaches used to evaluate whether the model is fitting the conditional age-at-length data are now routinely used for fish stock assessment through the most recent versions of r4ss package[13]. All of these features are now being included in assessments of data-rich fish stocks and could be included in assessments of whale stocks for which sufficient data are available.

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[13]See *https://github.com/r4ss/*.

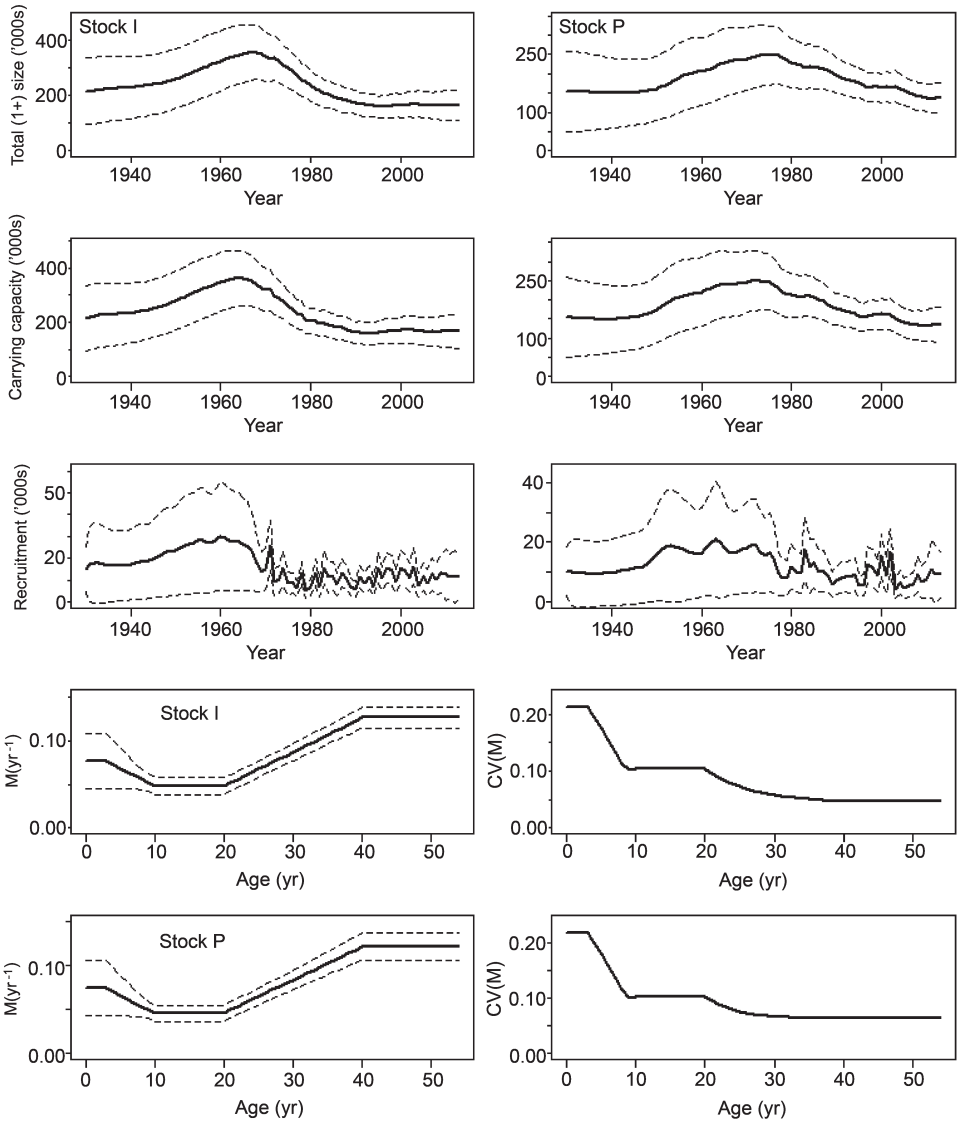

Fig. 4. Time-trajectories of total (1+) population size, carrying capacity, and recruitment (from 1930 and from 1975), and age-specific natural mortality by stock (estimates and CVs) for the reference case analysis of Punt *et al*. (2014). The dotted lines indicate 95% asymptotic confidence interval

Table 5

Reliability of conclusions from the SCAA as recorded in IWC (2014).

Model output	Conclusion
Historical trends in abundance	Relative trends generally consistent – modelled through changes in carrying capacity over about four decades, with abundance peaking in around 1970. The early and peak abundances are not quantitatively reliable. Recent abundance fitted to CPII and CPIII estimates
Extent of change from CPII to CPIII	Trends in abundance over the most recent 20 years are relatively flat. Differences can be explained as variability in distribution.
MSYR	Not robust.
M (natural mortality)	Weakly different by stock. CVs unrealistically low. Further investigation recommended.
Growth curves	Not reliable – a proxy for some unmodelled source of variation.
Stock identity	An input; variable spatial distribution used to account for variability in abundance estimates. Further exploration needed.
Errors in age-determination	Important to take into account.
JARPA/JARPA II abundance estimates	Biased low.
JARPA/JARPA II selectivity	Younger animals under-represented.

this review (even if it was a good thing to do in retrospect). He is, however, thanked for comments on an earlier version of this document as are Doug Butterworth, Greg Donovan, and to Toshihide Kitakado and Daniel Howell for providing reviews.

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Assessment of Antarctic minke whales using statistical catch-at-age analysis (SCAA)

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ABSTRACT

Statistical catch-at-age analysis (SCAA) is applied to data for Antarctic minke whales. The SCAA model is spatially-structured, can model multiple stocks of minke whales, and can utilise several data types for parameter estimation. The application to Antarctic minke whales considers two stocks (I and P) in five areas which cover Antarctic Areas III–E to VI–W. The parameters of the model (annual deviations about the stock-recruitment relationship, changes over time in carrying capacity, density-dependence parameters related to productivity and carrying capacity, and the parameters which determine growth by stock, age-specific natural mortality by stock, and vulnerability by area and 'fleet') are estimated by fitting the model to data on catches, catch-at-length, conditional age-at-length, and estimates of absolute and relative abundance. A reference case analysis is selected, and sensitivity explored using retrospective analyses and by varying the assumptions on which the reference case analysis is based. The reference case analysis is able to mimic all of the data sources adequately. Most of the analyses (reference and sensitivity) indicates that Antarctic minke whales in the assessed area increased from 1930 until the mid-1970s and have declined thereafter, with the extent of the decline greater for minke whales in Antarctic Areas III–E to V–W than for those further east. Natural mortality is consistently estimated to be higher for younger and older individuals than for individuals of intermediate age. Estimates of $MSYR_{1+}$ (the exploitation rate on animals 1 and older at which sustainable yield is maximised) are presented, but are unreliable owing to the lack of contrast.

KEYWORDS: CATCH-AT-AGE, ANTARCTIC MINKE WHALE, POPULATION MODEL; SOUTHERN HEMISPHERE; SURVEY-VESSEL; MODELLING; MSY RATE; ANTARCTIC; MORTALITY RATE; SCIENTIFIC PERMITS

INTRODUCTION

One of the fundamental tasks of the Scientific Committee of the International Whaling Commission (IWC) is to conduct 'assessments' to determine the status (e.g. relative to carrying capacity), trends and productivity of whale populations. Most of these assessments are based on fitting population dynamics models to estimates of absolute and relative abundance from surveys (e.g. Johnston *et al.*, 2011; Müller, 2011; Punt and Polacheck, 2006). In contrast, best practice for fishery assessments, which are conducted for largely the same purposes as IWC assessments, involve fitting population models to catch-at-age (CAA) and length-frequency data as well as to abundance indices (Maunder and Punt, 2013). Southern Hemisphere minke whales (*Balaenoptera bonaerensis*) are unique among cetacean stocks in that there is a long history and CAA and length frequency data have been collected.

In the early 1980s, the Scientific Committee's recommendations on catch limits for these minke whales followed from the Committee's acceptance that Antarctic minke whale numbers had been increasing prior their exploitation to any substantial extent. Amongst the evidence taken to point towards these conclusions, until these came under question in 1983 (IWC, 1984), were estimates of the slope of the descending limb of minke whale catch curves (Oshumi, 1979). Concern was expressed regarding assessments of minke whales based on CAA data (e.g. Sakuramoto and Tanaka, 1985; 1986) given difficulties estimating natural mortality and in particular how natural mortality changes with age (e.g. Chapman, 1983; Cooke, 1985; de la Mare, 1985a; 1985b), because trends in population size for minke whales are sensitive to the value for natural mortality (Butterworth *et al.*, 1999). The 'Japanese Whale Research Programme under Special Permit in the Antarctic' (or JARPA) stated that its primary objective was to estimate the age-specific natural mortality coefficient for minke whales in response to this situation (Government of Japan, 1987), although this was later changed to estimation of average (over age) natural mortality (Government of Japan, 1992).

Two classes of stock assessment method have recently been proposed for application to Antarctic minke whales (see Punt (2014) for a summary of recent applications of age-structured assessment models to Antarctic minke whales). One of these (ADAPT-VPA; Butterworth *et al.*, 2002; Butterworth *et al.*, 1999; Butterworth *et al.*, 1996) is based on the assumption that the CAA data are measured with limited error compared to the indices of abundance used to estimate the values for the parameters of the model. The other is Statistical catch-at-age Analysis (SCAA; Punt, 2011; Punt, 2014; Punt *et al.*, 2013; Punt and Polacheck, 2005; 2006; Punt and Polacheck, 2007; 2008). In contrast to ADAPT-VPA, SCAA does not assume that the age-structure of the catches is measured with limited error, and can account for both sampling error and age-reading error[4]. The specific SCAA model developed for Antarctic minke whales can account for multiple stocks in the assessed area, time-varying growth, multiple areas, fleet-specific vulnerabilities,

[4]Age-reading error has been quantified for Antarctic minke whales by Kitakado *et al*. (2013).

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changes over time in the proportion of each stock in each area and changes over time in vulnerability.

The range of issues which have motivated the analyses using these methods has increased over time in response to the needs and priorities of the Scientific Committee and the Commission. One specific issue was understanding the cause for the decline in estimates of abundance for minke whales from the 2nd to the 3rd circumpolar surveys of minke whales conducted as part of the International Decade of Cetacean Research (IDCR)/Southern Ocean Whale and Ecosystem Research (SOWER) programmes. Butterworth and Punt (1999) identified several hypotheses for a decline in minke whale recruitment including 'super-compensation', increased competition from other krill predators, poorer environmental conditions and bias in the estimation method. (IWC, 2002; 2003) identified further hypotheses which could address the reasons for the decline. IWC (2005) noted that population modelling could provide a way to address the plausibility of the hypothesis that the decline in recruitment is related to competition and other population dynamic-related factors. It considered that a SCAA modelling approach would provide the most appropriate modelling framework to address the population dynamics-related issue because a SCAA could allow *inter alia* for errors in CAA data, more than a single stock, environmental covariates, fleet-specific vulnerabilities (IWC, 2005)[5] and changes over time in vulnerabilities to be addressed and explored within a single model framework.

SCAA (Fournier and Archibald, 1982) involves developing a population dynamics model and fitting it by maximising an objective function (which under some circumstances can be interpreted as a likelihood function). Two key differences between original ADAPT-VPA approach of, for example, Butterworth *et al.* (1999) and SCAA analysis are that the latter does not assume that the age-composition data are known exactly (although it often makes fairly strong assumptions regarding age- (or length-) specific vulnerability and how it changes over time) and can calculate numbers-at-age for years for which catch age-composition data are not available.

The reference case model considers five areas (Antarctic Areas III–E, IV, V–W, V–E, and VI–W), selected primarily because of the availability of data. The hypothesis on stock structure used in this study is that there are two stocks: the I (Indian) stock – assumed to be found in Areas III–E, IV, and V–W, and the P (Pacific) stock – assumed to be found in Areas V–E and VI–W. The hypothesis of at least two stocks is based on the genetic (mtDNA and microsatellite) and non-genetic (morphometric, biological parameters) analyses based on JARPA data (IWC, 2008; Pastene, 2006) and has been corroborated by the genetic analysis of JARPA II data (Pastene *et al.*, 2014). The specific stock structure hypothesis follows from the assumption that the core of each stock is the western (Area III–E and IV–W) and eastern (Area V–E and VI–W) parts of the area surveyed by JARPA/JARPA II. These stocks could be related to breeding areas in lower latitude waters off the eastern Indian Ocean and western South Pacific where high sighting densities have been reported in October (Kasamatsu *et al.*, 1995).

This paper applies SCAA to data for the Antarctic minke whales in Management Areas III–E, IV, V, and VI–W. It first outlines the mathematical specifications for the model and its associated estimation scheme. The paper then provides specifications for a 'reference' case analysis which uses all of the available index, catch length-composition and conditional age-at-length data. Full results for this reference case are provided based on suggestions for model outputs and fit diagnostics by the Scientific Committee. A series of sensitivity tests are outlined which examine the sensitivity of the results to the assumptions of the model, including that carrying capacity may have changed over time, and the weights assigned to each of the many data sources and penalties.

MATERIALS AND METHODS

Mathematical specifications for the population model and likelihood function

The population dynamics model (Appendix A) considers multiple stocks, and represents each stock using an age- and sex-structured population dynamics model. The model includes 15 'fleets' consisting of three whaling types (Japan before 1987/88, Japan from 1987/88, and ex-Soviet Union) in each of the five areas considered in the model. Two Japanese whaling types are considered so that the data for commercial and Scientific Permit catches can be treated separately. Each 'fleet' can have a different length-specific vulnerability pattern (the combined effects of harvest selectivity and availability), which may change over time. Similarly growth, which depends on stock and sex, can change over time. Appendix B outlines the negative of the log-likelihood function which is minimised to find the best estimates for the parameters.

Data utilised

The data used when conducting assessments of the Antarctic minke whales consist of catches, abundance estimates, length frequency data, and conditional age-at-length data. The data include the catches and sighting survey information from the 2011/12 austral summer season.

Catches and length-frequency data

Catches are available by fleet and sex for two nations (Japan and ex-Soviet Union) and five Management Areas (III–E, IV, V–W, V–E, and VI–W). The catches prior to 1971/72 are not allocated to fleet because these catches were taken by several nations. There is no information on the length-frequency of these catches so the vulnerability patterns for the years prior to 1971/72 are assumed to be equal to that for in 1971/72, and the pre-1971/72 catches for Area V are split equally between Areas V–W and V–E. The results are unlikely to be sensitive to these assumptions given the small magnitude of the catches concerned.

Age-composition data

Age-composition data and hence conditional age-at-length data are only available for the Japanese catches. Earplugs from both sides of the whale were collected on the vessel and preserved in a 10% formalin solution. At the laboratory,

[5]Often also referred to as 'selectivities' by the Scientific Committee. Vulnerability combines the effect of age- (or length)-specific selectivity by the whalers with the relative probability of whalers encountering a whale of a given age or length given the spatial and temporal distribution of the whaling effort.

the plug surfaces were cut longitudinally to the centre, and the age of each whale determined by counting the growth layers using a stereoscopic microscope. One growth layer was assumed to be deposited each year (i.e. one pair of dark and pale laminae per year) based on Best (1982) and Lockyer (1984). Age-reading was conducted without knowledge of biological information. Four scientists participated in the reading of earplugs. Ages from whales captured in the period 1971/72–1979/80 (commercial whaling) were determined by reader-M (Y. Masaki). Ages from whales captured in the period 1980/81–1989/90 (commercial whaling and JARPA), and 1992/93 (JARPA) were determined by reader-K (H. Kato). Reader-Z (R. Zenitani) conducted age readings for whales captured in the period 1990/91–1991/92 and 1993/94–2004/05 (JARPA) and reader-B (T. Bando) conducted age readings for whales captured in the period 2005/06–2011/12 (JARPA II).

Indices of abundance

Table 1 lists the estimates of absolute abundance from the IDCR program (Okamura and Kitakado, 2012) and the indices of abundance based on the JARPA/JARPA II programme. The latter indices are corrected for $g(0)$. However, there may be biases which are not fully accounted for so the JARPA/JARPA II estimates of abundance are treated as indices, except for one sensitivity test where they are treated as estimates of absolute abundance.

The methods used for the abundance estimation for the JARPA/JARPA II surveys are outlined by Hakamada *et al.* (2013). The estimates of abundance and their coefficients of variation were estimated by stratum and survey mode (closing and passing) (Haw, 1991), using the 'standard methodology' of Branch and Butterworth (2001). The Okamura and Kitakado (2012) and Bravington and Hedley (2012) approaches for estimating minke whale abundance using IDCR/SOWER data resulted in estimates of $g(0)$ which were less than 1, especially for schools of size 1. However, these approaches cannot be applied directly to the sightings data from JARPA/JARPA II. Consequently $g(0)$ for these surveys is based on a regression model which provides relationship between $g(0)$ and mean school size by stratum (Hakamada *et al.*, 2013). AIC was used to choose amongst log-linear models for the effects of survey mode and survey timing. Weighted averages of abundance estimates over survey modes were calculated, where the weights were chosen to minimise the associated variances. The nominal abundance estimates needed to be adjusted using factors estimated from the model selected before the weighted average was taken.

Table 1a

The estimates of abundance (with CVs in parenthesis) – IDCR estimates.

Year	Estimate	Year	Estimate
Area III–E		**Area IV**	
1987/88	11,782 (0.440)	1988/89	46,763 (0.169)
1994/95	34,659 (0.237)	1998/99	55,873 (0.341)
Area V–W		**Area V–E**	
1985/86	105,951 (0.159)	1985/86	154,658 (0.189)
2001/02	43,640 (0.139)	2003/04	136,457 (0.134)
Area VI–W			
1990/91	20,438 (0.271)		
1995/96	48,206 (0.177)		

The reference case analysis

The reference case analysis ignores the length-frequency data for the ex-Soviet Union fleet because of concerns regarding the reliability of these data (there are no age-composition data for this fleet) and vulnerability for the ex-Soviet Union and the Japanese fleet are assumed to be the same. This latter assumption was made given information on

Table 1b

The estimates of abundance (with CVs in parenthesis) – JARPA/JARPA II indices of relative abundance.

Year	Estimate	Year	Estimate	Year	Estimate
Area III–E		**Area IV**		**Area V–W**	
1995/96	7,305 (0.655)	1989/90	50,736 (0.323)	1990/91	91,870 (0.305)
1997/98	4,362 (0.792)	1991/92	55,878 (0.448)	1992/93	61,918 (0.288)
1999/00	10,311 (0.975)	1993/94	44,286 (0.271)	1994/95	31,972 (0.385)
2001/02	53,619 (0.811)	1995/96	48,751 (0.371)	1996/97	41,475 (0.409)
2003/04	19,402 (0.717)	1997/98*	30,637 (0.331)	1998/99	133,867 (0.620)
2005/06	42,535 (0.440)	1999/00	87,345 (0.294)	2000/01	43,038 (0.885)
2007/08	10,952 (0.319)	2001/02	91,811 (0.289)	2002/03	122,469 (0.394)
		2003/04	53,434 (0.374)	2004/05	34,026 (0.411)
		2005/06	46,628 (0.464)	2005/06	119,437 (0.510)
		2007/08	40,243 (0.331)	2006/07	98,346 (0.409)
				2007/08	85,943 (0.478)
				2008/09	143,255 (0.450)
Area V–E		**Area VI–W**			
1990/91	132,914 (0.583)	1996/97	26,703 (0.682)		
1992/93	63,837 (0.371)	1998/99	39,866 (0.220)		
1994/95	152,534 (0.395)	2000/01	48,532 (0.640)		
1996/97	231,597 (0.500)	2002/03	25,483 (0.713)		
1998/99	67,442 (0.355)	2004/05	42,453 (0.605)		
2000/01	160,411 (0.311)	2006/07	36,540 (0.756)		
2002/03	65,040 (0.300)	2008/09	40,565 (0.271)		
2004/05	99,155 (0.235)				
2006/07	16,384 (0.379)				
2008/09	58,483 (0.468)				

*Survey covered only a small part of Prydz Bay.

possible misreporting of catch length distributions by the ex-Soviet Union (IWC, 2011). Vulnerability for the Japanese fleets (before 1987/88) is assumed to be a time-varying double-normal function of length in which a separate length-at-50%-vulnerability is estimated for each year (see Equation App.A.D.4c), while vulnerability for the JARPA/JARPA II fleet is assumed to be a logistic function of length and to be constant over space.

The other specifications of the reference case are:

(1) an age-specific availability factor, $\tilde{S}_a$, is estimated for age 1 (see Equation App.A.D.2);

(2) values for the change in growth rate ($\kappa_y^{g,s}$) are estimated for each year from 1963/64 until 2011/12 (see Equation App.A.E.3);

(3) there is no survey bias for the IDCR/SOWER estimates (i.e. $\chi = 1$ for the IDCR estimates) (See Equation App.B.B.1);

(4) separate survey bias parameters are estimated for the JAPRA / JARPA II indices in each of the five areas included in the analysis (see Equation App.B.B.1);

(5) the minus- and plus-group ages when fitting to the conditional age-at-length data, $a_{\min,y}$ and $a_{\max,y}$, are set to 1 and 45yr respectively (see Equation App.B.D.1);

(6) the minus- and plus-group lengths, $l_{\min,y}$ and $l_{\max,y}$ for females are set to 25ft and 32ft for the period of commercial whaling, and 17ft and 32ft for JARPA / JARPA II, and for males are set to 25ft and 31ft for the period of commercial whaling and 17ft and 31ft for JARPA / JARPA II. [These choices were made to avoid fitting the model to length-classes with few data] (See Equations App.B.C.1 and App.B.D.1);

(7) many of the parameters of the population dynamics model (the deviations in births, distribution, growth, carrying capacity, and vulnerability) are essentially random effects. The ideal way to estimate these parameters is within the context of a random effects formulation, in which the likelihood is integrated over the random effects. However, this is computationally infeasible for this model so a penalised likelihood estimation formulation is adopted instead. Punt (2014) investigated whether the method developed by Thompson and Lauth (2012) for estimating the variance of a random effect which does not involve maximising the marginal likelihood could be applied in this case but this method failed to provide reliable estimates. Consequently, the values for random effects standard deviations are pre-specified (Table 2) and sensitivity explored to alternative plausible values; and

(8) the ages at which natural mortality changes with age are set to 3, 10, 20 and 40. The justification for this particular selection is given in the first section under 'Results'.

Table 3 lists the estimable parameters of the reference case model.

Data weighting

The length-frequency and conditional age-at-length data are assumed to be multinomially distributed when fitting the model to the data (see Appendix B). Use of this likelihood function requires that the effective sample sizes be specified. Setting these sizes to the actual numbers of animals measured and aged would over-estimate the information content of these data sets because of a lack of independence between adjacent length-/age-classes. Previous applications of the SCAA have been based on setting the effective sample sizes as a pre-specified fraction of the observed numbers of animals measured and aged using the approach of McAllister and Ianelli (1997), which compares the variance of the standardised residuals about the fits to the data with the variance of the standardised residuals expected had the data been multinomially distributed. This approach has been criticised by Francis (2011) who noted that the residuals about the fits to length and conditional age-at-length data tend to be correlated between length-classes and ages given length. Francis (2011) proposed an alternative approach in which the effective sample size is based on how well the model mimics the mean lengths (and means ages given length for the conditional age-at-length data).

Fig. 1 summarises the application of the method of Francis (2011) given the other specifications for the reference case analysis. The model run on which this application is based

Table 2

Values for the parameters which determine the extent of the penalties on the deviation parameters.

Parameter	Value
Extent of variation in births, σ_R	0.3
Extent of variability in the vulnerability deviations, σ_S	10
Extent of variability in the proportion of each stock in each area, σ_P	0.3
Extent of variability in growth rate, σ_K	0.02
Extent of variability in carrying capacity, σ_K	0.05

Table 3

The estimable parameters of the population dynamics model and the objective function.

	Number of parameters	
Parameter	Stock I	Stock P
Carrying capacity in 1930, $\tilde{K}_{1930}^{1+,s}$	1	1
Natural mortality: M^s by stock, γ, δ	4	
Resilience, A	1	1
Recruitment deviation, ε_y	83	83
Expected proportion in each Area, $\overline{P^{s,A}}$	2	1
Annual deviations about the expected proportions in each area, φ_y^a	69	26
Exploitation rate by year, sex and fleet, $F_y^{g,f}$	291	125
Inter-annual deviations in carrying capacity, v_y^s	82	82
Parameters of the growth curve, L_∞^g, k^g, t_0^g, σ_γ^g	8	8
Inter-annual deviations in growth rate, υ_y	98	98
Parameters to define vulnerability, $L_{50,y}^{g,f}$, $L_{\text{diff}}^{g,f}$, $L_{\text{left}}^{g,f}$, $L_{\text{right}}^{g,f}$	22	12
Age-specific vulnerability, $\tilde{S}_a$	1	1
Inter-annual deviations in vulnerability, $\delta_y^{g,f}$	72	22
JARPA survey bias, χ	3	2
Total	1,199	

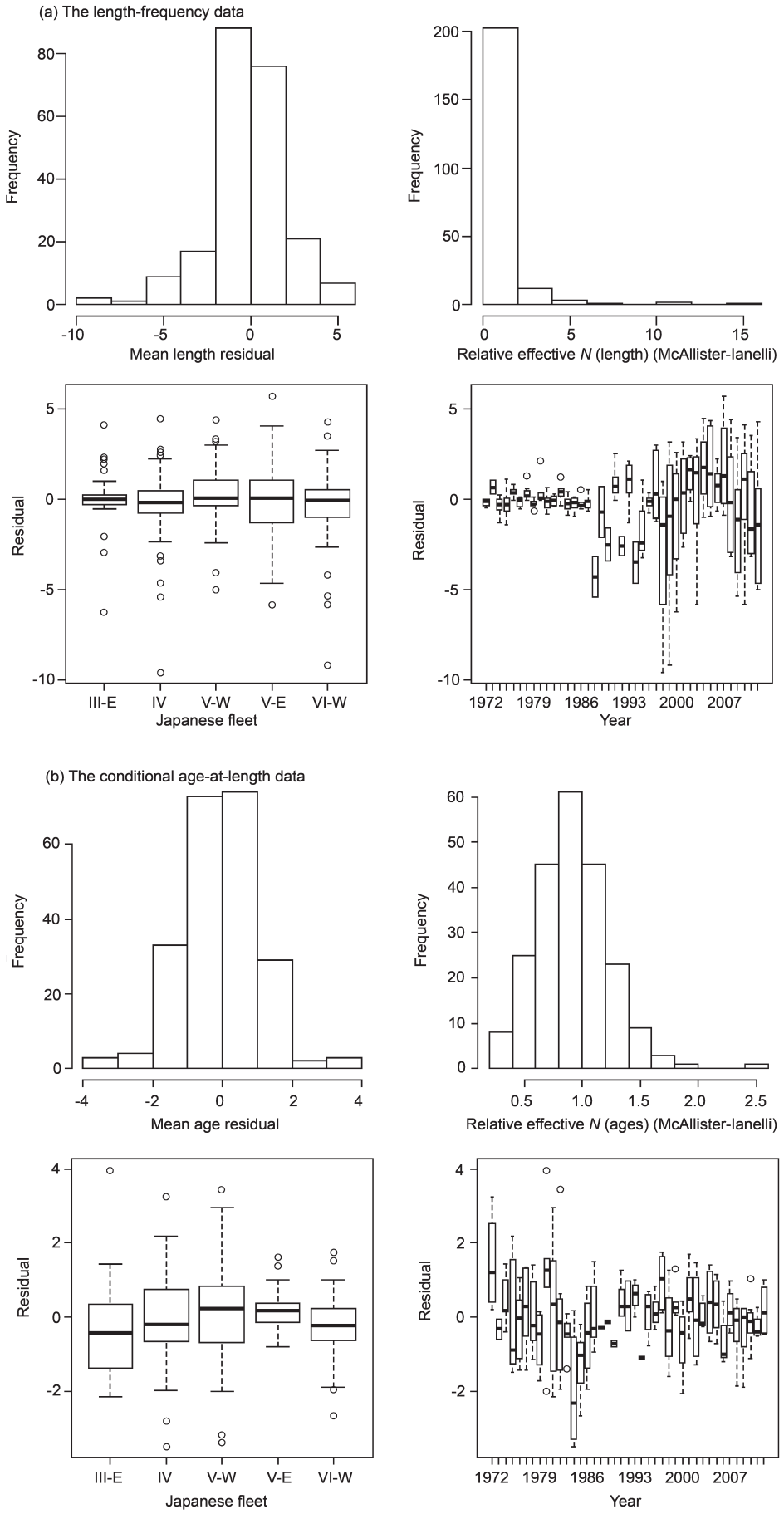

Fig. 1. Histograms of standardised residuals for the Japanese fleets about the mean length/ages (upper left panel), the ratio of the annual effective sample sizes to the observed numbers measured/aged based on the McAllister-Ianelli method (upper right panel), and the standardised residuals about the mean length/ages by area and year (lower panels).

set the effective sample sizes to the observed sample sizes. The residuals exhibit more variance than would be expected if the observed sample sizes reflect the effective sample sizes. Specifically, the ratio of the effective sample sizes to the observed sample sizes under the McAllister-Ianelli method (upper right panels of Figs 1a and 1b) also confirm

Table 4

The summary statistics and plots.

(a) Statistics

$b_{rec,1945–68}$ – slope of the linear regression of the estimates of the logarithms of the numbers of recruits (age 1 animals) on time (1945–68).
$b_{rec,1968–88}$ – slope of the linear regression of the estimates of the logarithms of the numbers of recruits on time (1968–88).
$b_{rec,1988–End}$ – slope of the linear regression of the estimates of the logarithms of the numbers of recruits on time (1988–last year).
$N_{tot,1945–68}$ – slope of the linear regression of the estimates of the logarithms of the numbers of 1+ animals on time (1945–68).
$N_{tot,1968–88}$ – slope of the linear regression of the estimates of the logarithms of the numbers of 1+ animals on time (1968–88).
$N_{tot,1988–Endr}$ – slope of the linear regression of the estimates of the logarithms of the numbers of 1+ animals on time (1988–last year).
$N_{\text{End–5,1}}/N_{1968,1}$ – ratio of the number of recruits in 2007 to that in 1968.
K_{1930} – carrying capacity in 1930.
K_{1960}/K_{1930} – ratio of K in 1960 to that in 1930.
K_{2000}/K_{1960} – ratio of K in 2000 to that in 1960.
Natural mortality (ages 3, 15, 35).
Average proportions in each management area.
Survey q for JARPA.
MSYR (1+).

(b) Plots

Assessment outputs

Total (1+) population size versus year (by stock and by area).
Age 1 animals (recruits) versus time.
Carrying capacity versus year.
Natural mortality versus age.
Body growth coefficient versus year.

Diagnostic plots

Survey estimates of abundance from IDCR with the associated model predictions (by area).

Table 5

The sensitivity tests.

Run	Description
	Reference case
Related to the population dynamics model	
A1	Siler natural mortality (Equation App. A.B.2).
A2	Autoregressive natural mortality deviations (Equation App. A.B.3).
A3	The proportion of each stock in each area is time-invariant.
A4	No time-varying growth.
A5	Carrying capacity (K) is time-invariant.
A6	Ignore ageing error.
Related to vulnerability patterns	
B1	JARPA/JARPA II vulnerability is constant.
B2	JARPA/JARPA II vulnerability is constant (and time-invariant); carrying capacity is time-invariant.
B3	JARPA/JARPA II abundance estimates are absolute.
B4	IDCR/SOWER estimates are assumed to be negatively biased, $g(0) = 0.60$.
B5	IDCR/SOWER estimates are assumed to be negatively biased, $g(0) = 0.80$.
B6	Time-invariant fishery vulnerability.
B7	Separate vulnerability patterns for JARPA/JARPA II.
B8	Time-varying declining vulnerability.
Related to data selection and data weighting	
C1	Decrease σ_s by 50%.
C2	Increase σ_s by 50%.
C3	Decrease σ_K by 50%.
C4	Increase σ_K by 50%.
C5	Decrease σ_p by 50%.
C6	Increase σ_p by 50%.
C7	Decrease σ_κ by 50%.
C8	Increase σ_κ by 50%.
C9	Decrease σ_R by 50%.
C10	Increase σ_R by 50%.
C11	Double weight on length data.
C12	Halve weight on length data.
C13	Double weight on conditional age-at-length data.
C14	Halve weight on conditional age-at-length data.
C15	All years of age and length data weighted equally.
C16	Increase cut-off lengths by 2ft.
C17	The length frequency and age composition data for the years until 1973/74 are down-weighted by 90%.

that the data are overdispersed relative to the multinomial. The residuals about mean length are higher for the period of JARPA /JARPA II (Fig. 1a, lower right panel), while the residuals for mean age given length are higher for the pre-JARPA period (Fig. 1b, lower right panel). There is no strong evidence for between-fleet differences in residual variance (Figs 1a and b, lower left panels). Consequently, the factor used to adjust the observed sample sizes to compute effective sample sizes are set to 1 for the commercial length-frequency data and 0.15 for the JARPA/ JARPA II length-frequency data. Furthermore, the factor used to adjust the observed sample sizes to compute effective sample sizes are set to 0.5 for the commercial conditional age-at-length data and 1 for the JARPA/ JARPA II conditional age-at-length data. 0.5 and 0.15 are rounded standard deviations of the residuals about mean length/age in Fig. 1.

Diagnostic statistics

Table 4 outlines the diagnostic statistics and plots. The statistics and some of the plots were originally selected by the Scientific Committee, but subsequently modified based on requests for additional analyses. The plots either summarise the key outputs from the assessments or aid understanding of those outputs somewhat better.

Sensitivity tests

Table 5 lists the specifications for the sensitivity tests. These sensitivity tests explore sensitivity to the weight assigned to the various data sources and penalties, the assumptions related to vulnerability, natural mortality and catchability, and to the use or otherwise of the JARPA/JARPA II index data. Results for the sensitivity tests are restricted to a set of 'core' statistics to keep the volume of results to minimum.

RESULTS

Modelling natural mortality

Table 6 and Fig. 2 contrast the results of analyses in which natural mortality is assumed to take the Siler form ('Siler', sensitivity test A1), in which natural mortality for ages 2–50

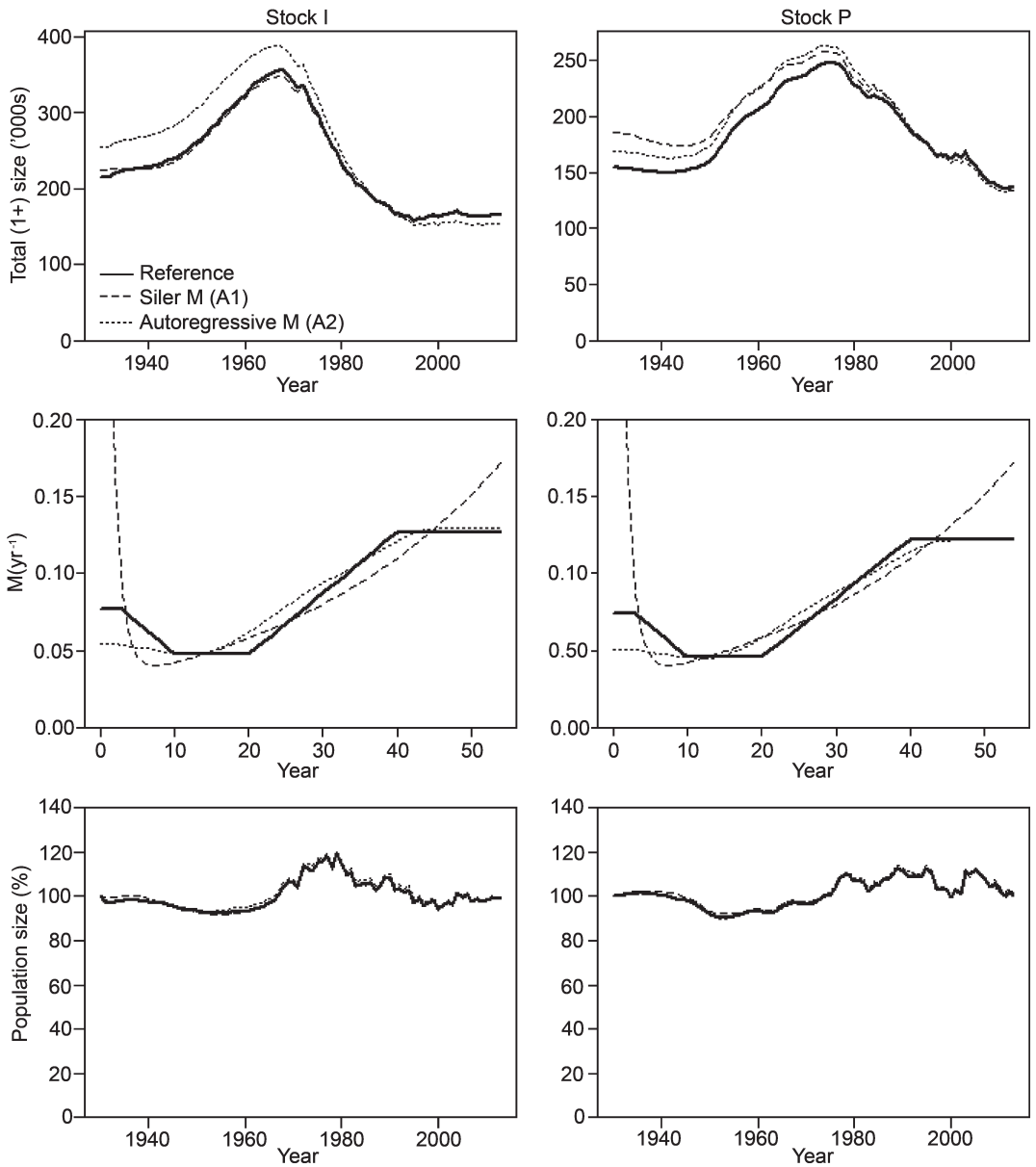

Fig. 2. Time-trajectories of total (1+) population size (upper panels), age-specific natural mortality (center panels), and total (1+) population size relative to carrying capacity (lower panels) for three ways to model natural mortality (the Siler model, autoregressive and piecewise linear).

Table 6a – Stock I

Results of the reference case analysis and the analyses to examine the sensitivity of the results to modifying some of the assumptions of the analysis method. The asymptotic standard errors for the estimates for natural mortality are given in parenthesis. The average proportions by area are given above the estimates for the JARPA χs (the numbers in parenthesis).

	b_{rec}			N_{tot}							Natural mortality (ages)			Mean proportion $\overline{b}^{N}$ (upper)/ JARPA χ^{A} (lower)			
Case	1945–68	1968–88	1988–End	1945–68	1968–88	1988–End	$N_{End-5,1}/N_{1968,1}$	K_{1930}	K_{1960}/K_{1930} (%)	K_{2000}/K_{1960} (%)	3	15	35	III–E	IV	V–W	MSYR (1+)
Reference	1.282	–2.931	0.956	1.912	–3.718	–0.168	0.539	214,922	162.1	49.2	0.077	0.048	0.107	0.156	0.376	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.658)	(0.947)	(1.013)	
A1	1.234	–2.905	0.880	1.933	–3.667	–0.114	0.527	224,852	153.1	50.0	0.089	0.042	0.094	0.157	0.376	0.468	0.218
											(0.03)	(0.004)	(0.004)	(0.692)	(1.009)	(1.077)	
A2	0.527	–3.400	1.141	1.539	–4.143	–0.439	0.517	253,935	151.9	41.3	0.054	0.049	0.107	0.150	0.371	0.479	0.221
											(0.009)	(0.006)	(0.007)	(0.707)	(0.989)	(1.008)	
A3	0.845	–3.565	0.908	1.581	–4.216	–0.391	0.495	228,085	149.6	42.1	0.072	0.053	0.110	0.214	0.344	0.442	0.221
											(0.017)	(0.005)	(0.005)	(0.565)	(1.276)	(1.265)	
A4	2.134	–1.810	–1.152	2.060	–2.549	–1.192	0.445	219,538	100	100	0.212	0.033	0.100	0.147	0.389	0.464	0
											(0.015)	(0.003)	(0.002)	(0.656)	(0.806)	(0.917)	
A5	1.775	–2.427	0.697	1.543	–3.178	0.108	0.627	219,047	100	100	0.055	0.039	0.106	0.156	0.375	0.469	0.002
											(0.013)	(0.003)	(0.002)	(0.631)	(0.926)	(0.979)	
A6	1.808	–5.272	0.572	2.245	–4.852	0.087	0.342	281,011	170.6	43.2	0.166	0.072	0.141	0.153	0.395	0.452	0.235
											(0.011)	(0.005)	(0.005)	(1.29)	(1.703)	(1.961)	
B1	1.309	–2.926	0.922	1.936	–3.683	–0.204	0.534	211,002	162.6	49.5	0.069	0.047	0.107	0.156	0.376	0.469	0.218
											(0.014)	(0.005)	(0.005)	(0.627)	(0.904)	(0.963)	
B2	1.829	–2.434	0.609	1.558	–3.156	0.060	0.605	217,579	100	100	0.062	0.039	0.106	0.156	0.375	0.469	0.001
											(0.013)	(0.003)	(0.002)	(0.619)	(0.907)	(0.96)	
B3	1.191	–2.983	1.000	1.836	–3.813	–0.156	0.541	225,183	159.7	47.9	0.088	0.049	0.108	0.126	0.381	0.494	0.220
											(0.018)	(0.005)	(0.005)	(1)	(1)	(1)	
B4	1.315	–2.300	0.970	1.951	–3.198	–0.083	0.601	299,225	164.0	54.7	0.082	0.047	0.106	0.158	0.369	0.473	0.219
											(0.016)	(0.005)	(0.005)	(0.419)	(0.628)	(0.648)	
B5	1.308	–2.629	0.954	1.938	–3.469	–0.124	0.567	245,298	163.3	51.9	0.080	0.047	0.107	0.157	0.372	0.471	0.219
											(0.016)	(0.005)	(0.005)	(0.541)	(0.796)	(0.837)	
B6	0.992	–3.332	0.337	1.917	–4.399	–0.470	0.983	272,981	163.9	42.7	0.192	0.050	0.109	0.152	0.385	0.462	0.224
											(0.012)	(0.005)	(0.005)	(0.951)	(1.260)	(1.414)	
B7	1.248	–2.953	1.605	1.888	–3.758	0.100	0.630	218,029	161.6	49.1	0.083	0.048	0.107	0.156	0.383	0.461	0.219
											(0.017)	(0.005)	(0.005)	(0.725)	(0.973)	(1.095)	
B8	1.042	–3.069	0.809	1.767	–4.143	0.189	0.587	242,359	169.6	47.3	0.216	0.053	0.106	0.159	0.385	0.456	0.226
											(*)	(*)	(*)	(1.216)	(1.739)	(1.964)	
Reference	1.282	–2.931	0.956	1.912	–3.718	–0.168	0.539	214,922	162.1	49.2	0.077	0.048	0.107	0.156	0.376	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.658)	(0.947)	(1.013)	
C1	1.314	–2.903	0.928	1.927	–3.697	–0.166	0.538	213,477	162.5	49.6	0.079	0.047	0.107	0.156	0.377	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.655)	(0.943)	(1.009)	
C2	1.277	–2.936	0.958	1.910	–3.721	–0.168	0.539	215,098	162.1	49.2	0.077	0.048	0.107	0.156\	0.376	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.658)	(0.948)	(1.013)	
C3	1.742	–2.329	1.197	1.946	–3.131	0.256	0.666	220,982	149.3	60.2	0.061	0.041	0.105	0.151	0.391	0.458	0.215
											(0.014)	(0.004)	(0.003)	(0.56)	(0.763)	(0.865)	
C4	1.277	–2.934	0.963	1.909	–3.721	–0.167	0.540	215,138	162.0	49.2	0.077	0.048	0.107	0.156	0.376	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.659)	(0.949)	(1.014)	
C5	1.155	–3.218	0.873	1.789	–3.960	–0.318	0.499	212,021	156.8	45.6	0.076	0.049	0.108	0.193	0.350	0.452	0.219
											(0.016)	(0.005)	(0.005)	(0.583)	5(1.13)	(1.154)	
C6	1.328	–2.691	0.986	1.957	–3.520	–0.102	0.567	231,531	164.1	51.7	0.078	0.047	0.106	0.127	0.400	0.467	0.218
											(0.016)	(0.005)	(0.005)	(0.726)	7(0.78)	(0.918)	
C7	1.479	–2.654	0.482	2.096	–3.530	–0.459	0.480	199,409	172.2	49.4	0.099	0.046	0.105	0.155	0.376	0.468	0.218
											(0.017)	(0.005)	(0.005)	(0.66)	(0.933)	(1.000)	
C8	1.197	–3.030	1.128	1.841	–3.785	–0.051	0.580	220,632	158.2	49.4	0.063	0.048	0.108	0.155	0.37	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.655)	6(0.945)	(1.008)	
C8	1.199	–2.953	0.939	1.871	–3.754	–0.207	0.531	220,187	160.7	48.5	0.078	0.048	0.107	0.155	0.376	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.662)	(0.946)	(1.008)	
C10	1.438	–3.051	0.962	1.979	–3.660	–0.129	0.522	205,653	163.5	50.3	0.071	0.047	0.106	0.157	0.376	0.467	0.218
											(0.016)	(0.005)	(0.005)	(0.643)	(0.935)	(1.003)	
C11	1.444	–2.846	0.563	2.020	–3.605	–0.480	0.528	208,700	167.4	48.7	0.102	0.046	0.106	0.154	0.377	0.469	0.218
											(0.017)	(0.005)	(0.005)	(0.704)	(0.977)	(1.053)	
C12	1.139	–3.086	1.319	1.825	–3.798	0.096	0.564	219,679	157.9	49.4	0.054	0.049	0.108	0.157	0.375	0.468	0.219
											(0.017)	(0.005)	(0.005)	(0.625)	(0.929)	(0.979)	
C13	0.835	–3.294	1.125	1.610	–4.017	–0.117	0.527	254,363	154.0	44.9	0.045	0.053	0.111	0.155	0.379	0.465	0.221
											(0.012)	(0.005)	(0.005)	(0.615)	(0.88)	(0.948)	
C14	1.750	–2.585	0.664	2.167	–3.373	–0.267	0.556	184,671	167.1	53.5	0.102	0.042	0.103	0.155	0.372	0.472	0.216
											(0.018)	(0.006)	(0.005)	(0.698)	(1.007)	(1.058)	
C15	1.938	–2.700	0.429	2.069	–3.366	–0.885	0.538	211,783	164.0	48.0	0.124	0.039	0.108	0.148	0.379	0.473	0.216
											(0.01)	(0.005)	(0.004)	(0.728)	(0.942)	(1.027)	
C16	1.209	–3.060	1.313	1.938	–3.685	0.076	0.595	204,153	163.4	51.4	0.053	0.049	0.107	0.157	0.375	0.468	0.218
											(0.017)	(0.005)	(0.005)	(0.646)	(0.95)	(1.007)	
C17	1.354	–3.154	0.915	2.068	–3.712	–0.182	0.548	205,748	167.9	49.8	0.081	0.048	0.106	0.156	0.377	0.468	0.219
											(0.017)	(0.005)	(0.005)	(0.663)	(0.952)	(1.02)	

Table 6b – Stock P

Results of the reference case analysis and the analyses to examine the sensitivity of the results to modifying some of the assumptions of the analysis method. The asymptotic standard errors for the estimates for natural mortality are given in parenthesis. The average proportions by area are given above the estimates for the JARPA χs (the numbers in parenthesis).

	b_{rec}			N_{tot}							Natural mortality (ages)			Mean proportion $\overline{b}^{v}$ (upper)/ JARPA χ^{A} (lower)		
Case	1945–68	1968–88	1988–End	1945–68	1968–88	1988–End	$N_{End-5,1}/N_{1968,1}$	K_{1930}	K_{1960}/K_{1930} (%)	K_{2000}/K_{1960} (%)	3	15	35	V–E	VI–W	MSYR (1+)
Reference	1.958	–2.957	–0.298	2.127	–0.779	–1.612	0.345	154,239	143.5	73.9	0.074 (0.016)	0.046 (0.005)	0.103 (0.005)	0.788 (0.685)	0.212 (1.190)	0.217
A1	1.704	–3.044	–0.542	1.76	–0.947	–1.721	0.343	185,636	128.2	68.8	0.089 (0.03)	0.042 (0.004)	0.094 (0.004)	0.788 (0.726)	0.212 (1.265)	0.218
A2	1.689	–3.283	0.023	2.121	–1.009	–1.83	0.327	168,575	142.5	66.2	0.050 (0.008)	0.046 (0.005)	0.100 (0.007)	0.793 (0.671)	0.207 (1.217)	0.219
A3	1.956	–3.008	–0.202	2.189	–0.831	–1.632	0.347	156,638	145.8	72.4	0.067 (0.016)	0.049 (0.005)	0.102 (0.005)	0.791 (0.683)	0.209 (1.27)	0.218
A4	3.476	–1.367	–2.527	3.079	0.618	–1.382	0.331	82,732	181.1	116.1	0.185 (0.016)	0.029 (0.004)	0.087 (0.004)	0.783 (0.65)	0.217 (1.093)	0.210
A5	1.403	–1.637	0.697	0.667	–0.178	–0.449	0.650	167,899	100	100	0.051 (0.012)	0.036 (0.002)	0.098 (0.002)	0.779 (0.638)	0.221 (1.017)	0.004
A6	3.759	–3.757	–0.227	2.710	–1.133	–1.286	0.436	145,631	151.7	75.8	0.146 (0.012)	0.064 (0.005)	0.124 (0.005)	0.780 (1.445)	0.220 (2.397)	0.230
B1	1.995	–2.927	–0.317	2.143	–0.734	–1.619	0.344	153,032	143.1	74.7	0.066 (0.013)	0.046 (0.005)	0.103 (0.005)	0.789 (0.646)	0.211 (1.126)	0.217
B2	1.413	–1.625	0.644	0.668	–0.176	–0.460	0.643	167,575	100	100	0.057 (0.012)	0.035 (0.002)	0.098 (0.002)	0.779 (0.622)	0.221 (0.991)	0.004
B3	1.865	–3.044	–0.236	2.085	–0.889	–1.608	0.346	145,149	143.5	71.8	0.085 (0.018)	0.047 (0.005)	0.104 (0.005)	0.725 (1)	0.275 (1)	0.218
B4	1.948	–2.925	–0.329	2.118	–0.756	–1.602	0.346	255,302	143.5	74.2	0.079 (0.016)	0.046 (0.005)	0.103 (0.005)	0.788 (0.417)	0.212 (0.723)	0.217
B5	1.957	–2.942	–0.322	2.125	–0.765	–1.615	0.344	192,064	143.5	74.0	0.077 (0.016)	0.046 (0.005)	0.103 (0.005)	0.788 (0.551)	0.212 (0.958)	0.217
B6	1.923	–3.789	–0.667	2.136	–1.217	–1.576	0.325	154,436	153.8	69.4	0.182 (0.016)	0.047 (0.005)	0.104 (0.005)	0.781 (1.055)	0.219 (1.77)	0.221
B7	1.905	–2.994	0.359	2.101	–0.835	–1.425	0.392	155,601	143.4	73.2	0.080 (0.017)	0.047 (0.005)	0.104 (0.005)	0.791 (0.712)	0.209 (1.302)	0.218
B8	1.551	–3.262	–0.366	1.857	–1.507	–1.416	0.346	173,619	148.8	63.7	0.213 (*)	0.052 (*)	0.105 (*)	0.777 (1.437)	0.223 (2.340)	0.225
Reference	1.958	–2.957	–0.298	2.127	–0.779	–1.612	0.345	154,239	143.5	73.9	0.074 (0.016)	0.046 (0.005)	0.103 (0.005)	0.788 (0.685)	0.212 (1.190)	0.217
C1	1.957	–2.960	–0.329	2.123	–0.783	–1.638	0.341	154,824	143.4	73.5	0.076 (0.016)	0.046 (0.005)	0.103 (0.005)	0.788 (0.683)	0.212 (1.191)	0.217
C2	1.960	–2.955	–0.294	2.129	–0.777	–1.610	0.346	154,098	143.5	73.9	0.074 (0.016)	0.046 (0.005)	0.103 (0.005)	0.788 (0.685)	0.212 (1.19)	0.217
C3	1.902	–2.387	0.485	1.301	–0.409	–0.968	0.489	165,158	120.2	84.2	0.059 (0.013)	0.04 (0.003)	0.100'(0.003)	0.784 (0.649)	0.216 (1.077)	0.214
C4	1.959	–2.953	–0.291	2.129	–0.779	–1.605	0.346	154,111	143.5	74.0	0.074 (0.016)	0.046 (0.005)	0.103 (0.005)	0.788 (0.685)	0.212 (1.19)	0.217
C5	1.988	–2.942	–0.293	2.160	–0.763	–1.604	0.347	153,074	144.4	74.3	0.072 (0.016)	0.046 (0.005)	0.103 (0.005)	0.801 (0.664)	0.199 (1.294)	0.217
C6	1.971	–2.934	–0.257	2.132	–0.759	–1.574	0.350	159,794	143.6	74.6	0.075 (0.016)	0.046 (0.005)	0.103 (0.005)	0.699 (0.783)	0.301 (0.751)	0.217
C7	2.164	–2.716	–0.855	2.266	–0.566	–1.750	0.319	142,307	148.9	77.1	0.095 (0.017)	0.045 (0.005)	0.101 (0.005)	0.789 (0.672)	0.211 (1.18)	0.217
C8	1.852	–3.142	–0.143	2.056	–0.902	–1.545	0.36	160,772	140.6	72.5	0.061 (0.015)	0.047 (0.005)	0.104 (0.005)	0.788 (0.685)	0.212 (1.188)	0.217
C9	1.918	–2.987	–0.283	2.098	–0.828	–1.679	0.35	157,151	143.2	73.2	0.075 (0.016)	0.047 (0.005)	0.103 (0.005)	0.789 (0.685)	0.211 (1.198)	0.218
C10	2.051	–3.15	–0.325	2.207	–0.676	–1.552	0.334	149,854	143.5	74.2	0.069 (0.015)	0.045 (0.005)	0.102 (0.005)	0.788 (0.669)	0.212 (1.161)	0.217
C11	2.036	–2.905	–0.742	2.167	–0.690	–1.745	0.343	149,744	146.2	74.8	0.099 (0.017)	0.044 (0.005)	0.102 (0.005)	0.789 (0.708)	0.211 (1.242)	0.217
C12	1.920	–3.012	0.020	2.110	–0.824	–1.537	0.355	157,484	141.5	73.2	0.052 (0.016)	0.047 (0.005)	0.104 (0.005)	0.787 (0.665)	0.213 (1.151)	0.217
C13	1.816	–3.331	–0.116	2.479	–1.026	–1.690	0.311	153,933	152.4	68.9	0.043 (0.011)	0.050 (0.004)	0.105 (0.005)	0.788 (0.667)	0.212 (1.164)	0.219
C14	2.100	–2.529	–0.506	1.778	–0.437	–1.520	0.388	152,573	133.9	81.2	0.099 (0.018)	0.041 (0.005)	0.100 (0.005)	0.788 (0.688)	0.212 (1.192)	0.215
C15	2.444	–2.999	–1.147	2.390	–0.607	–2.058	0.372	144,813	150.9	74.2	0.122 (0.011)	0.039 (0.004)	0.107 (0.004)	0.792 (0.700)	0.208 (1.253)	0.216
C16	1.892	–3.236	–0.057	2.085	–0.908	–1.623	0.360	161,866	140.7	71.4	0.052 (0.016)	0.048 (0.005)	0.104 (0.005)	0.789 (0.681)	0.211 (1.189)	0.218
C17	1.905	–3.023	–0.405	2.116	–0.854	–1.680	0.334	157,087	144.0	72.0	0.079 (0.017)	0.047 (0.005)	0.103 (0.005)	0.788 (0.693)	0.212 (1.209)	0.218

is modelled using an autoregressive process ('Autoregressive M', sensitivity test A2), and in which natural mortality changes at ages of 3, 10, 20 and 40 ('Reference'). Treating natural mortality as an autoregressive series leads to higher estimates of 1+ abundance for the pre-1980 period compared to the other two analyses. The Siler M analysis also leads to higher estimates of pre-1980 1+ abundance for stock P. Age-specific natural mortality from the Siler-based analysis implies much higher rates of natural mortality for very young and old animals than the autoregressive formulation, unrealistically so for the young ages (Fig. 2, center panels).

The breakpoints for the reference case model were set so that the profile of M-at-age matches than from the autoregressive M analysis quite well. The remaining analyses of this paper are consequently based on modelling natural mortality as a piecewise linear function of age, with breakpoints at ages 3, 10, 20 and 40, given that this is more parsimonious than the autoregressive M approach and does not lead to unrealistically high values for M-at-age for the younger ages,

Reference case analysis

Both stocks are estimated to have increased from 1930 until the early 1970s, with both stocks having declined subsequently thereafter (Fig. 3). The increase in abundance is due primarily to an increase in recruitment owing in turn to an increase in carrying capacity (Fig. 3). Carrying capacity is estimated to have declined subsequently for both stocks, but the effect of this on recruitment and hence total population size is much smaller for stock P than for stock I (Fig. 3). The total (1+) population size is estimated to track carrying capacity quite closely. Stock I is estimated to have initially been larger than stock P, but stock P is currently the larger of the two stocks (Fig. 3, Table 6). The estimates of the recruitment deviations (Fig. 3) suggest that there have been periods of good and poor recruitment. The estimates of natural mortality indicate that natural mortality is highest for the youngest and (particularly) oldest animals (Fig. 3; Table 6). Natural mortality for stock I is estimated to be slightly higher at large age than for stock P ($0.107yr^{-1}$ for animals of age 35, compared to $0.103yr^{-1}$; Table 6). The CV for natural mortality is highest for young ages and approximately 10% for ages 10–30 (Fig. 3).

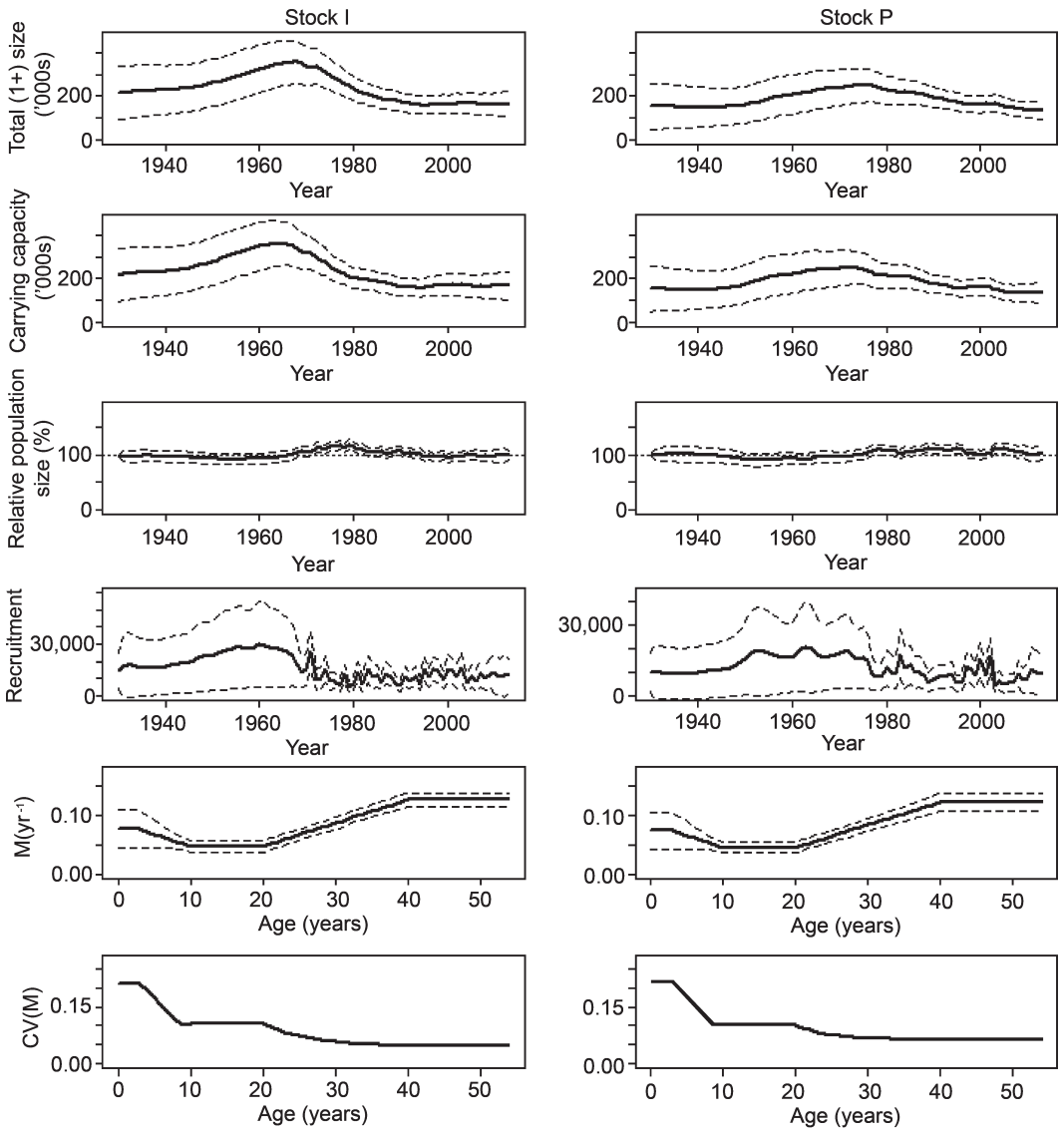

Fig. 3. Time-trajectories of total (1+) population size, carrying capacity, total (1+) population relative to carrying capacity, and recruitment (from 1930 and from 1975), and age-specific natural mortality by stock (estimates and CVs) for the reference case analysis. The dotted lines indicate 95% asymptotic confidence intervals.

The estimates of the proportions of the total population in each area changes over time, and vary inter-annually to better fit the abundance estimates, while there is also evidence for time-varying growth (Fig. 4). The initial declining trends in the proportion of the total population in Areas III–E, IV and V–W is due to the faster estimated rate of increase for the P stock. The von Bertalanffy growth rate is estimated to have peaked in the mid-1980s and to have declined thereafter (Fig. 4).

Figs 5 and 6 illustrate how well the model is able to mimic the estimates of absolute and relative abundance given the estimated changes in abundance as well as inter-annual variation in the proportion of the population in each area. The confidence intervals for the abundance estimates generally intersect the population trajectory, indicating that the extent of process error in the proportion of the stocks in each area is sufficient to capture additional variance.

Results are not shown for the fits to the length-frequency and conditional age-at-length data given the large number of associated plots. However, the fits to the commercial length-frequency data are generally excellent, except when sample sizes are very small. However (and expected from Fig. 1), the fits to the length-frequency data for JARRA/JARPA II are occasionally quite poor. Most of the poor fits occur when sample sizes are small. There are also no major concerns with the fits to the mean ages-at-length, suggesting that the extent of time-varying growth is sufficient to mimic the changes in growth over time.

Sensitivity tests

There are many sensitivity tests, and the results are generally insensitive to changes to specifications of the reference case analysis (Table 6). Consequently plots of results are only shown for 'interesting' cases. Not allowing for time-varying growth (sensitivity test A4) leads a markedly faster rate of increase for stock P and also to higher estimates of natural mortality for very young animals for both stocks (Fig. 7), but the fit of the model to the data is much poorer than for the reference case analysis (Table 7). As expected, the rate of increase is least over the initial years of the projection period when carrying capacity is constant (sensitivity tests A5 & B2, Fig. 7, 8). The results for stock I are very sensitive to whether allowance is made for age-reading error or not, with abundance for this stock increasing to much higher levels if age-reading error is ignored (sensitivity test A6). In terms of estimates of natural mortality, ignoring ageing error leads to higher rates of natural mortality.

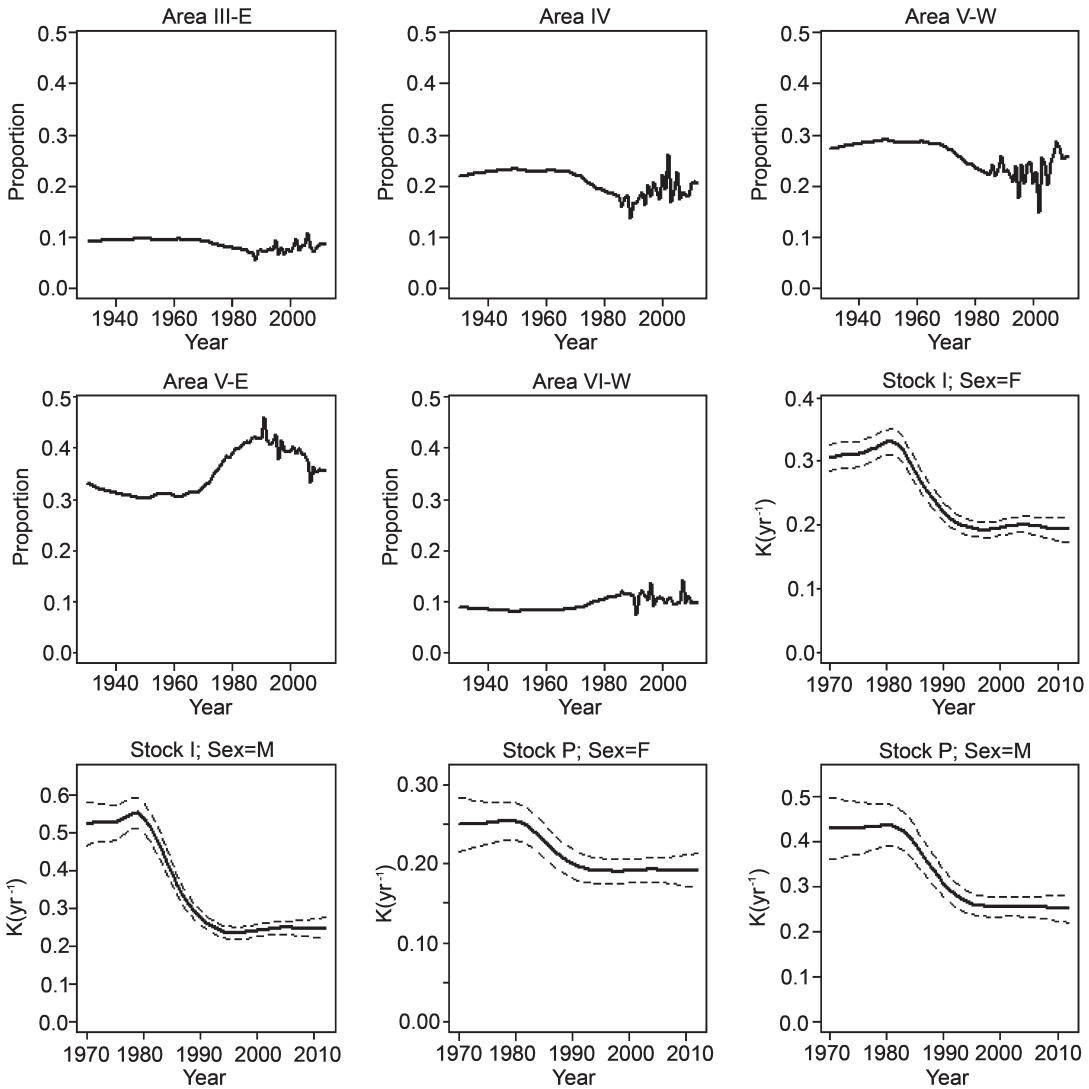

Fig. 4. Time-trajectories of the proportion of the total population in each of the five areas considered in the model as well as those of the growth rate parameter κ (by stock and sex) for the reference case analysis.

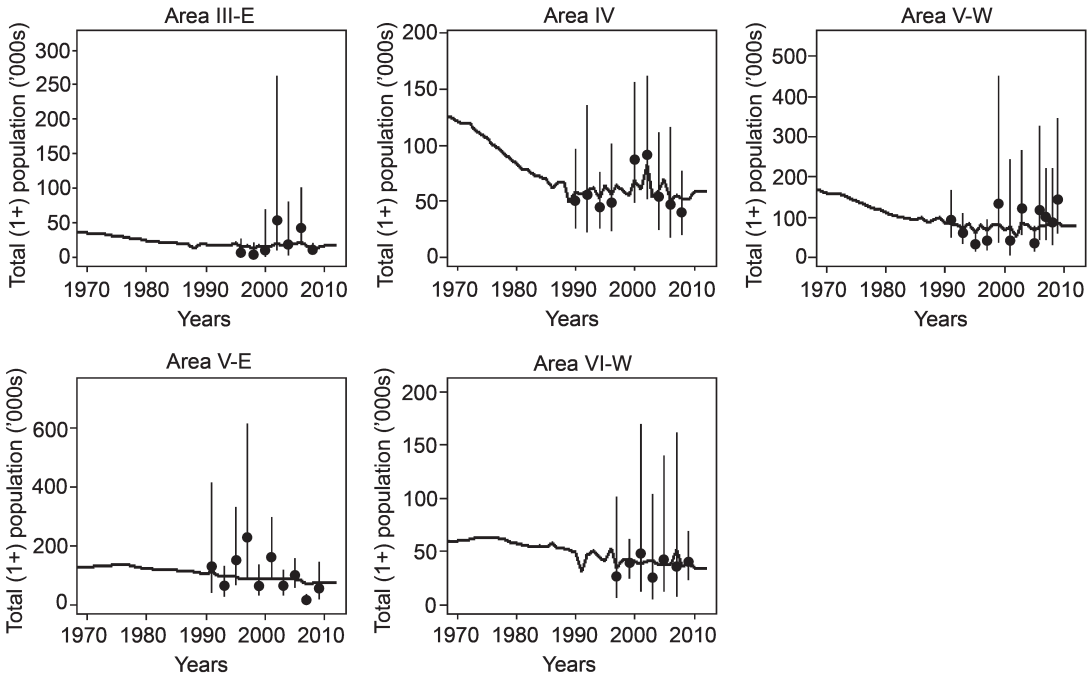

Fig. 5. Fits to the indices of relative abundance (from JARPA) for the reference case analysis. The bars indicate 95% confidence intervals based on the supplied sampling standard errors.

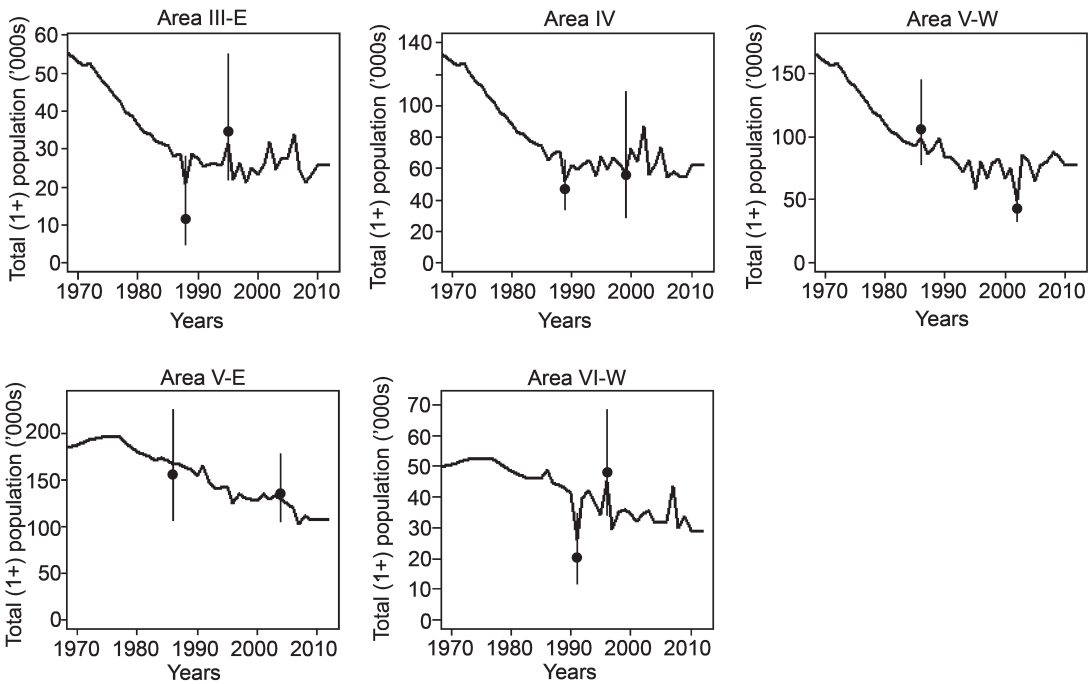

Fig. 6. Fits to the indices of absolute abundance (from IDCR) for the reference case analysis. The bars indicate 95% confidence intervals based on the supplied sampling standard errors.

As expected, assuming $g(0) = 0.8$ or 0.6 (sensitivity tests B4 & B5) leads to higher numbers in an absolute sense (Fig. 8), but the fits are hardly different in an AIC sense (Table 7). The numbers of animals in stock I are predicted to be higher before 1970 if vulnerability is time-invariant (sensitivity test B6), but not allowing for time-varying vulnerability leads to markedly poorer fits to the data. The numbers in stock I are also higher when allowance is made for time-varying declining vulnerability (sensitivity test B8) (and this is supported by AIC; Table 7). However, the Hessian matrix was not positive definite for this case, suggesting that the model is over-parameterised for this sensitivity test. Natural mortality for the younger animals is higher when vulnerability is assumed to be time-invariant and when allowance is made for time-varying declining vulnerability (but the lack of convergence for this case means the results should be interpreted with caution).

The time-trajectory of 1+ abundance and age-specific natural mortality are insensitive to treating the JARPA/JARPA II indices as absolute or relative indices of abundance (results not shown). The assumption $g(0) = 1$ for the IDCR surveys would have much stronger support if the JARPA/

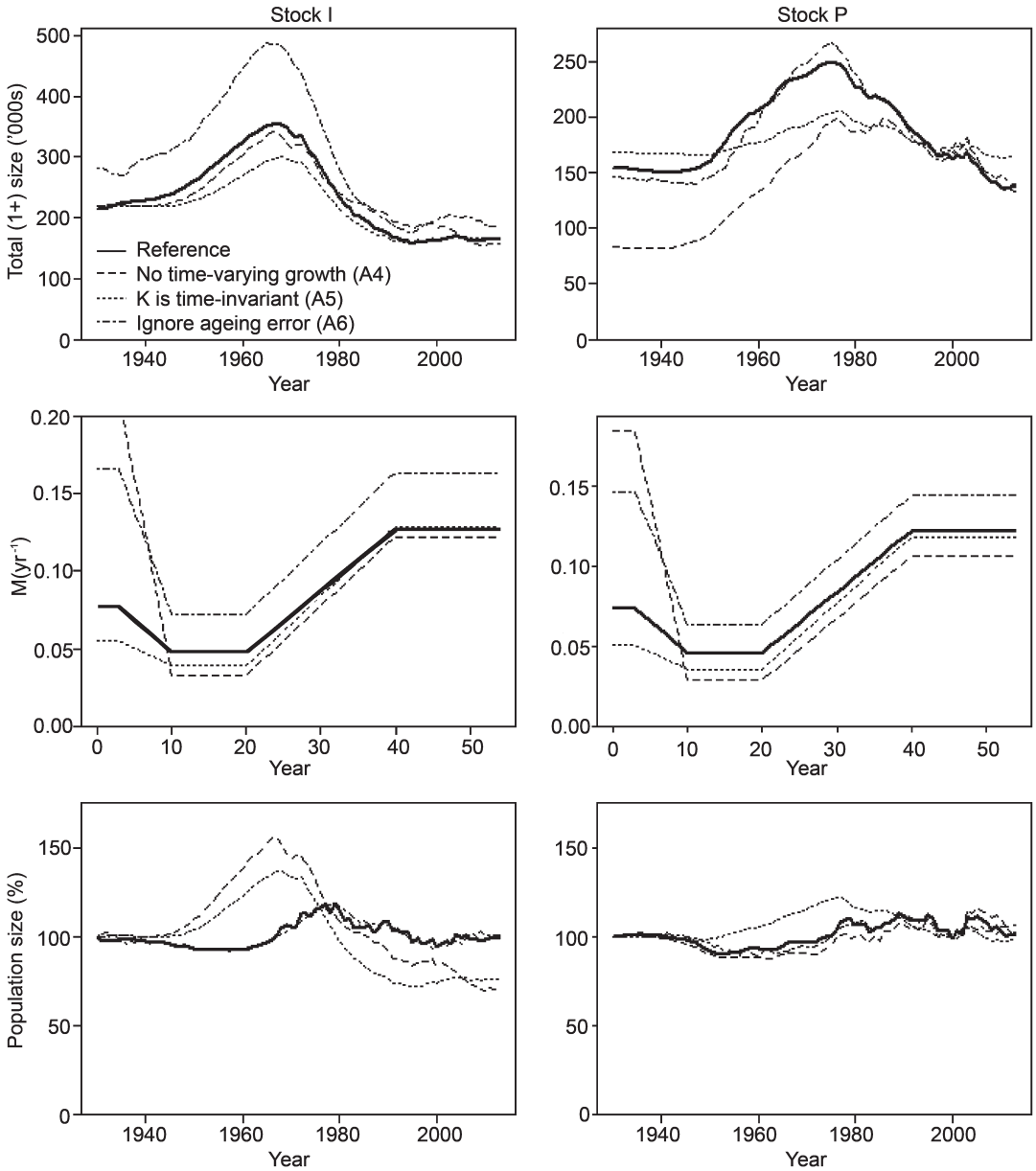

Fig. 7. Time-trajectories of total (1+) population size (upper panels), age-specific natural mortality (center panels), and total (1+) population size relative to carrying capacity (lower panels) for the reference case analysis and a sub-set of the sensitivity tests.

Table 7

Number of parameters, AIC and ΔAIC (relative to the reference case) for the sensitivity tests which are comparable in terms of likelihood formulation with the reference case analysis.

Case	No. parameters	AIC	ΔAIC
Reference	1,199	34,332.8	0
A1	1,201	34,324.4	–8.4
A2	1,246	34,452.6	119.8
A3	1,104	34,182.8	–150
A4	1,003	35,487	1,154.2
A5	1,035	34,186	–146.8
A6	1,199	33,769.8	–563
B1	1,199	34,324.8	–8
B2	1,031	34,163.4	–169.4
B3	1,194	34,327.2	–5.6
B4	1,199	34,326	–6.8
B5	1,199	34,329.4	–3.4
B6	1,105	36,168.4	1,835.6
B7	1,203	34,338.2	5.4
B8	1,293	34,171.2	–161.6

JARPA II indices are assumed to be absolute indices of abundance.

Retrospective analyses

Fig. 9 shows the time-trajectories of 1+ population size and recruitment for the reference case analysis and for analyses in which the data for the last two, last four, etc. years are ignored. In general, the qualitative results are robust to ignoring recent data. However, leaving out historical data leads to higher numbers (recruitment and in total) before 1970 for stock I. The sensitivity of the results for stock P to ignoring recent data is more complicated, with lower numbers before 1970, but to higher numbers for recent years. The estimates of natural mortality, M, for ages 0–3 decline with increasing years of data from $0.101yr^{-1}$ for stock I when the data set is restricted to the years 2002 and earlier to $0.077yr^{-1}$ for the reference case while they decline from $0.095yr^{-1}$ to $0.074yr^{-1}$ for stock P. The estimates of M for ages

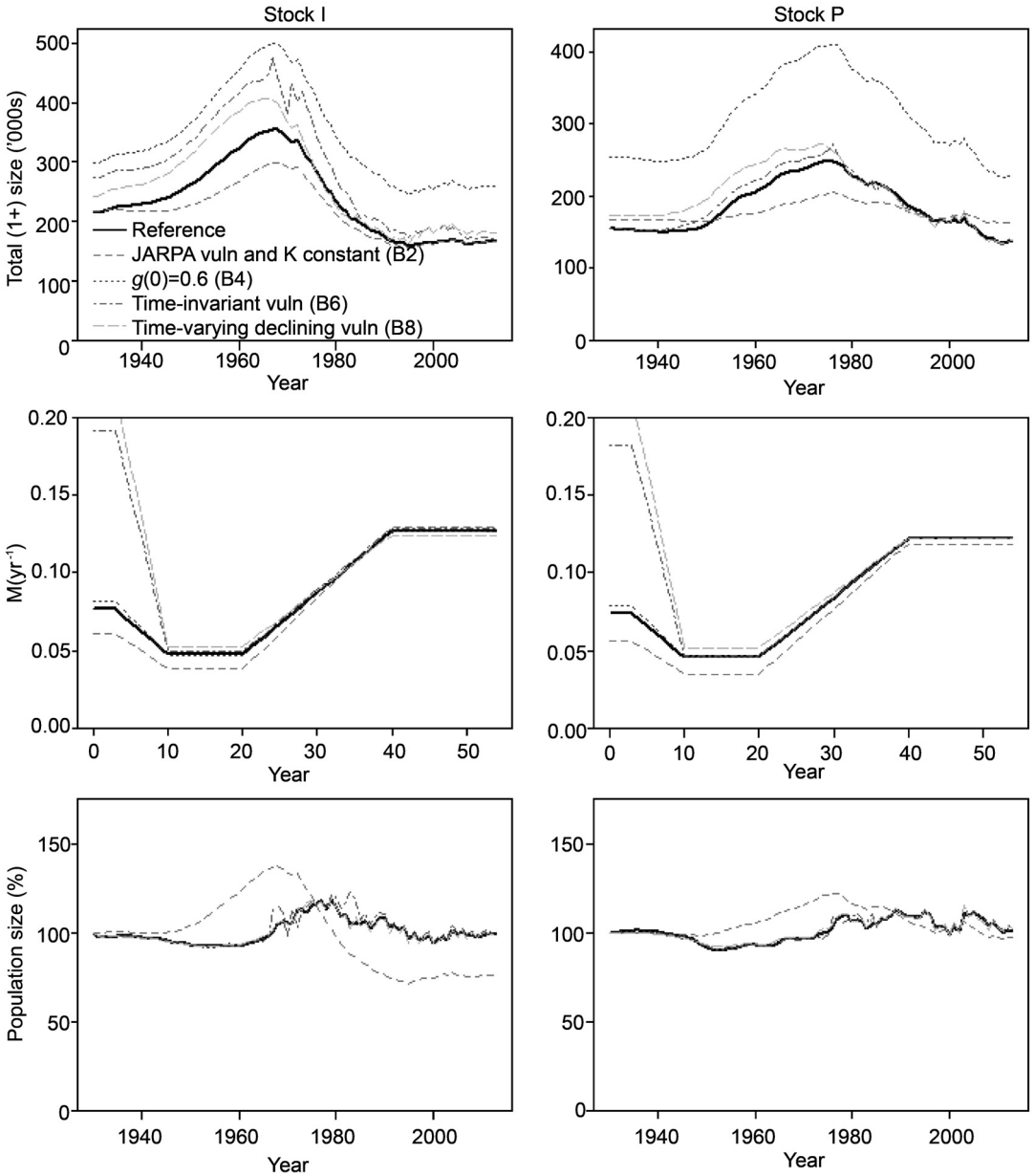

Fig. 8. Time-trajectories of total (1+) population size (upper panels), age-specific natural mortality (center panels), and total (1+) population size relative to carrying capacity (lower panels) for the reference case analysis and a sub-set of the sensitivity tests.

10+ are, however, insensitive to leaving data out of the analysis. The standard error of the estimate of *M* for age 3 declined from 0.020yr^{-1} when the data set is restricted to the years 2002 and earlier to 0.016yr^{-1} for the reference case.

Ignoring the JARPA/JARPA II data

Dropping the JARPA/JARPA II length-frequency and conditional age-length data means that it is not possible to estimate vulnerability for the period of scientific catches. Consequently, the sensitivity tests in this section are based on setting the vulnerability pattern for the JARPA / JARPA II catches to that estimated for the reference case analysis. This assumption has no impact for the analyses which ignore both the age and length data because it is impossible to estimate vulnerability without composition data. However, this assumption will give some additional information to the analyses which ignore either, but not both, of the conditional age-at-length and length-frequency data.

Fig. 10 shows 1+ abundance (as a function of time), natural mortality (as a function of age), and total (1+) population size relative to carrying capacity for the reference case analysis and analyses in which the JARPA/JARPA II conditional age-at-length, length-frequency and index data are ignored. As suggested by Punt (2014) the results are very insensitive to ignoring the JARPA/JARPA II abundance estimates. However, results for stock I are very sensitive to the ignoring the JARPA/JARPA II conditional age-at-length data, while ignoring the JARPA/JARPA II length-frequency and conditional age-at-length data simultaneously lead to a qualitative change to the time-trajectory of 1+ abundance for stock P.

DISCUSSION

Population status and trends

All of the analyses indicate that Antarctic minke whales in the assessed area increased from 1930 until the mid-1970s and, with the exception of the analysis in which growth rates do not change over time (sensitivity A4 in Table 6), declined

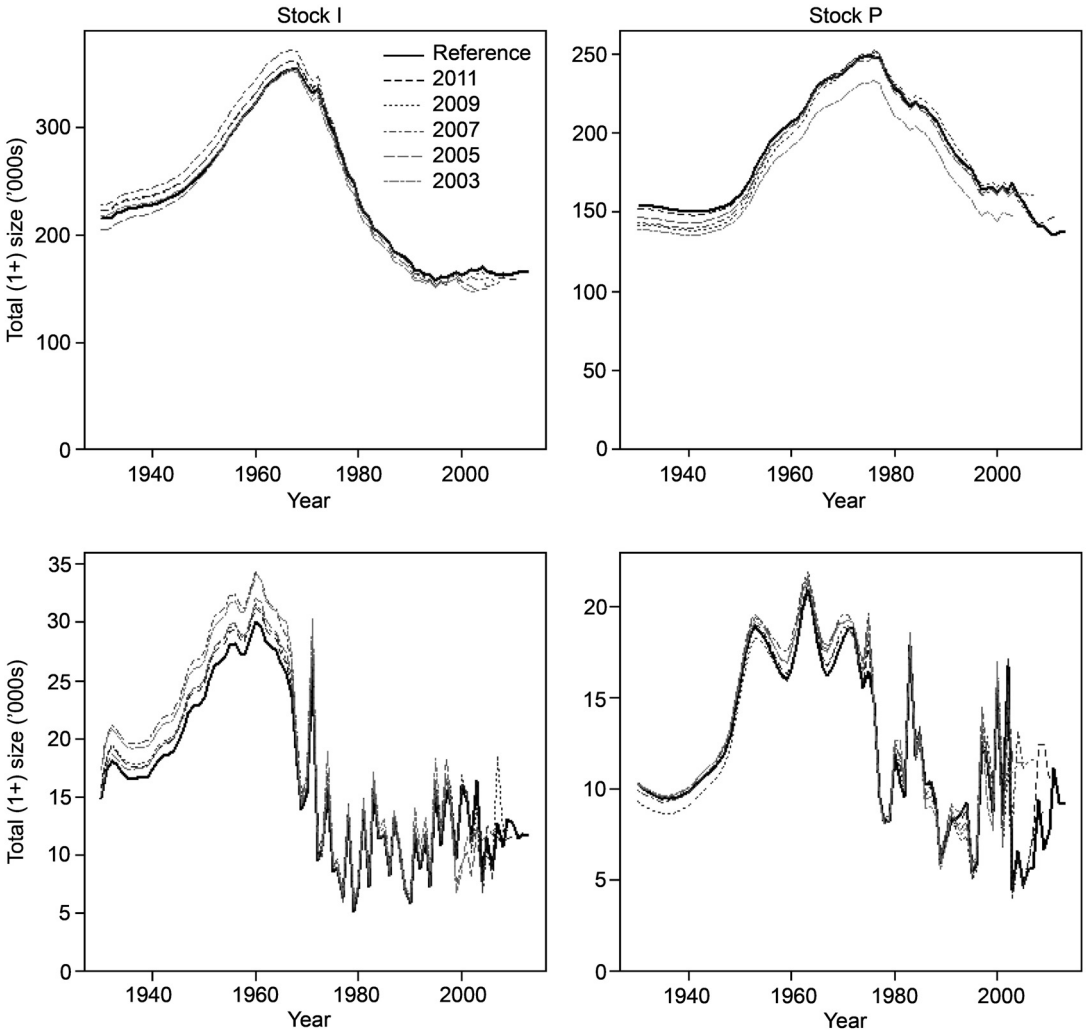

Fig. 9. Time-trajectories of 1+ population size and recruitment for the reference case analysis and for analyses when the data series are ignored after the indicated year.

over the period from the mid-1970s until 1988. The increase rate for total abundance size is 1.9% (SE 0.7%) annually for stock I and 2.1% (SE 1.1%) for stock P (Table 6). The extent of increase from 1945 to 1968 is estimated to be higher for stock P (Antarctic Areas V–E to VI–W) than for stock I (Antarctic Areas III–E to V–W). This result is robust to changes to the assumptions of the assessment. The recent (1988 onwards) trend in total abundance from the reference case analysis is downward (–0.2% (SE 0.5%) annually for stock I and –1.6% (SE 0.5%) for stock P). The conclusion that abundance is declining for stock P is robust to the changes to the assumptions, but the trend estimate for stock I for recent years is not statistically different from zero and some of the sensitivity tests for stock I (A5, A6, B2, B7, B8) suggest a slightly increasing trend (in point estimate terms).

The trends in recruitment mimic those in the total population size. However, given the time-lags involved in the model, even though total population size is estimated to be declining for stock I according to the reference case analysis, recruitment during 1988 onwards for this stock is estimated to be increasing by about 1% annually across almost all of the sensitivity tests.

With the exceptions of the trials in which carrying capacity is assumed to be time-invariant (A5 and B2), the analyses suggest that carrying capacity was higher in 1960 than in 1930 (reference case 162% (SE 28%) for stock I and 144% (SE 34%) for stock P), while carrying capacity in 2000 was about half (stock I) and 75% (stock P) of that in 1960. Consequently, carrying capacity in 2000 is estimated to be about 80% of that in 1930 for stock I and 110% of that in 1930 for stock P.

Parameter estimation

Natural mortality can be estimated with high precision (reference case: CVs of 20% for the youngest animals and 5% for the older ages, Fig. 3). Analyses conducted by Punt (2014) based on a previous version of the SCAA showed that this high precision is not a result of using an asymptotic method to estimate standard errors. Natural mortality is consistently estimated to be higher for younger and (particularly) older individuals. The functional form for natural mortality was forced to follow a piecewise linear formulation which should reduce the variance of the estimates of natural mortality. However, even allowing natural mortality to follow an auto-regressive process (sensitivity test A2) did not lead to markedly less precise estimates of natural mortality.

The Siler model for natural mortality was expected to be a parsimonious way to model age-specific natural mortality rather than pre-specifying breakpoints in the relationship

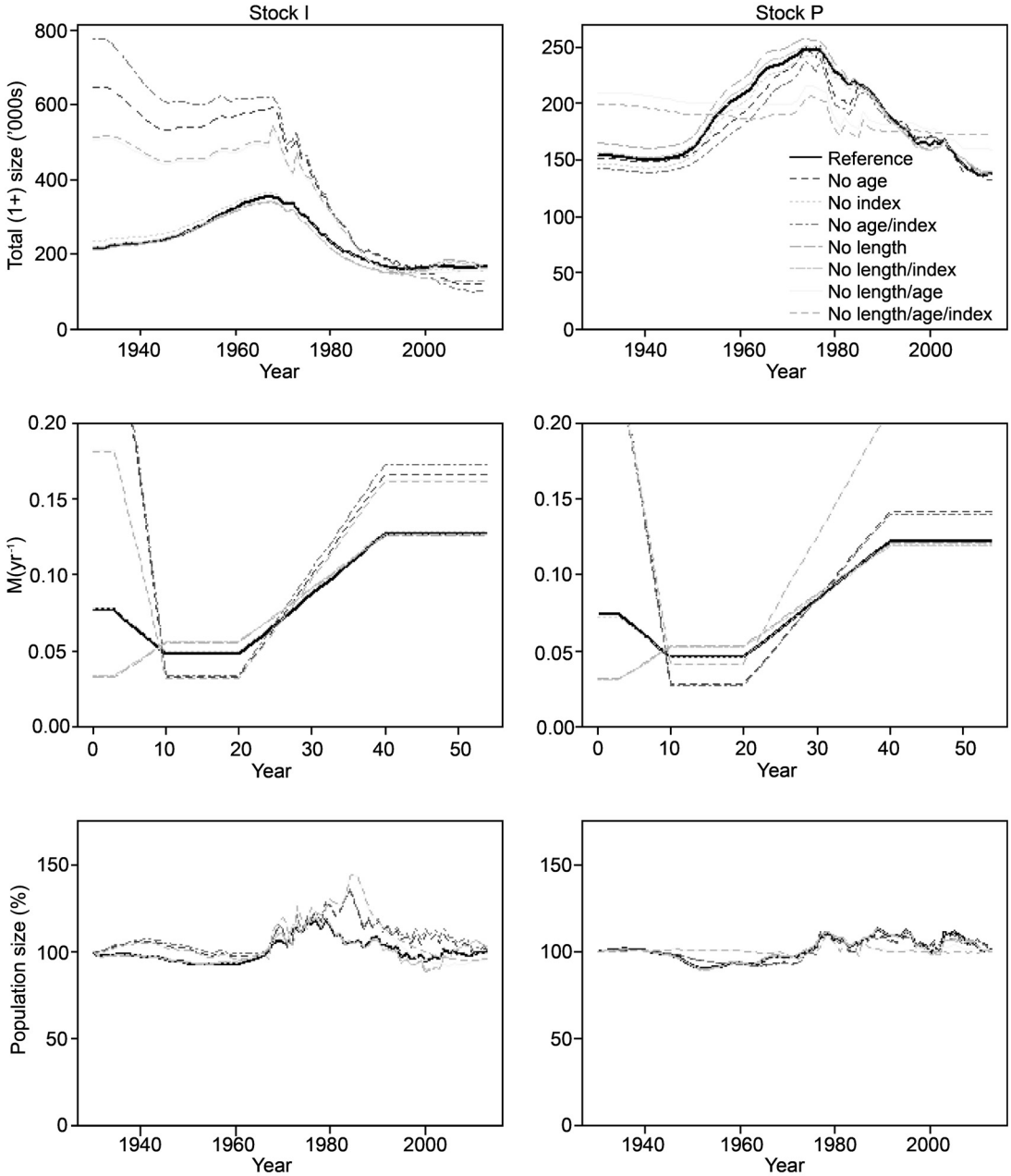

Fig. 10. Time-trajectories of total (1+) population size (upper panels), age-specific natural mortality (center panels), and total (1+) population size relative to carrying capacity (lower panels) for the reference case analysis, and variants thereof in which various combinations of the JAPRA/JARPA II index, the JAPRA/JARPA II conditional age-at-length and JAPRA/JARPA II length-frequency data are ignored when fitting the model.

between natural mortality and age. However, the estimates of natural mortality for very young animals based on the Siler relationship are unrealistically high (Fig. 2). Age-0 animals are not recorded while age-1 animals are poorly selected. Consequently the high natural mortality predicted for very young animals is an extrapolation based on natural mortality estimated for older animals.

The reference case estimates of $MSYR_{1+}$[6] are generally very high (>0.2), but some of the sensitivity tests led to estimates of $MSYR_{1+}$ which are essentially zero. A primary reason for the inability to estimate $MSYR_{1+}$ is that the stock is estimated to be close to carrying capacity throughout the assessment period (Figs 3, 7, and 8) for most of the analyses. It is noteworthy that $MSYR_{1+}$ is estimated to be essentially zero when carrying capacity is assumed to be a piecewise linear function of time (as was the case for previous SCAA configurations).

[6]The exploitation rate at which maximum sustainable yield is achieved when vulnerability is uniform on all animals aged one year and older.

Value and impact of JARPA/JARPA II data

Fig. 10 shows that the results are insensitive to dropping the JARPA/JARPA II abundance estimates while retaining other JARPA/JARPAII data. This contrasts with the results by Butterworth and Punt (1990) who highlighted the value of index data to reduce uncertainty regarding estimate of natural mortality. The JARPA/JARPA II abundance estimates are, however, not ignored (even though they are fairly imprecise; Table 1) because replacing the actual estimates by artificial data which exhibit strong trends in abundance resulted in estimated time-trajectories of population size which differed markedly from those for the reference case analysis (results

not shown). This suggests that the JARPA/JARPA II abundance data are providing similar information on trends in abundance to the other data sources.

In contrast to the abundance indices, the results of the SCAA are very sensitive to simultaneously ignoring the JARPA / JARPA II length-frequency and conditional age-at-length data (Fig. 10), which suggests that these data are the primary reason that it is possible to resolve between different trends in abundance and values for natural mortality, a fact also expected from the analysis of Butterworth and Punt (1990). In addition, the standard errors for the estimates of natural mortality are higher (by up to 75% for the young ages and 40% for age 15) when the JARPA/JARPA II age and length data are ignored (results not shown).

Caveats and model structure issues

The model on which the assessment is based is very complicated because it explicitly models five areas and two stocks, allows for time-varying vulnerability, and consequently has over 1,100 parameters. The complexity arises because: (1) some of the parameters (those related to natural mortality) are shared between stocks, necessitating that the two stocks are modelled simultaneously; and (2) the estimates of absolute abundance from IDCR are area-specific, which implies that the proportion of the population in each area needs to be modelled. In principle, the IDCR data could have been treated as relative indices of abundance, but then a constraint would have had to have been imposed on the survey catchability coefficients so that they sum to 1 over all areas in which a stock is found. Explicit allowance for spatial structure would also be needed if mixing of stocks was desired.

The analyses are based on many assumptions, several of which have been explored in the tests of sensitivity. In general, the results are robust to those assumptions. Assumptions which could not be explored in detail in this study related to stock structure are perhaps of greatest concern. In particular, the analyses of this paper assume that there are two stocks of minke whales in Antarctic Areas III–E through VI–W and that there are no areas of mixing.

The application of SCAA in this case is unusual because the fishing mortality rates are generally very small, and the population dynamics are driven primarily by the impact of changes in year-class strength. In this situation, the availability of estimates of absolute abundance is essential. Without such data, it would be impossible to determine the 'scale' of the population. This is evident from sensitivity tests B4 and B5 which vary a key parameter which determines the scale of the population ($g(0)$ for the IDCR estimates of abundance) but the change in AIC is fairly small (Table 7).

Future analyses

Although the SCAA-based assessment is 'mature' in that it has been under development for almost a decade and has been refined through the suggestions and advice of the Scientific Committee, there remain areas for future work. Most of these either require information not yet available or are computationally prohibitive (at least at present). Some key areas where future work could focus on are as follows:

(1) The analyses are based on a somewhat simple stock structure hypothesis, namely that there are two stocks with a hard boundary between them. Other stock hypotheses are worth considering in future work, including a single stock with an isolation-by-distance structure (IWC, In press) and two stocks that mix with each other in part of Area V–W (Pastene, 2006). Further, analyses that used genetic and non-genetic data from JARPA and JARPA II suggested that the spatial distribution of the two stocks has a soft boundary in Areas IV–E and V–W, which depends on year and sex (Kitakado *et al.*, 2014). The analyses by Kitakado *et al.* (2014) have yet to be finalised so could not be used in this paper. In any case, accounting for sex-specific mixing patterns would require a fairly substantial change to the model.

(2) Evaluating the performance of the estimation method using simulations. Some preliminary simulation-estimation analyses were undertaken by Punt and Polacheck (2008). However, the structure of the model as well as the method of parameter estimation has changed substantially since those analyses were undertaken. If simulation testing of the assessment method is desired, it would be sensible to drop the area-structure and move to a parameterisation in which the catchability coefficients for IDCR add to 1 over space as this should substantially speed up the time it takes to fit the model.

(3) Considering alternative likelihood functions for the length-frequency and conditional age-at-length data. The approach of Francis (2014) in particular warrants consideration in this regard.

(4) Basing the analysis on Bayesian techniques. While currently computationally infeasible, use of Bayesian methods should allow the parameters controlling the variance of the random effects for calf survival, growth, spatial distribution, etc. to be estimated rather than being pre-specified.

(5) Analysing the estimates of deviations in calf survival rate to identify the likelihood of possibly causal mechanisms for the changes in recruitment over time. This exercise should, however, be conducted carefully because evidence from fisheries is that relationships between measures of recruitment success and environmental variables can be spurious and can disappear given additional information (e.g. Howell *et al.*, 2013; Myers, 1998). Haltuch and Punt (2011) provide a framework to assess the likelihood of spurious correlations and ways to structure an evaluation of which environmental variables are indeed related to recruitment success.

Can the reason or reasons be determined for the decline in abundance of Antarctic minke whales?

In simple terms, the answer to this question is no. However, some progress has been made. In particular, the results point to the possibility that carrying capacity has changed over time (first increasing then decreasing). However, 'carrying capacity' in the model relates to trends in at least four processes: pregnancy rates, infant survival rates, age-0 survival rates and changes in maturity – the data included in the current paper do not allow these processes to be distinguished. Even if this could be achieved, it would be a

substantial undertaking to link any driving process to the underlying environmental cause. One of the original motivations for the development of an SCAA model was to evaluate the hypothesis of competition effects (IWC, 2005). The changes in carrying capacity may reflect such effects, but the model is not structured to test this hypothesis directly.

As noted above, the results of the paper do provide the types of data (deviations in age-1 abundance from the expectations given the number of mature females – under the assumption that maturity has not changed over time) which could allow an evaluation of which biological and environmental factors may have driven the changes in recruitment success.

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APPENDIX A

SPECIFICATIONS FOR THE POPULATION DYNAMICS MODEL

A. The population dynamics model

Under the assumption that harvesting occurs instantaneously at the start of the year, the number of animals of stock s, sex g and age a at the start of year y, $N_{y,a}^{g,s}$, is given by:

$$N_{y,a}^{g,s} = \begin{cases} 0.5\,\tilde{N}_{y,0}^{s} & \text{if } a = 0 \\ (N_{y-1,a-1}^{g,s} - C_{y-1,a-1}^{g,s})e^{-M_{a-1}^{s}} & \text{if } 1 \le a \le x-1 \\ (N_{y-1,x-1}^{g,s} - C_{y-1,x-1}^{g,s})e^{-M_{x-1}^{s}} + (N_{y-1,x}^{g,s} - C_{y-1,x}^{g,s})e^{-M_{x}^{s}} & \text{if } a = x \end{cases} \quad \text{(App.A.A.1)}$$

where $\tilde{N}_{y,0}^{s}$ is the number of births to stock s at the start of year y (see Equation App.A.C.1, here the sex-ratio at birth is assumed to be 50:50), $C_{y,a}^{g,s}$ is the catch of animals of stock s, sex g and age a during year y, calculated as the sum of the catch of such animals over all fleets i.e.:

$$C_{y,a}^{g,s} = \sum_{f} C_{y,a}^{g,s,f} \quad \text{(App.A.A.2)}$$

$C_{y,a}^{g,s,f}$ is the catch of animals of stock s, sex g and age a by fleet f during year y, M_a^S is the instantaneous rate of natural mortality on animals of stock s and age a (assumed to be time-invariant), and x is the plus-group (set equal to 54).

B. Natural mortality-at-age

The relationship between natural mortality and age is taken to be piecewise linear, with natural mortality for stock I assumed to be a constant proportion of that for stock P:

$$M_a^s = \begin{cases} \delta M^s & \text{if } a \le a_1 \\ M^s[\delta + (1-\delta)\dfrac{(a-a_1)}{(a_2-a_1)}] & \text{if } a_1 < a < a_2 \\ M^s & \text{if } a_2 \le a \le a_3 \\ M^s[1 + (\gamma-1)\dfrac{(a-a_3)}{(a_4-a_3)}] & \text{if } a_3 < a < a_4 \\ \gamma M^s & \text{if } a \ge a_4 \end{cases} \quad \text{(App.A.B.1)}$$

where σM^S is the rate of natural mortality for animals of stock s aged a_1 and younger, M^S is the rate of natural mortality for animals of stock s aged between a_2 and a_3, and γM^S is the rate of natural mortality for animals of stock s aged a_4 and older.

Sensitivity is explored to alternative formulations for natural mortality as a function of age. The Siler (Siler, 1979) relationship between natural mortality and age is:

$$M_a^s = \tilde{M}_1 e^{-\tilde{M}_2 a} + M^s + \tilde{M}_3 e^{-\tilde{M}_4 a/x} \quad \text{(App.A.B.2)}$$

where $\tilde{M}_1$, $\tilde{M}_2$, $\tilde{M}_3$, and $\tilde{M}_4$, are the parameters of the Siler relationship between natural mortality and age.

The second alternative model for the relationship between natural mortality and age is an AR(1) relationship, i.e.

$$\varepsilon_a^M = \varepsilon_{a-1}^M + \phi_a^M \quad \text{(App.A.B.3a)}$$

$$M_a^s = M^s e^{\varepsilon_a^M} \quad \text{(App.A.B.3b)}$$

where ε_a^M is the log of the deviation in the natural mortality between ages a and a–1 (the ϕ_a^M are subject to a normal penalty with standard deviation 0.05).

C. Births

The number of births to stock s during year y depends on the number of females that have reached the age-at-first-parturition at the start of year y and the extent of density-dependence in pregnancy rate and infant survival[1]:

$$\tilde{N}_{y,0}^s = 0.5\, f_0^s B_y^{\mathrm{F},s}\, e^{A^s(1-B_y^{1+,s}/K_y^{1+,s})}\, e^{\varepsilon_y^s} \quad \text{(App.A.C.1)}$$

where $B_y^{\mathrm{F},s}$ is the number of females of stock s that have reached the age-at-first-parturition at the start of year y, i.e.:

$$B_y^{\mathrm{F},s} = \sum_{a=1}^{x} \beta_a N_{y,a}^{g,s} \quad \text{(App.A.C.2)}$$

$B_y^{1+,s}$ is the number of animals aged 1 and older in stock s at the start of year y:

$$B_y^{1+,s} = \sum_g \sum_{a=1}^{x} N_{y,a}^{g,s} \quad \text{(App.A.C.3)}$$

$K_y^{1+,s}$ is the carrying capacity of stock s (expressed in terms of the size of the 1^+ component of the population) at the start of year y, β_a is the proportion of animals of age a that have reached the age-at-first-parturition, f_0^s is the pregnancy rate / infant survival rate in absence of harvesting for stock s, A^s is the resilience parameter for stock s, ε_y^s is the logarithm of the ratio of the expected to actual number of births for stock s during year y. The values for the ε_y^s are not treated as estimable parameters because Equation App.A.C.1 can lead to more calves than mature females for some values for ε_y^s. Therefore, a parameter θ_y^s is estimated for each year and stock, and the number of calves defined as:

$$\tilde{N}_{y,0}^s = 0.5 \frac{\exp(\theta_y^s)}{1+\exp(\theta_y^s)} B_y^{\mathrm{F},s} \quad \text{(App.A.C.4)}$$

The values for the ε_y^s are then computed as:

$$\varepsilon_y^s = \ell n\left(\frac{\exp(\theta_y^s)}{1+\exp(\theta_y^s)} / (f_0^s e^{A^s(1-B_y^{1+,s}/K_y^{1+,s})})\right) \quad \text{(App.A.C.5)}$$

β_a is defined by a logistic curve where 50% of animals reach first parturition at 8.5 years and 95% by 11.5 years. The first age at which an animal may reach first parturition is set equal to 3 years. These specifications were made for consistency with the analyses conducted by Butterworth and Punt (1999).

Allowance is made for the possibility that carrying capacity has changed over time as an autocorrelated time-series, i.e.:

$$K_y^{1+,s} = K_{1930}^{1+,s}\, e^{\xi_y^s} \quad \text{(App.A.C.6a)}$$

$$\xi_y^s = \xi_{y-1}^s + \nu_y^s \quad \text{(App.A.C.6b)}$$

where ν_y^s is the extent to which the logarithm of carrying capacity changes from year y–1 to year y for stock s.

D. Catches and vulnerability

The model-estimate of the catch of animals of stock s, sex g and age a by fleet f during year y depends on the number of animals of stock s, sex g and age a, the exploitation rate by fleet f on animals of sex s during year y, the proportion of animals of stock s in the area where fleet f operates, and the relative vulnerability of animals of sex g and age a during year y to fleet f (assumed to be independent of stock). $C_{y,a}^{g,s,f}$ is computed using the formula:

$$C_{y,a}^{g,s,f} = \sum_l C_{y,a,l}^{g,s,f} \quad \text{(App.A.D.1)}$$

where $C_{y,a,l}^{g,s,f}$ is the catch during year y by fleet f of animals of stock s, sex g and age a that are in length-class l:

$$C_{y,a,l}^{g,s,f} = \tilde{S}_a S_{y,l}^{g,f} F_y^{g,f} X_{y,a,l}^{g,s} P_y^{A,s} N_{y,a}^{g,s} \quad \text{(App.A.D.2)}$$

[1]As calves are not harvested, this formulation for density-dependence conceptually encompasses density-dependent effects in the survival rate of calves.

$S_{y,l}^{g,f}$ is the vulnerability of animals of sex g and length l to fleet f during year y, $\tilde{S}_a$ is a factor to reduce the availability of animals of certain (younger) ages to the fishery, $F_y^{g,f}$ is the exploitation rate due to fleet f on fully-selected (i.e. $S_{y,l}^{g,f} \rightarrow 1$) animals of sex g during year y, $P_y^{A,s}$ is the proportion of stock s that is in the area A (where fleet f is found in area A) during year y (the model assumes that there is no sex- or age-structure to distribution):

$$P_y^{A,s} = \overline{P^{A,s}} e^{\varphi_y^{A,s}} / \sum_{A'} e^{\varphi_y^{A',s}} \qquad \text{(App.A.D.3)}$$

$\overline{P^{A,s}}$ is the expected proportion of stock s that is in area A, $\varphi_y^{A,s}$ is the deviation from the expected proportion for stock s in area A during year y, and $X_{y,a,l}^{g,s}$ is the proportion of animals of stock s, sex g and age a that are in length-class l during year y.

Vulnerability by fleet is assumed to be a function of length, fleet and sex. The model has options which allow vulnerability to be uniform (Equation App.A.D.4a), logistic (Equation App.A.D.4b), or domed-shaped (Equation App.A.D.4c), and to vary over time:

$$S_{y,l}^{g,f} = 1 \qquad \text{(App.A.D.4a)}$$

$$S_{y,l}^{g,f} = (1 + e^{-\ell n 19 (L_l - L_{50,y}^{g,f})/L_{\text{diff}}^{g,f}})^{-1} \qquad \text{(App.A.D.4b)}$$

$$S_{y,l}^{g,f} = \begin{cases} \exp(-(L_l - L_{50,y}^{g,f})^2 / L_{\text{left}}^{g,f}) & \text{if } L_l \le L_{50,y}^{g,f} \\ \exp(-(L_l - L_{50,y}^{g,f})^2 / L_{\text{right}}^{g,f}) & \text{otherwise} \end{cases} \qquad \text{(App.A.D.4c)}$$

where $L_{50,y}^{g,f}$ is the length-at-50%-vulnerability (logistic vulnerability) / length-at-full-vulnerability (dome-shaped vulnerability) for fleet f during year y for animals of sex g:

$$L_{50,y}^{g,f} = L_{50,y-1}^{g,f} + \delta_y^{g,f} \qquad \text{(App.A.D.5)}$$

$\delta_y^{g,f}$ is the 'vulnerability deviation' during year y for fleet f for animals of sex g, $L_{\text{diff}}^{g,f}$ is the width of the length-specific vulnerability ogive for fleet f for animals of sex g, $L_{\text{left}}^{g,f}$ and $L_{\text{right}}^{g,f}$ are the parameters that determine the extent of dome-shapedness for the length-specific vulnerability ogive for fleet f for animals of sex g, and L_l is the length (in ft) corresponding to the mid-point of length-class l.

Time-dependence in vulnerability is modelled by allowing the length-at-50%-/full-vulnerability to change from one year to the next, i.e. the shape of the vulnerability given is the same each year, but the point at which vulnerability first equals 1 change. Time-dependence in vulnerability was modelled in this way to avoid the over-parameterization that might occur if allowance was also made for time-dependence in the parameters that determine the shape of the vulnerability give (this possibility is explored in one of the tests of sensitivity in which $L_{\text{left}}^{g,f}$ changes over time according to Equation App.A.D.5.).

E. Growth

The proportion of animals of stock s and sex g in age-class a that are in length-class l during y, $X_{y,a,l}^{g,s}$, is given by:

$$X_{y,a,l}^{g,s} = \int_{L_l - \Delta L}^{L_l + \Delta L} \frac{1}{\sqrt{2\pi}\sigma_\gamma^{g,s}} e^{-\frac{(L - \bar{L}_{y,a}^{g,s})^2}{2(\sigma_\gamma^{g,s})^2}} dL \qquad \text{(App.A.E.1)}$$

where ΔL is half of the width of each length-class (0.5 ft), $\sigma_\gamma^{g,s}$ is the extent of variability about the growth curve for sex g for animals of stock s, $\bar{L}_{y,a}^{g,s}$ is the expected length of an animal of stock s, sex g and age a during year y, assuming that length-at-age is governed by a von Bertalanffy growth curve and that the growth rate parameter $\kappa_y^{g,s}$ varies over time:

$$\bar{L}_{y,a}^{g,s} = \begin{cases} L_0^{g,s} & \text{if } a = 0 \\ L_\infty^{g,s} - (L_\infty^{g,s} - \bar{L}_{y-1,a-1}^{g,s}) e^{-\kappa_{y-1}^{g,s}} & \text{otherwise} \end{cases} \qquad \text{(App.A.E.2)}$$

$L_\infty^{g,s}$ is the asymptotic length for animals of stock s and sex g, $\kappa_y^{g,s}$ is the value of the Brody growth coefficient for animals of stock s and sex g during year y:

$$\kappa_y^{g,s} = \kappa_{y=1}^{g,s} e^{\upsilon_y^s} \qquad \text{(App.A.E.3)}$$

$L_0^{g,s}$ is the length of an animal of age zero for animals of stock s and sex g, and υ_y^s is the extent to which the growth rate changes from year y–1 to year y for stock s.

F. Initial conditions

The initial conditions ($y_1 = 1930$) correspond to a population at its unexploited equilibrium level:

$$N_{y_1,a}^{g,s} = \begin{cases} 0.5 \tilde{N}_{y,0}^s & \text{if } a = 0 \\ N_{y_1,a-1}^{g,s} e^{-M_{a-1}^s} & \text{if } 1 \le a \le x-1 \\ N_{y_1,x-1}^{g,s} e^{-M_{x-1}^s} / (1 - e^{-M_x^s}) & \text{if } a = x \end{cases} \qquad \text{(App.A.F.1)}$$

where $\tilde{N}_{y,0}^s$ is the expected number of calves in the absence of exploitation for stock s.

The value of the parameter f_0^s is chosen so that the population remains in balance in the absence of exploitation:

$$f_0^s = \left[\sum_{a=1}^{x-1} \beta_a \, e^{-\sum_{a'=0}^{a-1} M_{a'}^s} + \beta_x e^{-\sum_{a'=0}^{x-1} M_{a'}^s} / (1 - e^{-M_x^s}) \right]^{-1} \quad \text{(App.A.F.2)}$$

APPENDIX B

SPECIFICATIONS FOR THE REFERENCE CASE OBJECTIVE FUNCTION

The objective function contains contributions from the data and from penalties on some of the parameters:

$$L = \sum_i O_i \, \ell \mathrm{n} L_i + \sum_j PEN_j \quad \text{(App.B.1)}$$

where ℓnL_i is the contribution of the ith data source to the objective function, PEN_j is the contribution of the jth penalty term to the objective function, and O_i is a factor to account for overdispersion.

The data included in the assessment are the annual catches (by fleet and sex), the estimates of abundance (IDCR and JARPA/JARPA II), the catch length-frequency data and the conditional age-at-length data, while there are penalties on the magnitudes of the deviations from the expected number of births (Equation App.A.C.1), on the inter-annual deviations in the carrying capacity (Equation App.A.C.6b), on the inter-annual deviations in the growth rate (Equation App.A.E.3), on the inter-annual variation in the proportion of the population in each area (see Equation App.A.D.3), and on the inter-annual deviations in vulnerability (Equation App.A.D.5). Each of these contributions is discussed in turn below. The equations listed below assume that data for each data-type are available for every year, and for all areas and fleets. This is not the case in reality, and the equations are modified appropriately in the absence of data for specific years, areas and fleets.

A. Catches

The contribution of the catches to the objective function is based on the assumption that any errors when measuring the catch are log-normally distributed[1]:

$$\tilde{}\mathrm{n}L_1 = \sum_y \sum_g \sum_f \left\{ \frac{1}{2\sigma_C^2} \sum_y (\tilde{}\mathrm{n}\tilde{C}_y^{g,f} - \tilde{}\mathrm{n}C_y^{g,f})^2 \right\} = Const \quad \text{(App.B.A.1)}$$

where $\tilde{C}_y^{g,f}$ is the actual catch by fleet f of animals of sex g during year y, $C_y^{g,f}$ is the model-estimate of total catch by fleet f of animals of sex g during year y:

$$C_y^{g,f} = \sum_s \sum_a C_{y,a}^{g,s,f} \quad \text{(App.B.A.2)}$$

σ_C quantifies the extent of variation in catches.

B. Estimates of abundance

The contribution of the estimates of abundance to the objective function is based on the assumption that sampling error is log-normally distributed:

$$\tilde{}\mathrm{n}L_2 + \sum_A \sum_y \left\{ \frac{1}{2(\tilde{\sigma}_y^A)^2} (\tilde{}\mathrm{n}V_y^A = \tilde{}\mathrm{n}(\chi^A \, B_y^{\mathrm{Surv},A}))^2 \right\} = Const \quad \text{(App.B.B.1)}$$

where V_y^A is the estimate of abundance for area A and year y, χ^A is the uncorrected bias factor for area A, $\tilde{\sigma}_y^A$ is the measurement error standard deviation, determined from the observation error standard deviation and the extent of additional variance:

$$(\tilde{\sigma}_y^A)^2 = \tau^2 + (\phi_y^A)^2 \quad \text{(App.B.B.2)}$$

τ^2 is the extent of additional variance (set to 0 for the calculations of this paper), ϕ_y^A is the coefficient of variation of V_y^A, $V_y^{\mathrm{Surv},A}$ is the model-estimate of the total (1+) abundance in area A at the start of year y:

$$B_y^{\mathrm{Surv},A} = \sum_s \sum_g \sum_{a>0} \sum_l P_y^{A,s} X_{y,a,l}^{g,s} S_{y,l}^{g,f^*} N_{y,a}^{g,s} \quad \text{(App.B.B.3)}$$

f^* is the fleet to which the abundance estimates pertain (set to the post-1987 Japanese fleet for the JARPA / JARPA II indices; set to uniform selectivity for the IDCR indices).

[1]Note that very high weight is assigned to this component of the objective function so the model effectively replicates the actual catches exactly.

C. Length-frequency data

The contribution of the length-frequency data to the objective function is based on the assumption that the catch by sex and fleet is taken multinomially from the vulnerable population:

$$\ell \mathrm{n}L_3 = -\sum_y \sum_f \sum_g M_y^{g,f} \sum_{l=l_{\min,y}}^{l_{\max,y}} \rho_{y,l}^{g,f} \ell \mathrm{n}(\hat{\rho}_{y,l}^{g,f} / \rho_{y,l}^{g,f}) + Const \qquad \text{(App.B.C.1)}$$

where $M_y^{g,f}$ is the effective sample size for the length-frequency data for animals of sex g taken by fleet f during year y (set equal to the number of animals of sex g taken by fleet f during year y for which information on length is available, potentially multiplied by an year-specific overdispersion factor), $\rho_{y,l}^{g,f}$ is the observed fraction of the catch of animals of sex g taken by fleet f during year y that is in length-class l, $\hat{\rho}_{y,l}^{g,f}$ is the model-estimate of the fraction of the catch of animals of sex g taken by fleet f during year y that is in length-class l:

$$\hat{\rho}_{y,l}^{g,f} = \frac{\sum_s \sum_a C_{y,a,l}^{g,s,f}}{\sum_{s'} \sum_{a'} \sum_{l'} C_{y,a',l'}^{g,s',f}} \qquad \text{(App.B.C.2)}$$

Lengths $l_{\min,y}$ and $l_{\max,y}$ define the plus and minus groups for the length-frequency data for year y (data and model-predictions for animals with length less than $l_{\min,y}$ are pooled in the $l_{\min,y}$ length-class while data and model-predictions for animals with length greater than $l_{\max,y}$ are pooled in the $l_{\max,y}$ length-class).

D. Conditional age-at-length data

The age data are included in the objective function under the assumption that sampling for age is multinomial conditioned on length:

$$\tilde{}\mathrm{n}L_4 + \sum_y \sum_f \sum_g \sum_{l=l_{\min,y}}^{l_{\max,y}} \tilde{M}_{y,l}^{g,f} \sum_{a=a_{\min,y}}^{a_{\max,y}} \theta_{y,a,l}^{g,f} \tilde{}\mathrm{n}\left(\hat{\theta}_{y,a,l}^{g,f} / \theta_{y,a,l}^{g,f}\right) + Const \qquad \text{(App.B.D.1)}$$

where $\tilde{M}_{y,l}^{g,f}$ is the effective sample size for the age breakup of the animals of sex g in length-class l taken by fleet f during year y (set equal to the number of animals of sex g in length-class l taken by fleet f during year y for which information on length and age is available, potentially multiplied by a year-specific overdispersion factor), $\theta_{y,a,l}^{g,f}$ is the observed fraction of the catch of animals in length-class l of sex g taken by fleet f during year y that were aged to be age a, $\hat{\theta}_{y,a,l}^{g,f}$ is the model-estimate of the fraction of the catch of animals in length-class l of sex g taken by fleet f during year y that were aged to be age a:

$$\hat{\theta}_{y,a,l}^{g,f} = \frac{\sum_s \tilde{C}_{y,a,l}^{g,s,f}}{\sum_{s'} \sum_{a'} \tilde{C}_{y,a',l}^{g,s,f}} \qquad \text{(App.B.D.2)}$$

$\tilde{C}_{y,a,l}^{g,s,f}$ is the model-estimate of the number of animals of sex g and stock s in length-class l caught by fleet f during year y that would have been aged to be age a:

$$\tilde{C}_{y,a,l}^{g,s,f} = \sum_{a'} Y_{a,a',y} C_{y,a',l}^{g,s,f} \qquad \text{(App.B.D.3)}$$

$Y_{a,a',y}$ is the fraction during year y of animals of sex g and age a' that are aged to be age a (the age-reading error matrix):

$$Y_{a,a',y} = \int_{a-0.5}^{a+0.5} \frac{1}{\sqrt{2\pi}\sigma_{a',y}^{''}} e^{-\frac{(\lambda-\beta_{a',y})^2}{2(\sigma_{a',y}^{''})^2}} d\lambda \qquad \text{(App.B.D.4)}$$

$\tilde{\beta}_{a,y}$ is the expected age based on age-readings for an animal of true age a during year y, and $\sigma_{a,y}''$ is the standard error of the age-estimate for an animal of true age a during year y. The year-dependence of $\tilde{\beta}_{a,y}$ and $\sigma_{a,y}''$ is related to the ager who conducted the age-readings in year y (Table App.B.1), while age-dependence is modelled by allowing and $\sigma_{a,y}''$ to change linearly with age.

$$\tilde{\beta}_{a,y} = \tilde{\beta}_{L,y} + (\tilde{\beta}_{H,y} - \tilde{\beta}_{L,y})\frac{a}{70}; \quad \sigma_{a,y}^{''} = \sigma_{L,y}^{''} + (\sigma_{H,y}^{''} - \sigma_{L,y}^{''})\frac{a}{70} \qquad \text{(App.B.D.5)}$$

Table App. B.1

Parameters which determine the age-reading error matrix. These values correspond to the 'Lockyer unbiased' analysis of Kitakado *et al*. (2013). The values for L and H are 0 and 70 respectively.

Year	Reader	$\tilde{\beta}_L$	$\tilde{\beta}_H$	σ_L''	σ_H''
1971/72–1979/80	Masaki	3.0837	58.7940	1.5531	1.5531
1980/81–1989/90	Kato	2.4545	56.0060	0.5391	7.3718
1990/91–1991/92	Zenitani	1.0300	62.8530	0.4637	3.6614
1992/93	Kato	2.4545	56.0060	0.5391	7.3718
1993/94–2004/05	Zenitani	1.0300	62.8530	0.4637	3.6614
2005/06–2011/12	Bando	1.6355	63.6440	0.6588	3.4128

Ages $a_{\min,y}$ and $a_{\max,y}$ define the plus and minus groups for the ageing data for year y, i.e. data and model-predictions for animals with age greater than $a_{\max,y}$ are pooled at age $a_{\max,y}$ [2] and those with age less than $a_{\min,y}$ are pooled at age $a_{\min,y}$.

E. Penalties

The penalty on the deviations from the expected number of births is based on the assumption that these deviations are log-normally distributed:

$$PEN_1 = \frac{1}{2\sigma_R^2}\sum_s\sum_y(\varepsilon_y^s)^2 \qquad \text{(App.B.E.1)}$$

where σ_R is the standard deviation of ε_y^s.

The penalty on the changes over time in the vulnerability deviations is based on the assumption that these deviations are normally distributed:

$$PEN_2 = \frac{1}{2\sigma_S^2}\sum_g\sum_y\sum_f(\delta_y^{g,f})^2 \qquad \text{(App.B.E.2)}$$

where σ_S is the extent of inter-annual variation in the age-at-50%-vulnerability.

The penalty on the annual deviations in the proportion of each stock in each area is based on the assumption that these deviations are normally distributed:

$$PEN_3 = \frac{1}{2\sigma_P^2}\sum_s\sum_y\sum_A(\varphi_y^{A,s})^2 \qquad \text{(App.B.E.3)}$$

where σ_P is the extent of variation in the distribution of the stock.

The penalty on the inter-annual changes in the von Bertalanffy growth rate parameter is based on the assumption that these deviations are normally distributed:

$$PEN_4 = \frac{1}{2\sigma_\kappa^2}\sum_s\sum_y(\upsilon_y^s)^2 \qquad \text{(App.B.E.4)}$$

where σ_κ is the extent of variation in changes in growth rate.

The penalty on the inter-annual changes in the logarithm of carrying capacity is based on the assumption that these deviations are normally distributed:

$$PEN_5 = \frac{1}{2\sigma_K^2}\sum_s\sum_y(\nu_y^s)^2 \qquad \text{(App.B.E.5)}$$

where σ_k is the extent of variation in changes in carrying capacity.

[2]Note that the evaluation of the impact of age-reading error is determined before the application of the plus-group.

Validation of the use of firearms for euthanising stranded cetaceans

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ABSTRACT

Efforts to euthanise stranded cetaceans remain highly variable in their outcomes, with few field tested operational procedures available. This study sought to validate the efficacy of using modern firearms technology to euthanise small (<6m length) stranded cetaceans. Post-mortem evidence was gathered from the standardised shooting of cetacean cadavers (n = 10), representing six species, using .30 caliber (7.62mm) firearms and blunt solid copper-alloy non-deforming projectiles, in southwestern Australia. The six species studied were Risso's dolphin, common dolphin, bottlenosed dolphin, pygmy sperm whale, Cuvier's beaked whale, and humpback whale. Post-mortem data revealed that 100% of bullet wound tracts fully penetrated the skulls of shot animals, with associated indirect skull fracturing, secondary bone missiles and brain parenchyma laceration. The results suggest that appropriate firearms technology is fully capable of inducing instantaneous fatal pathology to the central nervous system of these species. In comparison to alternative methods for the euthanasia of stranded cetaceans, the use of firearms is associated with superior animal welfare outcomes, public safety levels and accessibility. This paper provides a template for the safe, humane and repeatable use of this technique to euthanise <6m length stranded cetaceans.

KEYWORDS: AUSTRALASIA; STRANDINGS; STRESS; EUTHANASIA

INTRODUCTION

In cetacean stranding events, euthanasia is considered a desirable animal welfare outcome when animals are deemed non-viable for release. The novel size and physiology of cetaceans dictates that routine euthanasia techniques (AVMA, 2013) are rarely applicable. Methods for euthanising stranded cetaceans remain highly variable and poorly standardised (Barco *et al.*, 2012). With recent research showing increases in cetacean stranding incidence (e.g. Coughran *et al.*, 2013), increasing anthropogenic causes for stranding events (Barlow and Gisiner, 2006), the projected effects of climate change (Schumann *et al.*, 2013), and suggestions of declining marine mammal health worldwide (Gulland and Hall, 2007), reliable euthanasia methods for stranded cetaceans are increasingly required. Acceptable euthanasia methods must offer high safety levels for personnel and public health, be publicly acceptable and cost-effective (Harms *et al.*, 2014) but above all else, must be humane and offer the most rapid death possible (Øen and Knudsen, 2007).

Approaches to cetacean euthanasia have included the use of chemical injection (Harms *et al.*, 2014), explosives (Coughran *et al.*, 2012), exsanguination (Harms *et al.*, 2014) and firearms (Blackmore *et al.*, 1995). Despite extensive research into humane killing methods for whale hunting (Gales *et al.*, 2008; Kestin, 1995; Knudsen and Øen, 2003; O'Hara *et al.*, 1999; Øen and Knudsen, 2007), little of this knowledge has been applied to stranding scenarios. Animal welfare studies into livestock slaughter and marine mammal hunting have produced the most scientifically rigorous templates for assessing killing methods. The two key parameters identified for assessing the humaneness of any killing method are the duration and intensity of suffering induced before the animal becomes permanently insensible (Mellor and Littin, 2004; Newhook and Blackmore, 1982). While the intensity of suffering is a difficult parameter to quantify or objectively assess, duration of suffering is relatively simple to measure (Knudsen, 2005). A recent scientific focus on quantifying animal welfare outcomes has seen the parameter time to death (TTD) commonly adopted as a parameter for assessing wildlife killing techniques (e.g. Cowled *et al.*, 2008; Hampton *et al.*, 2014a; Gales *et al.*, 2008). Physical euthanasia methods are generally considered to be the only killing methods capable of providing instantaneous deaths (Grandin, 2006). As such, the proportion of animals for which TTD is zero, known as the instantaneous death rate (IDR) is commonly cited to benchmark physical killing methods (Hampton *et al.*, 2014a), in particular for marine mammals (Gales *et al.*, 2008). The International Whaling Commission (IWC) has used TTD and IDR to assess cetacean killing methods for more than thirty years (IWC, 1981; 2012).

Firearms have been used for killing cetaceans (<6m length) in commercial and indigenous whale harvesting operations for decades (IWC, 1981; Øen and Knudsen, 2007). The studies of Ingling (1997) and Øen and Knudsen (2007) demonstrated that large calibre rifles are adequate for the rapid euthanasia of harpooned bowhead whales (*Balaena mysticetus*) and minke whales (*Balaenoptera acutorostrata*). However, the techniques described by Øen and Knudsen (2007) have not been widely utilised for euthanising stranded cetaceans (Barco *et al.*, 2012). One of the impediments to the employment of these methods is the inaccessibility of the large centre-fire calibers described (.577, Ingling, 1997; .375,

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.458, Øen and Knudsen, 2007) to wildlife management staff. For management techniques to receive widespread uptake, they must be accessible. In Australia, North America and New Zealand, .30 calibre (7.62mm) centre-fire firearms are used extensively for terrestrial wildlife management (Choquenot *et al.*, 1999; Hunt *et al.*, 2006; IWC, 2012; Thomas, 2013). Blackmore *et al.* (1995) identified the need for further ballistic research to develop or identify suitable projectiles for euthanising medium-size cetaceans.

Protocols for testing the ballistic properties of any particular firearm-projectile pairing have been well described (Thali *et al.*, 2002). The method of firing standardised shots into appropriate cadavers has been widely utilised in both humans (Kaplan *et al.*, 1998; Voiglio *et al.*, 2004) and animal species (Blackmore *et al.*, 1995; Daoust and Cattet, 2004; Grund *et al.*, 2010). This technique is more scientifically rigorous than the use of ballistic gel (Ingling, 1997; Zhang *et al.*, 2005) and allows relevant ballistic parameters to be repeatedly quantified without impacting on animal welfare (see Blackmore *et al.*, 1995). This paper attempts to scientifically validate the efficacy of .30 calibre firearms and appropriate projectiles as a euthanasia tool for moribund cetaceans <6m in length. We used cadaver studies to examine the cranial pathology induced by firearms euthanasia in a variety of smaller cetacean species commonly subjected to stranding. Following the approaches of Blackmore *et al.* (1995), Øen and Knudsen (2007) and Mörner *et al.* (2013), we combined a standardised shooting method with detailed post-mortem examinations. The research was a collaborative project between the Department of Parks and Wildlife (DPaW) and the Perth Zoo, and was conducted in the southwest of Western Australia during 2013.

MATERIALS AND METHODS

Animal specimens

Ten dead stranded cetaceans, representing six species: Risso's dolphin (*Grampus griseus*), Common dolphin (*Delphinus delphis*), Common bottlenosed dolphin (*Tursiops truncatus*), Pygmy sperm whale (*Kogia breviceps*), Cuvier's beaked whale (*Ziphius cavirostris*) and humpback whale (*Megaptera novaeangliae*), were accessed opportunistically between April and September 2013 in southwestern Australia. Past studies have identified cetaceans with a body length of 5–9m as an appropriate upper limit for the use of firearms for euthanasia (Barco *et al.*, 2012; Blackmore *et al.*, 1995; Greer. *et al.*, 2001; IWC, 2006). As such, only animals <6m in length were considered for inclusion in the study. Southwestern Australia was selected as a field site due to the high diversity of species available for experimentation, combined with a relatively high incidence of stranding events (Coughran *et al*., 2013). A long term cetacean stranding record (Groom and Coughran, 2012) for Western Australia reports 37 cetacean species observed off the coast and 34 species in the stranding record. All animals were freshly dead, with evidence of post-mortem change indicating they had been dead for less than 12 hours.

Shooting methodology

All cadavers were shot in a standardised manner (see Fig.1a), using a single dorsal midline aim point, while in ventral recumbency, following the methodology of Blackmore *et al.* (1995). The aim point is described as 40–100mm caudal to the blowhole, at a 45° angle towards the middle of an imaginary line connecting the anterior edges of two flippers (Blackmore *et al.* 1995). Shots were fired 0.5–1.0m from the surface of the animal. All cadavers were shot on land, rather than in water, over sandy substrate. Three *Browning* hunting rifles, of calibre .300 *Winchester* Magnum (.300 WM; one cadaver), .300 *Winchester* Short Magnum (.300 WSM; six cadavers), and .308 *Winchester* (.308 WIN; three cadavers) were used (Fig. 1b; Table 1).

All rifles fired the same projectiles; 12g/180 grain *Woodleigh* hydrostatically stabilised blunt non-deforming solid bullets (Table 1; Fig. 1b). These projectiles are constructed from copper-alloy (see Thomas, 2013) and have been developed to allow deep tissue penetration in large, thick-boned game species. These projectiles were chosen on the basis that blunt-nosed non-deforming projectiles have previously been shown to successfully penetrate cetacean craniums (Øen and Knudsen, 2007) while shotgun solids,



Fig. 1. Standardised shooting methodology used in this study. (a) Standardised shooting technique for post-mortem ballistic testing on a neonate humpback whale (*Megaptera novaeangliae*) in ventral recumbency. (b) The non-traditional design of the .30 calibre blunt solid copper-alloy non-deforming *Woodleigh* hydrostatic projectiles used for standardised shooting. The shell casings are .300 *Winchester* Short Magnum (left) and .308 *Winchester* (right).

Table 1

Ballistic properties of .30 caliber (7.62mm) firearms used in this study (Barnes, 2009).

Calibre	Projectile grain	Projectile weight (g)	Muzzle velocity (ms^{-1})	Muzzle energy (J)
.300 *Winchester* Magnum	180	12	959	5,385
.300 *Winchester* short Magnum	180	12	943	5,190
.308 *Winchester*	180	12	800	3,890

expanding projectiles and pointed-nosed projectiles have proven unreliable (Blackmore *et al.*, 1995; IWC, 2000). The sectional density (SD) of a projectile, the ratio of a projectile's mass to its cross-sectional area, is an important terminal ballistic parameter influencing tissue penetration (see Ordog *et al.*, 1984). In terminal ballistics, the SD of a firearm projectile is calculated as the weight of the projectile, in pounds (lb), divided by the square of the projectile's diameter, in fractions of an inch, (w/d^2). The SD of the projectiles used in this study was 0.286. All projectiles were factory loaded.

Post-mortem examination

After shooting, cadavers were subjected to veterinary post-mortem examination to record the nature of cranial pathology sustained. The locations of entry and exit wounds were recorded, the head was dissected from the body at the atlanto-occipital joint (Fig. 2a) and the skull and brain were subjected to detailed post-mortem examination (Fig. 2b). Gross pathology of the brain and surrounding organs attributable to bullet wound tract injuries were recorded following the principles of Hollerman *et al.* (1990) and Di Maio (1999). Morphometric parameters were recorded from each animal, including total body length, and maximum head diameter, including cranium and surrounding soft tissues (Table 2). Radiographic documentation of the entire head was employed for the six animals with maximum cranial diameter <400mm (Fig. 2b), being the only animals for which our equipment possessed sufficient power for radiographic resolution.

All summary statistics are presented as mean ± standard deviation (range, sample size).

RESULTS

As noted, all animals were freshly dead cetaceans under 6m in length. Six species were represented (Table 2). Mean total body length was 2.7 ± 1.1 (range 1.3–4.3, n = 10) meters. Mean maximum head diameter was 0.37 ± 0.15 (range 0.18–0.60, n = 10) meters. In all cases, bullet placement was sufficiently accurate to achieve penetration of the cranial cavity. All specimens were shot through the midline hindbrain with complete penetration of the dorsal and ventral surfaces of the skull (Fig. 2a, b). The permanent bullet wound tracts through the brain parenchyma were limited to a tract roughly the diameter of the projectile (Fig. 2b). There was widespread evidence of meningeal trauma in all cases. Intra-cranial in-driven bone fragments and extensive indirect skull fracturing were present in all cases (Fig. 2b). No projectiles or projectile fragments were recovered from any cranial tissues from any animals upon dissection, and evidence of intra-animal projectile fragmentation was not detected radiographically in any of the six animals x-rayed (Fig. 2b).

DISCUSSION

Wound ballistics

The field of science relating to the interaction between a projectile and a target is known as terminal ballistics. When the target struck is living tissue, the patterns observed constitute the field of study known as wound ballistics (Fackler, 1988). The killing power of a projectile is a function of the energy it carries and the behaviour of the projectile. There are three distinct mechanisms of ballistic injury: crushing of tissue producing a permanent tract; temporary cavitation; and hydrostatic shock (Caudell, 2013). The predominant mechanism of injury for any individual gunshot is highly dependent on the behaviour of the individual projectiles. Based upon their terminal ballistic behaviour, centre-fire projectiles can be divided into three

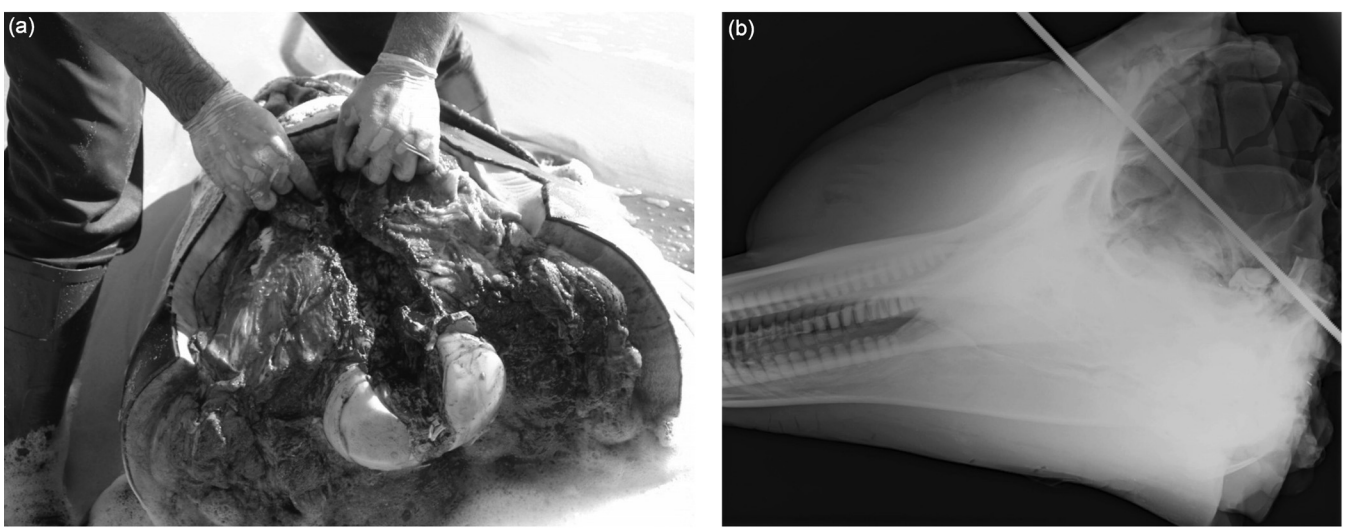

Fig. 2. Patterns of ballistic pathology evident at post-mortem examination. (a) Gross dissection of the permanent bullet wound tract from a neonate humpback whale (*Megaptera novaeangliae*) in ventral recumbency, dissected through the atlanto-occipital joint. (b) Contrast radiographic study using a .30 inch diameter threaded metallic rod passed through the permanent bullet wound tract in a bottlenosed dolphin (*Tursiops aduncus*) in ventral recumbency, dissected through the atlanto-occipital joint.

Table 2
Individual cadavers examined in this study.

Species	Length (m)	Head diameter (m)	Firearm calibre	Projectile	Aim point	Dorsal skull penetration	Ventral skull penetration	Projectile fragmentation	Indirect skull fractures
Risso's dolphin	2.7	0.36	.308 WIN	Hydrostatic 180 grain	Dorsal	Yes	Yes	No	Yes
Common dolphin	1.8	0.18	.308 WIN	Hydrostatic 180 grain	Dorsal	Yes	Yes	No	Yes
Bottlenose dolphin	1.3	0.18	.300 WSM	Hydrostatic 180 grain	Dorsal	Yes	Yes	No	Yes
	2.7	0.26	.300 WSM	Hydrostatic 180 grain	Dorsal	Yes	Yes	No	Yes
Pygmy sperm whale	2.5	0.41	.300 WSM	Hydrostatic 180 grain	Dorsal	Yes	Yes	No	Yes
	1.8	0.29	.300 WSM	Hydrostatic 180 grain	Dorsal	Yes	Yes	No	Yes
	1.9	0.31	.308 WIN	Hydrostatic 180 grain	Dorsal	Yes	Yes	No	Yes
Cuvier's beaked whale	4.2	0.55	.300 WSM	Hydrostatic 180 grain	Dorsal	Yes	Yes	No	Yes
Humpback whale	4.2	0.51	.300 WM	Hydrostatic 180 grain	Dorsal	Yes	Yes	No	Yes
	4.3	0.60	.300 WSM	Hydrostatic 180 grain	Dorsal	Yes	Yes	No	No

groups; rapid expansion (RE), controlled expansion (CE) and non-deforming projectiles (Caudell *et al.*, 2012). Expanding projectiles (RE and CE) are designed to expand and/or fragment upon penetration, and are commonly used to hunt thin-skinned terrestrial mammal species. Non-deforming projectiles are designed to penetrate deep into the body after striking without fragmenting, and are used for very large, heavily boned or muscled mammal species. Projectile shape also has an important bearing on wound ballistic patterns, with blunt-nosed projectiles more effective at penetrating rigid structures and less prone to trajectory deviation than pointed-nose projectiles (Øen and Knudsen, 2007).

While crushing of tissues is an important process for RE and CE projectiles, non-deforming projectiles are more reliant on temporary cavitation and hydrostatic shock to induce death. The killing effect of hydrostatic shock is of particular relevance for high energy and non-deforming projectiles. The process of temporary cavitation is particularly important to the pathology induced in inelastic tissues, especially the cranium (Karger *et al.*, 1998; Zhang *et al.*, 2005). The structure of the cranium generates wound ballistic features not encountered with other parts of the anatomy (Karger *et al.*, 1998). The inelastic nature of the cranium ensures that the temporary wound cavity created by a high velocity projectile plays a much larger part in the creation of pathology than in more elastic tissues (Zhang *et al.*, 2005). The high intracranial pressures generated by the temporary cavitation process within the inelastic environment of the skull create indirect skull fractures, cortical contusions and perivascular haemorrhage (e.g. Øen and Knudsen, 2007). The generation of secondary bone projectiles from penetrating skull injuries is also an important mechanism underlying the killing potential of cranial gunshot wounds (Karger *et al.*, 1998). These principles are well established in human medicine (Quatrehomme and İşcan, 1999; Zhang *et al.*, 2005) but their application in wildlife shooting studies has lagged (Caudell, 2013).

In the present study, extensive cranial trauma was observed in all cadavers, with full penetration of the dorsal and ventral skull in all cases. Despite the absence of projectile fragmentation or expansion, the temporary cavitation effect of the high energy projectiles induced widespread indirect skull fractures, in-driven bone fragments and meningeal trauma. The use of specialised, blunt-nosed projectiles that are designed to withstand fragmentation, deformation or trajectory deviation (see Thomas, 2013) resulted in 'through-and-through' permanent wound tracts in all cases. The findings of this study provide strong evidence that insensibility and death would have been instantaneous in all cases. The results of this study suggest that rifle calibres smaller than those recommended in the past for the shooting of larger cetaceans (Ingling, 1997; Øen and Knudsen, 2007) can be effective if used with specialised projectiles for euthanising smaller cetaceans.

Results from other cetacean shooting studies

The IWC actively encourages member nations to provide it with records from all whale killing events, including details on TTD and IDR (Brakes and Donoghue, 2006), as determined according to the criteria of Knudsen (2005), and recognised by the IWC. The results are made publicly available on the IWC's website every year, and include methods and outcomes but provide limited detailed information when compared to a peer-reviewed case study. We searched all reports for case studies involving the use of .30 calibre firearms to euthanise stranded cetaceans and found 218 cases, comprising five species and three different .30 calibers (Table 3). Firearms used were .30–06, .308 and .303 calibers, and projectiles were 150 grain soft-point bullets. While firearm calibres and projectile design differed from our post-mortem study, all cases utilised an identical shooting method. All cases were recorded from New Zealand, where several recent mass stranding events necessitated the euthanasia of large numbers of cetaceans in an identical manner. Three animals were reported for which TTD was not

Table 3
Instantaneous death rates (IDRs) for .30 calibre (7.62mm) firearm euthanasia cases reported in published literature.

Year	Country	Species	*n*	Calibre	Projectile grain	Projectile design	Aim point	IDR (%)	Reference
2005	New Zealand	Long-finned pilot whale	41	.30–06	150	Soft point	Dorsal	100	IWC (2006)
2010–11	New Zealand	Long-finned pilot whale	48	.30–06	150	Soft point	Dorsal	100	IWC (2011)
2010–11	New Zealand	Long-finned pilot whale	48	.303	150	Soft point	Dorsal	100	IWC (2011)
2010–11	New Zealand	Dwarf minke whale	1	.30–06	150	Soft point	Dorsal	100	IWC (2011)
2010–11	New Zealand	Pygmy sperm whale	1	.303	150	Soft point	Dorsal	100	IWC (2011)
2011–12	New Zealand	Long-finned pilot whale	63	.30–06	150	Soft point	Dorsal	96.8	IWC (2012)
2011–12	New Zealand	Pygmy sperm whale	8	.30–06	150	Soft point	Dorsal	100	IWC (2012)
2011–12	New Zealand	Pygmy sperm whale	4	.303	150	Soft point	Dorsal	100	IWC (2012)
2011–12	New Zealand	Pygmy sperm whale	2	.308	150	Soft point	Dorsal	100	IWC (2012)
2011–12	New Zealand	Strap-toothed whale	1	.308	150	Soft point	Dorsal	100	IWC (2012)
2011–13	New Zealand	Humpback whale	1	.308	150	Soft point	Dorsal	0	IWC (2012)
Total			**218**					**Mean: 98.6**	

zero: two long-finned pilot whales, *Globicephala melas* and one humpback whale, *Megaptera novaeangliae* (IWC, 2012). The mean IDR for the 218 cases was 98.6% (Table 3).

Instantaneous death rate (or equivalent terminology) is considered the key parameter by which the welfare outcomes of many killing methods are benchmarked, including livestock slaughter methods (Grandin, 2006) and commercial whale harvesting techniques (Gales *et al.*, 2008). The calculated IDR of 98.6% from all published .30 calibre firearm cetacean euthanasia attempts reviewed is extremely high in comparison to other reported physical killing methods (e.g. Lewis *et al.*, 1997) including the stunning of domesticated livestock in controlled abattoir conditions (Grandin, 2006; Newhook and Blackmore, 1982). While the .30 calibre firearms used in New Zealand differ slightly from those used for cadaver studies, the result suggests that the professional shooting of smaller (<6m length) stranded cetaceans is one of the most humane killing methods documented.

Comparison with other euthanasia methods

In the field of small animal veterinary medicine, injectable chemical euthanasia is widely regarded as the preferred euthanasia method (AVMA, 2013). This preference, combined with high public acceptance of the technique and its 'aesthetically pleasing' nature, has led to the approach being preferred for cetacean euthanasia in some jurisdictions (Barco *et al.*, 2012; Harms *et al.*, 2014). There are important considerations when dealing with wild, rather than domesticated species, with chemical euthanasia methods requiring manual handling and restraint of animals that is likely stressful for non-domesticated species. In addition, the inherent difficulty in accessing the vasculature of cetaceans, as well as their sheer size, dictates that chemical euthanasia methods cannot generate instantaneous deaths and are invariably associated with prolonged TTD (Dunn, 2006; Kolesnikovas *et al.*, 2012; March, 2012). Harms *et al.* (2014) reported TTD ranging from minutes to hours for a recently developed chemical euthanasia approach. There is a compelling argument that the shortest TTD should be the overwhelming priority for euthanasia methods, over concerns such as public acceptance or aesthetics (Coughran *et al.*, 2012; Øen and Knudsen, 2007). In addition, methods involving protracted TTD are impractical for mass stranding scenarios (e.g. IWC, 2006). There are also increasing concerns surrounding the eco-toxicological risks associated with the use of chemical methods (Barco *et al.*, 2012). In particular, the high environmental pollution risks associated with the use of barbiturates have been acknowledged (Barco *et al.*, 2012; Harms *et al.*, 2014; Otten, 2001; Peschka *et al.*, 2006) and exemplified by a recent secondary toxicity or 'relay toxicity' case study (Bischoff *et al.*, 2011). Through the use of lead-free ammunition (Caudell *et al.*, 2012; Thomas, 2013), the method presented here poses negligible risk of eco-toxicity.

Physical methods, and particularly firearms, are used as the preferred euthanasia methods for many large mammal species (e.g. Blackmore *et al.*, 1995; Longair *et al.*, 1991), due to their capacity to deliver instantaneous killing, low levels of environmental contamination and their accessibility to non-veterinarians. Despite these benefits, perceptions of poor aesthetics, public acceptance and safety have seen the professional use of firearms decline in recent decades, particularly in charismatic species (e.g. Barco *et al.*, 2012; Herbert, 2004; Nimmo and Miller, 2007). The shooting method described in this study offers a high level of operator and public safety through the use of professional staff, appropriate equipment and adherence to a standard operating procedure (Hampton *et al.*, 2014b). However, there are possible limitations of the described technique including the difficulty of animal positioning on steep or rocky substrate, the availability of the specialised projectiles required and the importance of the shooter being familiar with anatomical landmarks.

Wider acceptance and use of firearms as a humane tool in wildlife management has been hindered by a lack of understanding of wound ballistics (Caudell, 2013), a scarcity of studies providing scientific validation of firearms efficacy (e.g. Parker *et al*., 2006; Hampton *et al.*, 2014a) and a lack of scientific rigor in shooting studies (Daoust *et al.*, 2014). The shooting approach presented here is a highly humane method for euthanising cetaceans of <6m using widely accessible equipment. We encourage further cadaver studies into the use of firearms to euthanise cetaceans in the medium size range (6–9m), for which firearm use is currently considered contentious (Blackmore *et al.*, 1995; Greer *et al.*, 2001; IWC, 2006).

CONCLUSIONS

The post-mortem evidence presented in this study demonstrate that shooting is a highly reliable and humane

method for euthanising moribund small sized cetaceans (<6m). Post-mortem results demonstrate consistent skull penetration and cerebral trauma in all cases, while ante-mortem data collected by the IWC indicates a very high IDR. The method was found to be effective in all species examined and was associated with low operator and eco-toxicity risks. The calibres of firearms examined are readily available worldwide and have common applications in wildlife management for the shooting of many terrestrial species. The firearms method presented here shares the advantages of being accessible to non-veterinarians and of not requiring specialised equipment, beyond projectiles. The cadaver examination approach, originally described by Blackmore *et al.* (1995), is recommended in determination of optimum caliber-projectile combinations for the euthanasia of other species where methods remain contentious. Humaneness, rather than concerns over aesthetics or public acceptance, should be the first criteria for any euthanasia method. The use of appropriate firearms for euthanising smaller cetaceans is associated with superior outcomes for animal welfare, public health and accessibility when compared to alternative approaches. Physical euthanasia methods are currently under-represented in wildlife management but can often provide more humane and expeditious alternatives to other killing methods.

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Evaluating critical dispersal rates for whale management under the IWCs Revised Management Procedure: An application for North Atlantic common minke whales

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ABSTRACT

A key consideration for any Revised Management Procedure (RMP) and Aboriginal Whaling Management Procedure (AMWP) *Implementation* is the choice of stock structure hypotheses, and the weighting of alternative stock structure hypotheses using available data. The RMP/AWMP-lite framework is applied to the North Atlantic common minke whales for three stock structure hypotheses and two RMP 'variants'. The stock structure hypotheses differ in terms of how many stocks are found in the North Atlantic and how they mix on the feeding grounds. Focusing on the eastern North Atlantic, simulations are undertaken to assess when management performance for two RMP variants is inadequate and how much effective dispersal between adjacent stocks is needed so that the performance of these variants becomes adequate.

KEYWORDS: WHALING; MANAGEMENT; NORTH ATLANTIC; MINKE WHALES

INTRODUCTION

The management strategies (or management procedures) applied by the International Whaling Commission (IWC) to determine catch (or strike) limits for commercial and aboriginal subsistence whaling are selected by means of simulation (the management strategy evaluation approach). This process involves a number of steps (Punt and Donovan, 2007):

(1) identification of management goals (and performance measures to quantify the extent to which those goals are achieved);

(2) selection of hypotheses that pertain to the situation at hand, and development of operating models that represent those hypotheses-the set of operating models forms the 'trials structure';

(3) conditioning of the operating models on the available data (and possible rejection of hypotheses [or combinations of hypotheses] that are not compatible with the data);

(4) identification of candidate management strategies; and

(5) simulation of the performance of the management strategies against agreed objectives by projecting the operating model forward in which catch limits are set using the management strategy.

A wide range of uncertainties are considered in the trials that are used to evaluate management strategies for whale populations. However, the two uncertainties that have consistently proved to be most challenging in terms of management strategies achieving conservation objectives, while still achieving goals related to high and stable catches (commercial whaling) and satisfying aboriginal need (aboriginal subsistence whaling) are the productivity of the resource usually quantified through the exploitation rate at which maximum sustainable yield rate [MSYR] is achieved, and the number of stocks in the area being managed and how they mix.

It is well known that managing multiple stocks as if they are a single stock can lead to a failure to achieve conservation objectives (e.g. Dougherty *et al.*, 2013; Fu and Fanning, 2004; IWC, 1992; Martien *et al.*, 2013; Spies, 2014). Therefore, information on stock structure can be important for the purpose of management. However, it is rarely the case that stock structure can be resolved with certainty. Uncertainty regarding stock structure and its implications for management under the IWC's Revised Management Procedure (RMP) and Aboriginal Whaling Management Procedure (AWMP) has therefore been a considerable focus for discussion during meetings of the Scientific Committee of the IWC, and the IWC Scientific Committee has attempted to adopt an approach to selecting stock structure hypotheses that makes use of genetic and non-genetic data (Donovan, 1991). A trials structure that allows for multiple stocks has been developed for the North Atlantic common minke whales, *Balaenoptera acutorostrata* (IWC, 1993), the Bering-Chukchi-Beaufort Seas bowhead whales, *Balaena mysticetus* (IWC, 2008a), the western North Pacific Bryde's whales, *Balaenoptera edeni* (IWC, 2008b), the North Atlantic fin whales, *Balaenoptera physalus* (IWC, 2009) and the western North Pacific minke whales, *Balaenoptera acutorostrata* (IWC, 2014).

The performance of a management strategy in terms of achieving conservation objectives when stock structure is uncertain depends on the management strategy being evaluated. For example, management strategies that aim for lower exploitation rates and that spread catches spatially are

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more likely to outperform strategies that allow for higher exploitation rates and that allow catches to be taken from a small fraction of the area being managed (IWC, 1992; Spies, 2014). Conservation performance will be better when there are multiple stocks if there is dispersal[3] among them because this provides an opportunity for a 'rescue effect' (Brown and Kodric-Brown, 1977). Thus, the need to understand stock structure (from a management perspective) is much reduced if there is high dispersal between stocks.

The statistical power of neutral genetic tests for stock structure relies on the sample size and the degree of genetic differentiation, measured using genetic distance metrics such as F_{ST}, among stocks (Taylor and Dizon, 1996). Genetic differentiation at neutral loci is influenced by the level of gene flow between stocks, which is a product of the migration rate (the probability m that an individual is a migrant) and the effective population size (N_e). When gene flow is restricted, genetic drift will promote genetic divergence. As a result, detecting stock structure using genetic approaches is straightforward when dispersal is limited (Mills and Allendorf, 1996; Taylor and Dizon, 1996). For example, variation in microsatellite markers in the Pacific cod, (*Gadus microcephalus*), has revealed a strong pattern of isolation by distance, suggesting restricted gene flow and considerable self-recruitment among populations in the northeastern Pacific (Cunningham *et al.*, 2009). Limited dispersal of Pacific cod was also detected between the Aleutian Islands and the eastern Bering Sea using a landscape genetics approach (Spies, 2012), leading to the reappraisal of the Aleutian Islands and eastern Bering Sea management unit (Spies, 2014). However, low genetic differentiation, e.g. due to ongoing or recent gene flow, reduces statistical power in genetic studies. This is problematic for detecting stocks, because the amount of dispersal required to achieve genetic homogeneity is often lower than the dispersal rate below which stocks should be assigned to different management units (Shaklee and Bentzen, 1998; Waples, 1998). The problem of low statistical power could be solved by investing in genotyping more individuals and/or increasing the number of genetic markers. However, it is seldom clear *a priori* how many samples or markers will be adequate to determine whether there are multiple stocks in a proposed management unit.

The aim of this paper is to develop a framework that integrates uncertainty regarding stock structure and rates of mixing[4] and dispersal amongst stocks within a management context. The aim of the framework is to identify levels of dispersal for which (conservation) performance is adequate, and can hence be used in studies of power to assess sample sizes for genetic studies (Palsboll *et al.*, 2007). The work is embedded within the actual management system because the critical level of dispersal will depend on the management system and how it addresses uncertainty, for example, regarding stock structure. The framework is applied for illustrative purposes to the situation of managing common minke whales in the North Atlantic using the IWC's Revised Management Procedure (RMP)[5].

[3]The term 'dispersal' is used here in the sense of 'effective dispersal' and refers to permanent movement of individuals among stocks. Such individuals become part of the population to which they move and contribute to future reproduction.

[4]'Mixing' is defined here as two stocks which overlap at some time on the feeding groups but do not interbreed.

METHODS

Outline of approach

The analyses in this paper are based on the RMP/AWMP-lite framework. This framework involves developing operating models using a general modelling structure to allow rapid evaluation of whether hypotheses are likely comparable with the data and the likely performance of candidate management strategies. In particular, RMP/AWMP-lite is based on representing populations using age- and sex-aggregated population dynamics models, and allows for scenarios in which multiple stocks are found in the region to be managed. RMP/AWMP-lite allows for dispersal among stocks, as well as mixing of stocks on the feeding grounds. Nevertheless, the framework could be applied with other types of population dynamics models (age- and sex-structured) commonly used when testing management strategies for the IWC, although at perhaps severe computational cost.

The approach for selecting the critical level of dispersal is as follows:

(1) select a set of stock structure hypotheses and a set of candidate management strategies (the critical dispersal rate will depend on the stock structure hypothesis and the management strategy);

(2) condition the stock structure hypotheses on the data (i.e. fit the operating model to the available monitoring data) for the lowest plausible value for MSYR (the conservation performance of a management strategy will be poorer for this value MSYR);

(3) identify 'problematic' combinations of management strategies and stock structure hypotheses[6] by conducting projections where the level of dispersal among stocks is set to zero (the worst case scenario); and

(4) conduct additional projections for the 'problematic' combinations in which dispersal is allowed between adjacent stocks and the level of dispersal is increased until the results are no longer 'problematic'.

It is possible that for a particular management strategy that there is no level of dispersal at which conservation performance is adequate. Such a strategy is too aggressive and does not warrant being considered further.

RMP/AWMP-LITE

The population dynamics are based on the Pella-Tomlinson model, i.e.:

$$N^i_{t+1} = N^i_t + r^i N^i_t \left(1 - [N^i_t / K^i]^{z^i}\right) - C^i_t \qquad (1)$$

[5]The specifications and definition of terms for the RMP can be found in IWC (2012b).

[6]'Problematic' combinations are those that lead to failure to achieve the conservation-related goals of the IWC. For this paper, a combination of stock structure hypothesis and management strategy is considered 'problematic' if the lower 95th percentile of final depletion for any stock is less than the (assumed) MSY level of 0.6, although criteria such as those used to define adequate conservation performance under the RMP (IWC, 2012a) could have been adopted instead. However, this paper is primarily illustrative and the approach of IWC (2012a) can be quite computationally intense.

where N_t^i is the number of stock i animals at the start of year t;

K^i is the carrying capacity of stock i;

r^i is the intrinsic rate of growth for stock i;

z^i is the degree of compensation (selected so that MYSL[1] – the population size at which MSY is achieved for stock i – equals a pre-specified value); and

C_t^i is the catch during year t from stock i.

The number of animals in stock i at the start of the first year of the model forecast (y_{init}) is $N_{y_{\text{init}}}^i = \delta^i K^i$. The catch by stock is determined by apportioning the catches by area, taking account of mixing (i.e. exposure to harvesting) matrices, according to:

$$C_t^i = \sum_A C_t^A \frac{X^{A,i} N_t^i}{\sum_j X^{A,j} N_t^j} \quad (2)$$

where C_t^A is the catch in area A during year t; and

$X^{A,i}$ is the relative exposure of stock i to harvesting in area A (i.e. the proportion of stock i in area A when catches are taken) – the catch mixing matrix.

Dispersal can be modelled under the assumption of no net movement of animals between stocks at carrying capacity, i.e.:

$$N_{t+1}^i \leftarrow N_{t+1}^i (1 - \lambda_{i-j}) + \lambda_{i-j} \frac{K^i}{J^j} N_{t+1}^i \quad (3)$$

where l_{i-j} is the dispersal rate between stocks i and j.

The values for the parameters of the population dynamics model are: (a) the intrinsic rate of growth by stock, (b) the stock-specific carrying capacities, (c) the ratio of the number of animals at the start of the modelled period to carrying capacity (if treated as estimable), (d) the dispersal rates and (e) the values for the entries of the catch mixing matrices. The fourth of these quantities must be pre-specified by the user for the purposes of this paper, while the values for the remaining parameters can either be pre-specified or estimated by minimising an objective function[7]. In principle, dispersal rates can be estimated if data on tagging (genetic or non-genetic) are available, but the need to use the framework of this paper is lower in these cases given a key source of information on movement is available.

The contribution of the estimates of abundance to the objective function is:

$$L_1 = \sum_A \sum_t \frac{\left(\ell n \hat{B}_t^A - \ell n B_t^{A,\text{obs}} \right)^2}{2\sigma_t^A} \quad (4)$$

where $B_t^{A,\text{obs}}$ is the abundance estimate for area A and year t;

$\hat{B}_t^A$ is the model-estimate of the abundance corresponding to $B_t^{A,\text{obs}}$:

$$\hat{B}_t^A = \sum_i \tilde{X}^{A,i} N_t^i \quad (5)$$

σ_t^A is the standard error of the logarithm of $B_t^{A,\text{obs}}$, and

$\tilde{X}^{A,i}$ is the relative exposure of stock i when surveys taken place in area A (i.e., the proportion of stock i in area A when surveys are undertaken) – the sightings mixing matrix.

The projections are based upon the assumption that survey estimates of abundance become available on a pre-specified frequency. A removal limit for each area is set as a catch limit from the RMP tuned to achieve a median final depletion for the 'D1' trial of 0.72 (see IWC, 2012b). The CV for future surveys is assumed to be 0.25 for the illustrative analyses of this paper.

Application to North Atlantic common minke whales

Specifications: Operating models

The *Implementation* for the North Atlantic common minke whales was completed in 1993 (IWC, 1994) based on operating models specified in IWC (1993). Two *Implementation Reviews* have been conducted for this group of whales (in 2003 and 2008; see (IWC, 2004; IWC, 2009)) and an *Implementation Review* is currently being undertaken (IWC, In press). The *Implementation Simulation Trials* for the North Atlantic minke whales are described in IWC (1993). Those trials involved ten sub-areas in the North Atlantic with three stocks ('W', 'C' and 'E'), each of which consists of sub-stocks (2 for the 'W' stock ('WC' and 'WG'), 4 for the 'C' stock ('CIP', 'CG', 'CIC' and 'CM'), and 4 for the 'E' stock ('EN', 'EC', 'ES', and 'EB'))[8]. The sub-areas on which the original trials were based (Fig. 1a) were modified during the 2003 *Implementation Review* to those in Fig. 1b, but the trials were not revised (IWC, 2004). The trials documented in IWC (1993) considered some variants of these basic stock structure hypotheses:

(1) sub-stock 'CM' is part of the 'E' stock;

(2) sub-stock 'EN' is a separate stock, sub-stocks 'WC', 'WG', 'CIP', 'CG', 'CIC' and 'CM' are components of one ('C') stock, and sub-stocks 'EC', 'ES', and 'EB' are components of one ('E') stock; and

(3) sub-stock 'CIP' is part of the 'W' stock.

The original *Implementation Simulation Trials* considered values for MSYR_{mat}[9] of 1% and 4%, two levels of current abundance, and various scenarios regarding catch and sightings mixing. Unlike the original *Implementation Simulation Trials*, there are now sufficient data points (Table 1) to estimate the sub-stock carrying capacities by fitting (conditioning) the operating model on the data. Only one scenario regarding $MSYR_{1+}$[10] is considered in this paper because it is well-known that the RMP performs adequately when MSYR_{mat} = 4% (IWC, 1993; 2008a; 2008b; 2009; 2014). MSYR in Equation 1 pertains to the total population size rather than mature component of the population Consequently, MSYR is set to 0.66% in this paper to roughly mimic MSYR_{mat} = 1%[11]. MSYL_{1+} is assumed to be 0.6,

[7]The values for the parameters of AWMP/RMP-lite can be estimated by fitting the model to mixing proportions by area, minimum abundance estimates and tagging data (Punt, 2013), but those data are not available for the North Atlantic minke whales.

[8]A new sets of trials is currently under development (IWC, In press) that include trials with one, two and three stocks, as well as a scenario of two cryptic stocks.

[9]MSYR defined in terms of harvesting of mature animals only.

[10]MSYR defined in terms of harvest of all animals aged 1 and older.

[11]De la Mare (2014) questions a simple relationship between MSYR_{1+} and MSYR_{mat} but this assumption is adequate for the purposes of this paper.

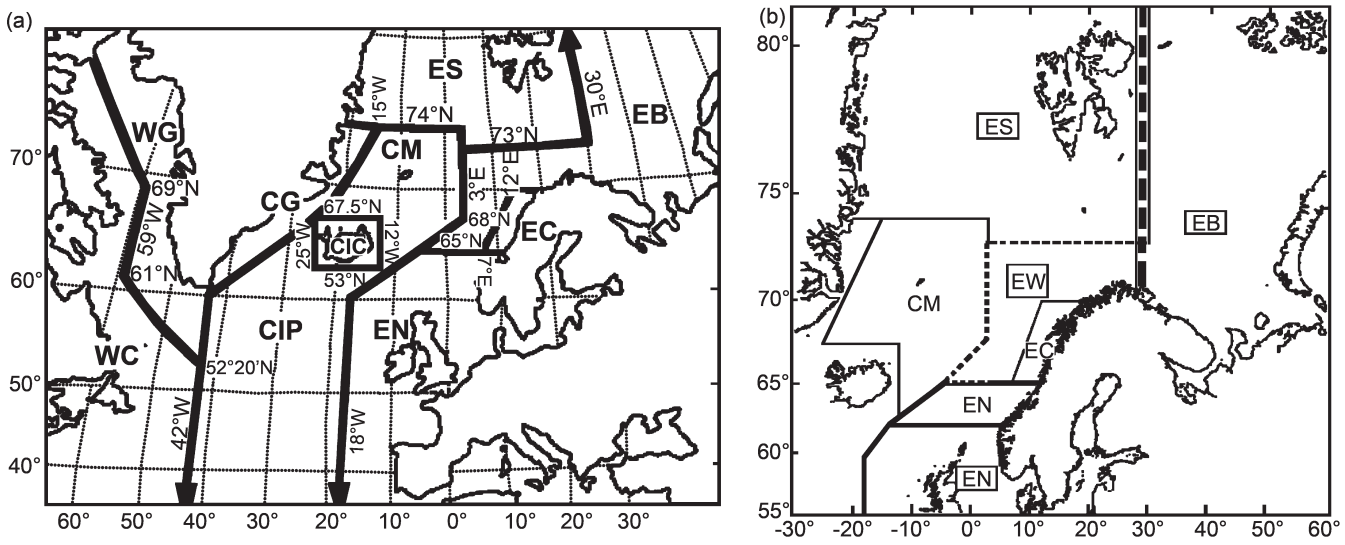

Fig. 1. Map of the North Atlantic outlining the ten sub-areas included in the original trials (left panel) and as the eastern area was modified during the 2003 *Implementation Review* (right panel).

Table 1

Abundance estimates used for conditioning.

Sub-area	Year	Estimate	CV	Sub-area	Year	Estimate	CV
WC	2007	20,741	0.30	EB	1989	21,868	0.21
WG	1993	8,370	0.43	EB	1995	29,712	0.18
WG	2005	10,790	0.59	EB	2000	25,885	0.24
WG	2007	16,100	0.43	EB	2007	28,625	0.23
CIP	2007	1,350	0.60	EN	1989	8,318	0.25
CG	2007	1,048	0.38	EN	1995	22,536	0.23
CIC	1987	24,532	0.32	EN	1998	13,673	0.25
CIC	2001	43,633	0.19	EN	2004	6,246	0.47
CIC	2007	10,680	0.29	ES	1989	13,070	0.13
CM	1988	4,732	0.229	ES	1995	24,891	0.10
CM	1995	12,043	0.28	ES	1999	17,406	0.14
CM	1997	26,718	0.14	ES	2003	19,377	0.28
CM	2005	26,739	0.45	EW	1989	20,991	0.17
				EW	1995	34,986	0.12
				EW	1996	23,522	0.13
				EW	2005	27,152	0.22

Table 2

Catch and sightings mixing matrix for stock structure hypothesis A. X denotes that the stock concerned can be found in the sub-area indicated by the column header.

	Sub-area									
Stock	WC	WG	CIP	CG	CIC	CM	EN	EC	ES	EB
W	X	X*	0	0	0	0	0	0	0	0
C	0	0	X	X*	X*	X*	0	0	0	0
E	0	0	0	0	0	0	X	X*	X*	X*

*Indicates an estimable parameter of the catch/sightings mixing matrix (there is one fewer parameter for each stock than the number of sub-areas in which a stock is found because the entries of a mixing matrix for a stock must sum to one).

y_{init} = 1938, and each stock is assumed to be at its unfished level at the start of 1938 (i.e. = 1).

This paper is based on a small set of (example) alternative stock structure hypotheses that might form the basis for future *Implementation Simulation Trials*. These are summarised below:

(1) Stock Structure Hypothesis A. There are three stocks (and no sub-stocks), the catch and sightings mixing matrices are assumed to be same (Table 2), with the parameters determining the proportion of each stock in each sub-area estimated (along with the carrying capacities by stock) to mimic the abundance estimates;

(2) Stock Structure Hypothesis B. There are ten stocks[12], each stock is in 'their' sub-area when catches and sightings occur (Table 3a); and

(3) Stock Structure Hypothesis C. There are ten stocks, each stock is in 'their' sub-area when catches occur (i.e. the catch mixing matrix is diagonal), but they are mixed on the feeding grounds when surveys take place (Table 3b).

Specifications: RMP variants

Only two RMP variants[13] are considered in these analyses primarily because the focus for these calculations was the performance of the RMP for the sub-stocks that constitute the eastern stock. The RMP variants are defined as follows:

[12]Mimicking a situation in which there are three stocks but each stock consists of a number of sub-stocks.

[13]RMP variants are specifications for how stock structure uncertainty will be addressed – they involve different ways to spread catches spatially. See IWC (2012b) for definitions for 'catch cascading', 'combination areas', etc.

Table 3
Sightings mixing matrices for the stock structure hypotheses B and C.

	Sub-area									
Sub-stock	WC	WG	CIP	CG	CIC	CM	EN	EC	ES	EB
(a) Stock structure hypothesis B										
WC	1	0	0	0	0	0	0	0	0	0
WG	0	1	0	0	0	0	0	0	0	0
CIP	0	0	1	0	0	0	0	0	0	0
CG	0	0	0	1	0	0	0	0	0	0
CIC	0	0	0	0	1	0	0	0	0	0
CM	0	0	0	0	0	1	0	0	0	0
EN	0	0	0	0	0	0	1	0	0	0
EC	0	0	0	0	0	0	0	1	0	0
ES	0	0	0	0	0	0	0	0	1	0
EB	0	0	0	0	0	0	0	0	0	1
(b) Stock structure hypothesis C										
WC	0.5	0.5	0	0	0	0	0	0	0	0
WG	0	1	0	0	0	0	0	0	0	0
CIP	0	0	0.45	0.1	0.25	0.2	0	0	0	0
CG	0	0.1	0.2	0.4	0.3	0	0	0	0	0
CIC	0	0	0.05	0.03	0.87	0.05	0	0	0	0
CM	0	0	0.25	0.1	0.25	0.4	0	0	0	0
EN	0	0	0	0	0	0.2	0.75	0.05	0	0
EC	0	0	0	0	0	0	0.15	0.8	0.05	0
ES	0	0	0	0	0	0.2	0.05	0.2	0.45	0.1
EB	0	0	0	0	0	0	0.05	0.35	0.05	0.55

(1) Sub-area 'CIC' (Iceland) is treated as a *Small Area*, and sub-areas 'EN', 'EC', 'ES' and 'EB' are treated as a *Combination Area*, with 'catch cascading' applied across these four sub-areas; and

(2) Sub-area 'CIC' (Iceland) is treated as a *Small Area*, and sub-areas 'EN', 'EC', 'ES' and 'EB' are treated as a *Small Area*, with all of the catch taken from sub-area 'EB'.

RMP variant (2) can be considered to be the most risky so it is the focus for the analyses.

Specifications: Calculating dispersal

The trials are initially conducted with no dispersal amongst the stocks. The output from these trials is then used to determine the distribution of stock size relative to carrying capacity in year 100 (final depletion) and hence the probability that the depletion is 0.6 or higher. 'Failure' is considered to occur when this probability is less than 0.95. Dispersal between the 'ES' and 'EB' sub-stocks is then implemented and the extent of dispersal increased until the probability that final depletion is 0.6 or higher exceeds 0.95. The choice of sub-stock 'ES' is arbitrary and was chosen here for illustrative purposes.

RESULTS

Model fits

Fig. 2 shows the fit of the operating model to the abundance estimates for the three example stock structure hypotheses. In terms of likelihood, the 3-stock operating model (hypothesis A, which, because it estimates mixing proportions, see Table 2, has the same number of parameters as the 10-stock operating models) has the lowest negative log-likelihood (47.9), although the fit is only marginally better than that of the 10-stock operating model with no mixing (stock structure hypothesis B; negative log-likelihood of 48.6). In contrast, the negative log-likelihood of the operating model that includes mixing (stock structure hypothesis C) is 60.1 (Fig. 2). The poor fit of stock structure hypothesis C is evident in the fits to the abundance estimates for sub-areas 'WG', 'CIP' and 'EN'. Poor fits to the abundance data are perhaps not unexpected for this stock structure hypothesis given that the mixing rates were selected 'by expert judgement' rather than by fitting the model to any data.

Projections (no dispersal)

Fig. 3 shows time-trajectories of stock size relative to carrying capacity for the 'E' stock for the 3-stock operating model and for the four easternmost sub-stocks for the two 10-stock operating models for the two RMP variants. The remaining stocks are never depleted to be below 60% of carrying capacity after 100 years. The solid line is the median over simulations while the shading covers 90% of the distributions.

The performance of both RMP variants is adequate when there are no sub-stocks (see Fig. 3, upper panels). Similarly, the performance of catch cascading is adequate for the two 10-stock stock structure hypotheses except for sub-stock 'EW' under RMP variant 1 (lower panels of Fig. 3). However, the performance of RMP variant 2 is poor for the 'EB' sub-stock, irrespective of whether there is or is not mixing on the feeding grounds when surveys take place.

The poor performance of RMP variant 1 for the 'EW' sub-stock when there is mixing on the feeding grounds when surveys take place occurs because even if the 'EW' sub-stock is extirpated, the estimates of abundance for the 'EW' sub-area do not reflect this. Consequently, the RMP allocates catches to sub-area 'EW' even though there are no animals in this sub-area when catches occur (Figs 3 and 4). The poor performance of RMP variant 2 occurs because all of the catch occurs in the 'EB' sub-area even though the catch limit is based on the abundance estimates for the entire 'E' management area.

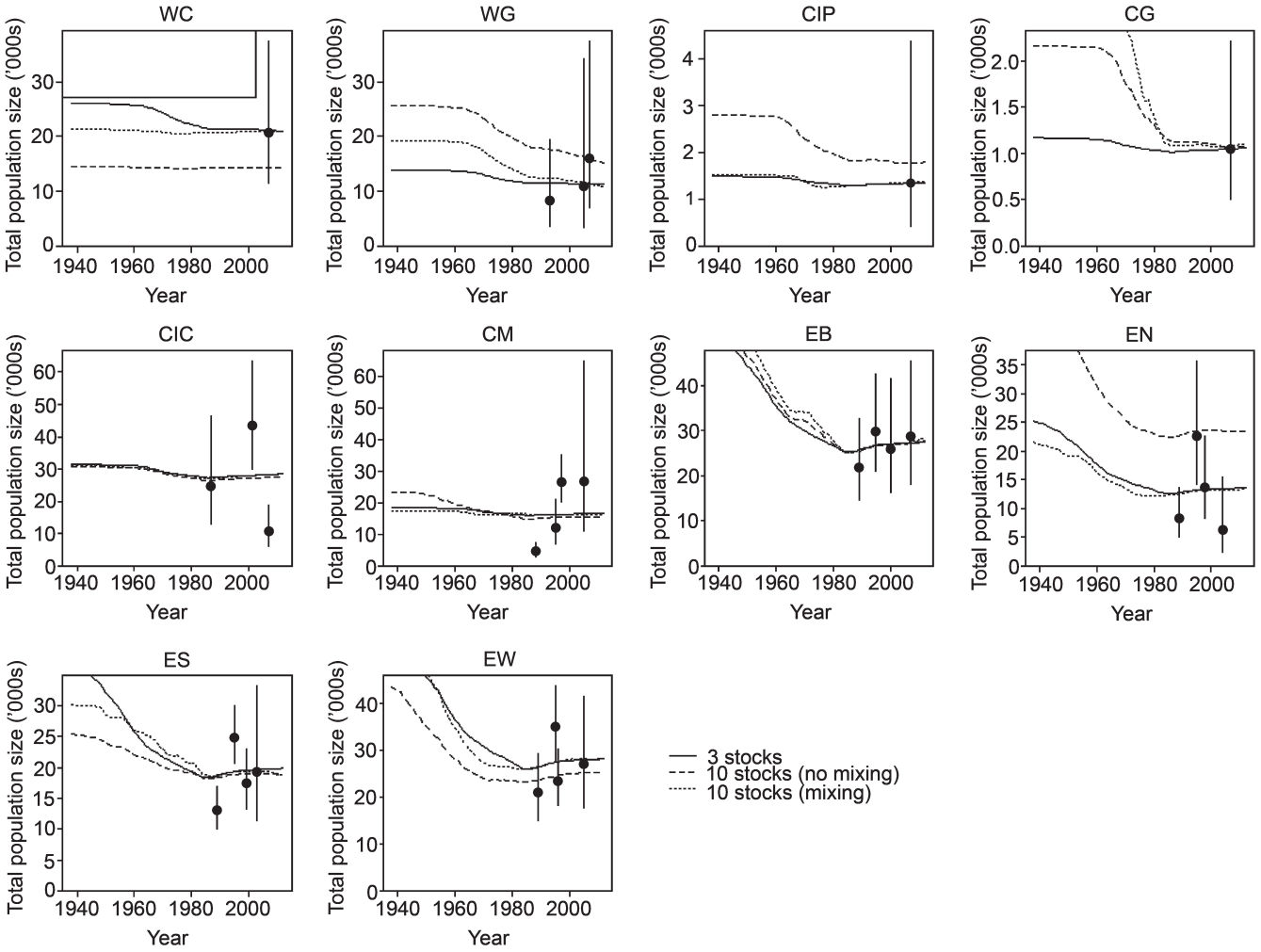

Fig. 2. Fits of the three operating model variants to the abundance data.

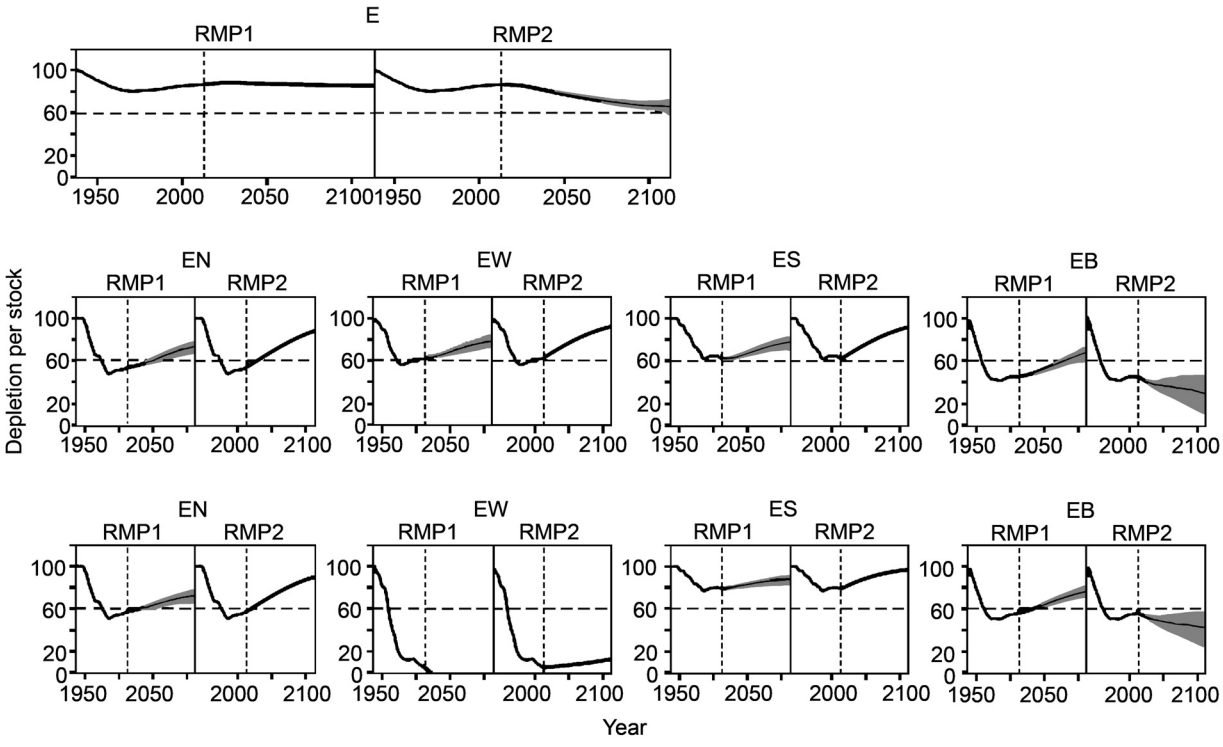

Fig. 3. 100-year time-trajectories of 1+ abundance relative to carrying capacity based on projections for the three operating models (upper panels: Stock structure hypothesis A; centre panels: Stock structure hypothesis B; lower panels: Stock structure hypothesis C). Results are shown for the two RMP variants. The light line denotes the historical estimates of abundance and the solid line the median of the forecasts in each panel, while the shaded area encompasses 90% of the simulated future trajectories.

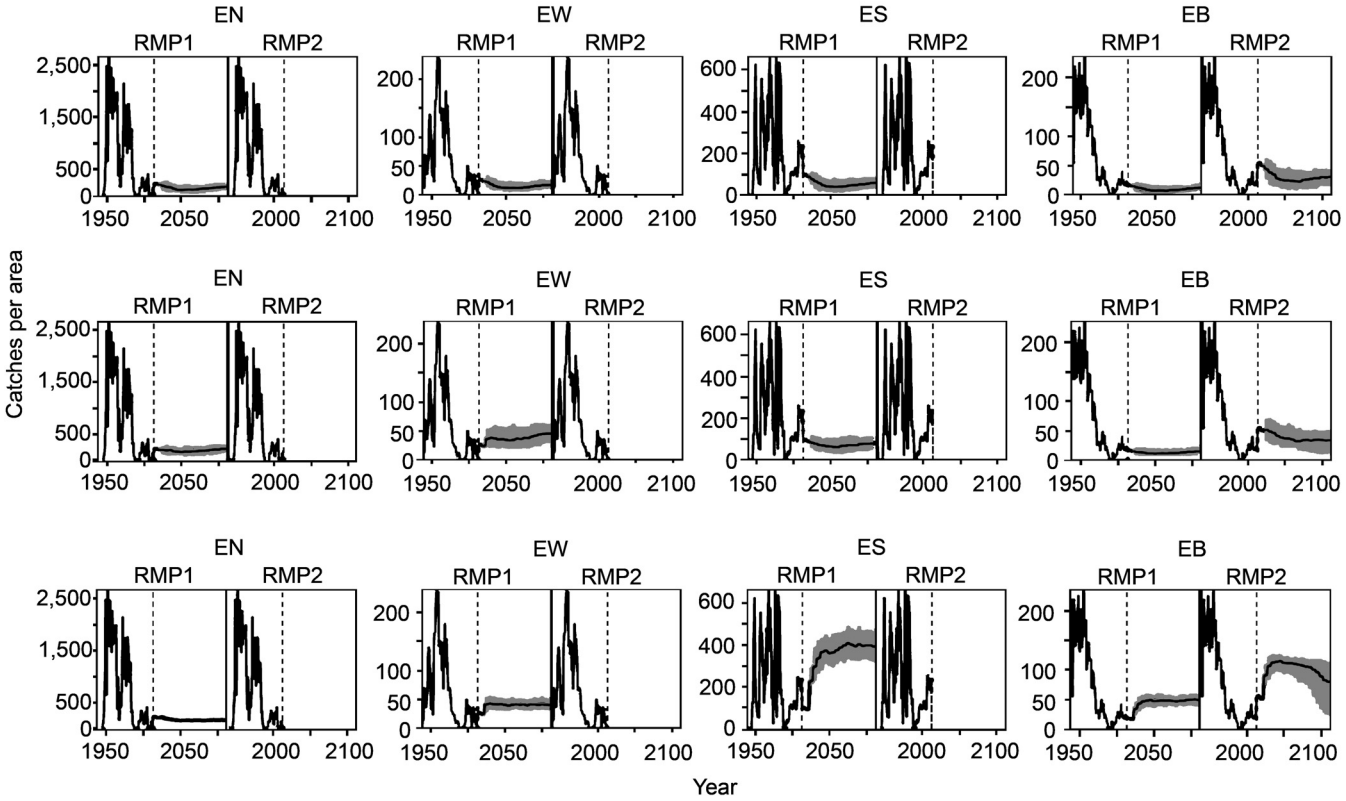

Fig. 4. Catches per area for the three operating models (upper panels: Stock structure hypothesis A; centre panels: Stock structure hypothesis B; lower panels: Stock structure hypothesis C). Results are shown for the two RMP variants. The light line denotes the historical catches and the solid line the median of the forecasts in each panel, while the shaded area encompasses 90% of the simulated future trajectories of catch.

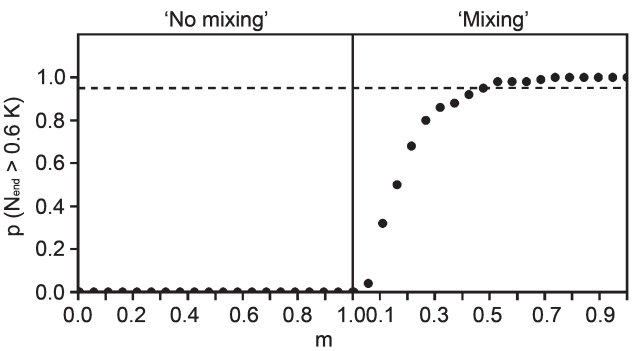

Fig. 5. The probability of final depletion being higher than 0.6 versus dispersal rate for stock structure hypotheses B ('no mixing') and C ('mixing') under RMP variant 2. The dashed line indicates the threshold value p = 0.95.

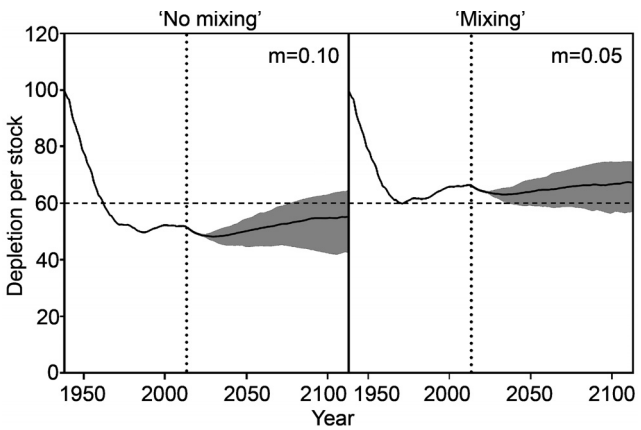

Fig. 6. Depletion trajectories for sub-stock EB at which management performance becomes adequate (or closest to adequate) for stock structure hypotheses B ('no mixing') and C ('mixing') under RMP variant 2. For stock structure hypothesis B the highest explored value of dispersal rate is shown. The light line denotes the historical estimates of abundance and the solid line the median of the forecasts, while the shaded area encompasses 90% of the simulated future trajectories.

Projections (with dispersal)

Fig. 5 shows the probability of RMP variant 2 satisfying the risk criterion that the probability that the final (year 100) depletion is 0.6 or higher exceeds 0.95 as a function of the rate of dispersal between sub-stocks 'ES' and 'EB'. This goal is achieved for a dispersal rate of 0.05 when there is mixing during sightings surveys (see the right panels of Figs 5 and 6). However, there is no dispersal rate that allows the risk criterion to be satisfied when there is no mixing during surveys and RMP variant 2 is applied (Fig. 5, left panel).

DISCUSSION

This paper outlines how RMP/AWMP-lite can be used to evaluate the consequences of different stock structure hypotheses given different RMP variants, and to assess the level of dispersal among areas, that may be consequential for management purposes. The results of the paper (and extended calculations based on alternative stock structure hypotheses/RMP variants) should help the process of conducting the *Implementation Review* for the North Atlantic common minke whales and other future *Implementations* and *Implementation Reviews* in at least three ways:

(1) Some RMP variants (e.g. variant 2 in this paper) may be unacceptable for all levels of dispersal for some stock structure hypotheses. In these cases, the RMP variant is

not a feasible candidate for implementation and does not need to be examined further, in particular using complex *Implementation Simulation Trials*;

(2) Assumptions regarding when mixing takes place are consequential. In particular, the poor performance of catch cascading for sub-stock 'EW' (lower row of Fig. 3) can be attributed almost totally to the assumption that there is mixing when surveys take place but not when catches occur. Those designing the trials structure need to consider whether this is a valid assumption; and

(3) The results in Fig. 5 provide a threshold level of mixing that should form the basis for evaluations of the power of genetic methods to detect population structure. However, the level of dispersal suggested is probably undetectable under most practical genetic analyses.

On a broader scale, the methodology described in this paper demonstrates the potential of species-specific demographic simulation frameworks, such as RMP/AWMP-lite, for assessing demographic independence in the context of pre-defined management goals. Solid genetic criteria for management units can be developed by determining the level of genetic divergence at the level of dispersal at which management performance is adequate. In addition, the number of genetic markers required to resolve population structure can be assessed upfront, which allows for an efficient targeted approach. This also prevents the waste of valuable conservation resources if the expected level of genetic divergence is too low to be detected by population genetic approaches and improves the integration of genetics into the management toolkit.

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Photo-identification confirms that humpback whales (*Megaptera novaeangliae*) from eastern Australia migrate past New Zealand but indicates low levels of interchange with breeding grounds of Oceania

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ABSTRACT

Recent photo-identification and genetic studies have identified at least five discrete breeding populations in Australia and Oceania: western Australia (D), eastern Australia (E (i)), New Caledonia (E (ii)), Tonga (E (iii)), French Polynesia and the Cook Islands (F). Also evident are low levels of intermingling among breeding populations consistent with the degree of genetic differentiation. Photo-identification has confirmed linkages between Area V feeding areas and eastern Australia breeding grounds and one genotype match has been reported between Area V feeding areas and Oceania breeding grounds. Recent abundance estimates show strong increases in the eastern Australian population, and some recovery in the New Caledonia and Tonga populations, but with little evidence of recovery at other known Oceania breeding grounds or New Zealand. Studies to date have provided no conclusive evidence of the migratory destination of humpback whales passing through New Zealand waters *en route* between Antarctic feeding areas and tropical breeding grounds. Photo-identification comparisons were undertaken between humpback whale fluke catalogues from eastern Australia (EA, 1315), Oceania east (OE, 513), Oceania west (OW, 166) and New Zealand (NZ, 13). Five matches were found between OE/OW, four matches between OW/EA and three matches between NZ/EA. The data are used to investigate and discuss the migratory destination and breeding ground migratory interchange of humpback whales travelling through New Zealand waters. The data confirm that humpback whales with site fidelity to eastern Australia migrate past New Zealand including through the Cook Strait and Foveaux Strait.

KEYWORDS: HUMPBACK WHALES; PHOTO-ID; MIGRATION; SITE FIDELITY; EASTERN AUSTRALIA; NEW ZEALAND; OCEANIA; ANTARCTIC WATERS; BREEDING GROUNDS; FEEDING AREAS

INTRODUCTION

A comprehensive investigation of humpback whales (*Megaptera novaeangliae*) migrating through New Zealand waters was undertaken during the 1950s (Dawbin, 1956; 1966; Dawbin and Falla, 1949). After reviewing a range of factors that might influence the migratory routes taken by humpbacks past New Zealand including ocean currents, bottom topography and geography of land masses encountered, Dawbin (1956) concluded that the primary factors determining the migratory route of humpbacks past New Zealand were feeding behaviour in Antarctic waters and the location of breeding grounds in eastern Australia and the islands of the western Pacific further to the east (Dawbin, 1956; 1964; 1966; Dawbin and Falla, 1949).

Initially, Dawbin considered the breeding ground destinations of humpback whales migrating from Antarctic feeding areas through New Zealand waters, and up along the eastern coast of Australia, were the eastern Coral Sea including the Chesterfields and New Caledonia, with the Tongan Group of islands being the northern limit of north

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bound humpbacks passing New Zealand (Dawbin and Falla, 1949). However, Dawbin subsequently noted that the 'great length of the eastern Australian coastline situated in the tropics should however provide a much more extended area of coastal conditions suitable for breeding than is available at near Pacific Islands' (Dawbin, 1956).

Geographic separation and isolation of discrete breeding groups was considered to occur and to influence breeding ground destinations of migrating humpback whales (Chittleborough, 1965; Dawbin, 1964; 1966; Mackintosh, 1942). The 'Discovery' marking programme[21] provided the first direct evidence of linkages between polar feeding areas and temperate breeding grounds and intermingling among discrete breeding groups (Chittleborough, 1965; Dawbin, 1959; 1964; 1966; Mackintosh, 1942; Rayner, 1940). This evidence supported the hypothesis that western Australia, eastern Australia and Oceania were discrete breeding grounds with little interchange among individuals and no evidence for permanent exchange of individuals (Chittleborough, 1965; Dawbin, 1964). Dawbin reported links between eastern Australia and Area V[22] with occasional interchange between eastern Australia and New Zealand and significant segregation between eastern Australia and the New Zealand/Oceania region (Dawbin, 1959; 1964; 1966).

Members of the South Pacific Whale Research Consortium and the Southern Cross University Whale Research Centre have been undertaking long-term photo-identification, genetic and satellite tagging studies on humpback whales in the Pacific basin and eastern Australia. The studies have substantiated that western Australia (Breeding Stock D) and eastern Australia (Breeding Stock E (i)) are discrete breeding populations (Anderson and Brasseur, 2007; Anderson *et al.*, 2010; Olavarria *et al.*, 2006a; 2006b). The data also substantiated that the IWC Breeding Stock E, which included eastern Australia, New Caledonia and Tonga, should be considered to be three discrete breeding sub-populations; eastern Australia (E (i)), New Caledonia (E (ii)) and Tonga (E (iii)) (Garrigue *et al.*, 2006; Olavarria *et al.*, 2007). The observed limited movements of individual humpback whales between eastern Australia and Oceania (Garrigue *et al.*, 2000; Garrigue *et al.*, 2011) and within Oceania (Garrigue *et al.*, 2002; Garrigue *et al.*, 2010; Hauser *et al.*, 2010; South Pacific Whale Research Consortium *et al.*, 2007) are consistent with the reported levels of genetic differentiation between Breeding Stock(s) E (i), E (ii) and E (iii). Similarly acoustic evidence substantiates low levels of intermingling between Breeding Stock D and E (i) (Noad *et al.*, 2000). Only six movements of humpback whales have been documented, by photo-identification, between Area V feeding grounds and eastern Australia (Franklin *et al.*, 2008a; Kaufman *et al.*, 1990; Rock *et al.*, 2006). Satellite tagging has documented a movement from the Cook Islands to Area VI (Hauser *et al.*, 2010). One recent genotype match was reported between New Caledonia and the Area V feeding area, and also a small number of genotype matches have been reported between Oceania breeding grounds and Area V, VI and I feeding areas (Steel *et al.*, 2008).

Genetic evidence in a recent study suggested that the humpback whales passing New Zealand may be closely related to the New Caledonia (E (i)) population (Olavarria *et al.*, 2006b) and a recent photo-identification matching of the New Zealand Catalogue with the Oceania catalogues produced only 3 matches: two matches with New Caledonia and one with Vava'u, Tonga (Constantine *et al.*, 2006). These studies have demonstrated links between New Zealand and tropical breeding grounds in Oceania but the relationship between New Zealand and Australia has yet to be carefully investigated. Some photo-identification data (Franklin *et al*. 2008b) and limited telemetry data (Gales *et al*., 2009; Garrigue *et al*., 2010) have indicated that whales from eastern Australia migrated past southern New Zealand and that whales from New Caledonia pass near northern New Zealand, respectively. However, there remains considerable uncertainty about the destination of humpback whales migrating past New Zealand from Area V feeding areas.

This paper examines photo-identification data collected from 1999–2004 to investigate movements of individual humpback whales between eastern Australia and Oceania and within Oceania and discuss the breeding ground migratory interchange and migratory destinations of humpback whales travelling through New Zealand waters.

METHODS

Photo-identification data

Vessel-based photo-identification of humpback whale pods in Hervey Bay, Queensland (25°S, 153°E) was undertaken between 1992 and 2005 as part of a long-term study of social behaviour. Photo-identification was also utilised in a study of humpback whales on the northern migration at Byron Bay (28°38'S, 153°38'E) and on the southern migration at Ballina (28°52'S, 153°36'E) between 2003 and 2004. The combined reconciled eastern Australian fluke catalogue for the years 1999–2004, after reconciliation within and between the catalogues and rejection of photographs of unsuitable quality, consists of 1,315 individuals.

Dedicated surveys of humpback whales in Oceania were conducted between 1999–2004 during the austral winter, in four primary sampling sites: New Caledonia; Tonga; the Cook Islands and French Polynesia. Surveys were conducted in only one or two seasons in other adjacent sampling sites: Vanuatu, Fiji, Samoa, and Niue. Sampling at American Samoa began in 2003. The combined Oceania fluke catalogue for 1999–2004, after reconciliation within and between the catalogues and rejection of photographs of unsuitable quality, consists of 692 individuals.

A comprehensive description of site sampling effort and the method used to compare the Oceania and eastern Australian catalogues, within and between regions, are fully reported in South Pacific Whale Research Consortium (2007) and Garrigue *et al.* (2011). Although some local site samples, e.g. Vanuatu, Fiji, Samoa and Niue are small, when combined with other sampling sites to create the sites of

[21] 'Discovery' marks were stainless steel numbered tags that were fired into the body of the whale and recovered if that animal was captured (Brown, 1978).

[22] The International Whaling Commission designated six management areas in the southern hemisphere for baleen whales (except Bryde's whales), areas I–VI. Area v covered the waters between 130°e and 170°w (see review in Donovan, 1991). Some papers refer to the humpback whales from this area as 'group v' humpback whales.

'Oceania West' and 'Oceania East' for analysis (Table 1, below), the combined site samples can be considered random samples from the E (ii) and E (iii) plus F populations, for the purposes of these analyses.

The eastern Australian and Oceania catalogues selected for inclusion in this study were the most recent, fully reconciled, photo-identification catalogues from each of the sample sites at the time of writing and are summarised in Table 1. Photo-identification survey work is still underway in most sites. Sampling site locations are shown in Fig 1.

Statistical analysis

For the analyses, fluke data from New Caledonia and Vanuatu were combined into an Oceania west (OW) catalogue (166) while Tonga, Fiji, American Samoa, Samoa, Niue, Cook Islands and French Polynesia were combined into an Oceania east (OE) catalogue (513). The eastern Australian (EA) catalogue (1,315) and New Zealand (NZ) catalogue (13) were treated as separate population catalogues (Table 1).

Several analyses were conducted investigating the number of matches found between sample site (SITE) and population

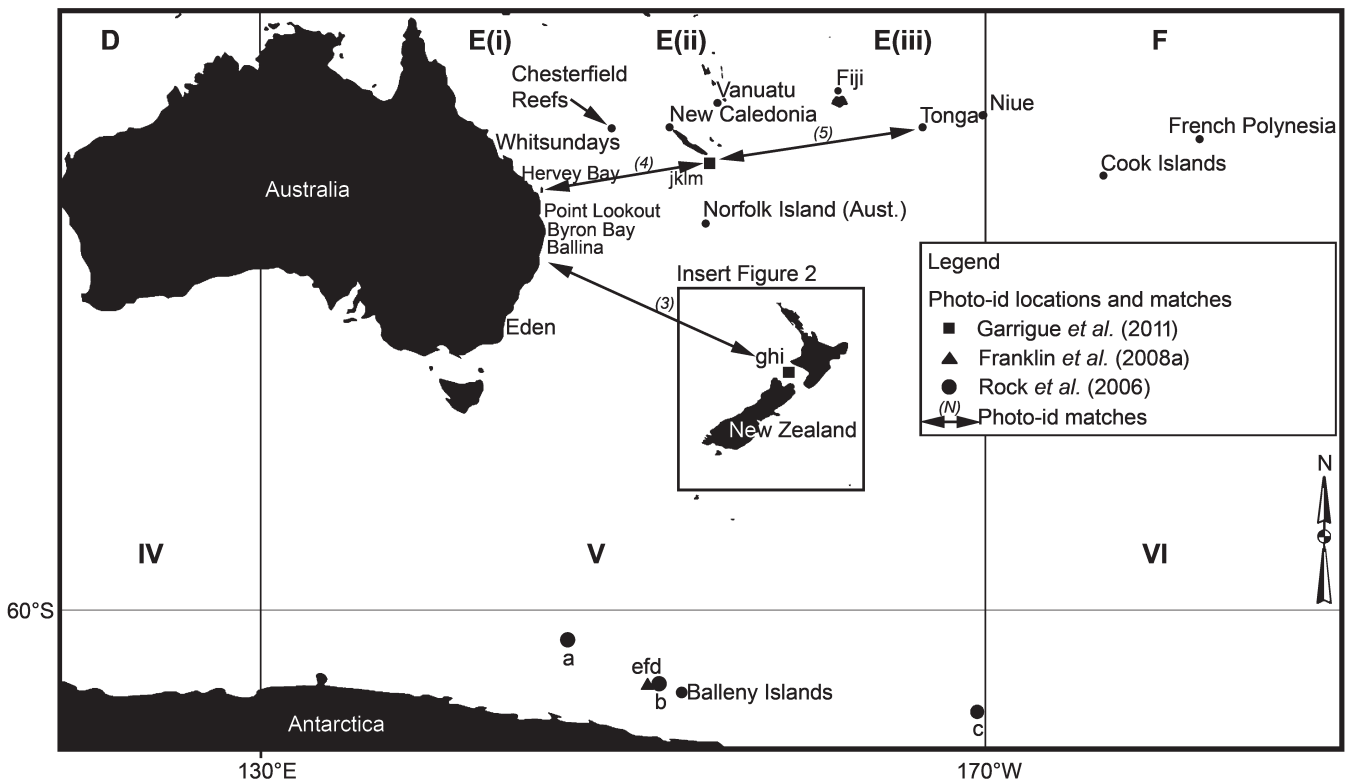

Fig. 1. Locations of the New Zealand (NZ), Eastern Australian (EA), Balleny Islands and Oceania photo-identification survey sites; Eastern Australia and Oceania breeding grounds (E (i), E (ii), E (iii), F); and Antarctic feeding areas IV, V and VI (IWC, 2006) and the photo-id matches reported between NZ/EA, EA/OW and OW/OE.

The circle symbols (a), (b) and (c) show the location of humpback whales reported in Rock *et al.* (2006); whale (a) was sighted in Point Lookout and Eden, (b) in the Whitsundays, Hervey Bay and Eden and (c) in Hervey Bay and Eden. The triangle symbols (e), (f) and (d) show the Balleny Island/EA matches reported in Franklin *et al*. (2008a); whale (d) was sighted in Ballina and (e) and (f) were sighted in Byron Bay and Hervey Bay but in different years. The square symbol marked (g), (h), (i) shows the NZ/EA matches reported in South Pacific Whale Research Consortium (2007); all three were resighted in Hervey Bay, two within the same season; June in NZ and September in Hervey Bay. The square symbol marked (j), (k), (l) and (m) shows the four New Caledonia/Hervey Bay matches reported in South Pacific Whale Research Consortium (2007).

Table 1

Summary of eastern Australian and Oceania reconciled catalogues 1999–2004 by population catalogues (POP)[1] and sampling sites (SITE)[2].

(A) eastern Australia (EA)		(B) Oceania west (OW)		(C) Oceania east (OE)		(D) New Zealand[3] (NZ)	
Site	Flukes (*n*)	Site	Flukes (*n*)	Site	Flukes (*n*)	Site	Flukes (*n*)
Hervey Bay	871	New Caledonia	160	Fiji	2	New Zealand	13
Byron Bay	415	Vanuatu	6	Tonga	282		
Ballina	29			Samoa	1		
				American Samoa	31		
				Niue	2		
				Cook Islands	36		
				French Polynesia	159		
Total EA	1,315	Total OW	166	Total OE	513	Total NZ	13

[1]The pooling of sample site catalogues into the population catalogue groupings of EA, OW, and OE population is based on: Olavarría *et al.* (2006a; 2006b); Anderson and Brasseur (2007) and Anderson *et al.* (2010).
[2]Although the sample size at some sites is small the combined site effort and samples are consistent with these being random samples from the populations and are considered such for this analysis.
[3]New Zealand is not considered a discrete population, however for the purposes of this analysis it was treated as such.

catalogues (POP), $m_{SITE\text{-}POP}$: NZ-EA, OW-EA, OE-EA, OW-OE, NZ-OW, NZ-OE. In each case, if the whales sighted at the sample site (SITE) were all members of the population catalogue (POP), the proportion of the SITE catalogue that would be expected to be matched to the POP catalogue should be equal to the proportion of the estimated population that was in the POP catalogue. Alternatively, if the whales sighted at the sample site (SITE) were not all members of the population, the proportion of the SITE catalogue that would be expected to be matched to the POP catalogue would be lower than the proportion of the estimated population in the POP catalogue.

This provides a means of estimating the expected number of matches under a null hypothesis that the whales identified at the SITE were all members of the POP catalogue for testing against the alternative hypothesis that they were not. The analysis is based on a test of association in a 2×2 cross-table of frequencies constructed as *'not seen'* or *'seen'* at the sample site by *'not seen'* or *'seen'* in the proposed population (Table 2).

Given these data and estimates, the expected numbers of matches, $_{POP\text{-}SITE}$, may be derived from expected equality of proportions, $m_{POP\text{-}SITE}/n_{SITE} = n_{POP}/N_{POP}$, and calculated as $_{POP\text{-}SITE} = (n_{POP}*n_{SITE})/N_{POP}$. This is both the standard way of calculating the expected frequencies under a null hypothesis of independence in a cross-table (row total by column total over grand total) and a simple transformation of the estimator, $= (n_1*n_2)/m_2$. The expected frequencies for each of the other cells were obtained in the standard way.

A one-tailed test of association is appropriate because the alternative hypothesis is that the observed frequency of whales seen at both locations will be lower than the expected frequency under the null hypothesis. We used one-tailed p-values from Fisher's Exact Test. This test is preferred over the asymptotic Pearson Chi-Square test when expected frequencies are small.

The sizes of sampling site catalogues (n_{SITE}), the sizes of population catalogues (n_{POP}) the estimated 2004 population sizes (N_{POP}) and the numbers of matches between the sampling site catalogues and the population catalogues ($m_{POP\text{-}SITE}$), except for the Ballina catalogue (Dan Burns, unpublished data), were derived from Garrigue *et al.* (2011), South Pacific Whale Research Consortium (2006) and Paton *et al*. (2011) and are reported in Table 3.

RESULTS

Matching between the eastern Australian and the Oceania catalogues, after reconciliation within and between the catalogues and rejection of photographs of unsuitable quality, resulted in: 3 matches between eastern Australia and New Zealand; 4 matches between eastern Australia and Oceania west (New Caledonia, Vanuatu) and 5 matches between

Table 2

Scheme for the cross-tables.

Sample site (SITE)	Hypothesised population (POP)		Total
	Not seen	Seen	
Not seen	$N_{POP} - n_{SITE} - n_{POP} + m_{POP\text{-}SITE}$	$n_{POP} - m_{POP\text{-}SITE}$	$N_{POP} - n_{SITE}$
Seen	$n_{SITE} - m_{POP\text{-}SITE}$	$m_{POP\text{-}SITE}$	n_{SITE}
Total	$N_{POP} - n_{POP}$	n_{POP}	N_{POP}

N_{POP}=estimated 2004 population size; n_{POP}=size of the population catalogue; n_{SITE}=size of the sample site catalogue; $m_{POP\text{-}SITE}$ =number of whales matched between the population and sample site catalogues.

Table 3

Data summary: sizes of sampling site catalogues, sizes of population catalogues, the estimated 2004 population sizes and the numbers of matches between the sampling site catalogues and the population catalogues.

SITE – POP	NZ-EA	OW-EA	OE-EA	OW-OE	NZ-OW	NZ-OE
Sample site catalogue (n_{SITE})	13	166	513	166	13	13
Population catalogue (n_{POP})	1,315	1,315	1,315	513	166	513
Estimated population size (N_{POP})[1]	7,090	7,090	7,090	3366	472	3,366
Site-population matches ($m_{POP\text{-}SITE}$)	3	4	0	5	0	0

[1]Estimated population sizes (n_{POP}) are based on comparable abundance estimates utilising photo-id data: Baker *et al.* (2006) and Paton *et al*. (2011).

Table 4

Frequencies of whales *not seen* and *seen* in sampling sites by whales *not seen* and *seen* in proposed populations with expected frequencies for site to population matches and Fisher's one-tailed p-values.

SITE – POP	NZ-EA	OW-EA	OE-EA	OW-OE	NZ-OW	NZ-OE
Not seen – Not seen	5,765	5,613	5,262	2,692	293	2,840
Not seen – Seen	1,312	1,311	1,315	508	166	513
Seen – Not seen	10	162	513	161	13	13
Seen – Seen	3	4	0	5	0	0
Expected matches	2.4	30.8	95.1	25.3	4.6	2.0
Fisher's one-tailed p-value	N/A	0.000	0.000	0.000	0.003	0.166

Oceania west and Oceania east (Tonga, Fiji, American Samoa, Samoa, Niue, Cook Islands and French Polynesia). No matches were found between New Zealand and any other of the Oceania catalogues in this comparison (but see Constantine *et al.*, 2006).

The frequencies of whales in sampling sites by whales in proposed populations with the expected frequencies for site to population matches and Fisher's one-tailed p-values are reported in Table 4.

Of the 13 whales sighted in New Zealand, three were matched to the eastern Australian catalogue. This is consistent with the 2.4 expected if the New Zealand whales were all members of the eastern Australian population. With the data falling in the wrong tail of the test distribution this result is entirely consistent with that hypothesis. Of the 166 whales sighted in Oceania west, four were matched to the eastern Australian catalogue. This is considerably and significantly fewer than the 30.8 expected if they were all members of the eastern Australian population. Of the 513 whales sighted in Oceania east, none were matched to the eastern Australian catalogue. This is significantly fewer than the 95.1 expected if they were all members of the eastern Australian population. Of the 166 whales sighted in Oceania west, five were matched to the Oceania east catalogue. This is significantly fewer than the 25.3 expected if they were members of the Oceania east population.

Of the 13 whales sighted in New Zealand, none were matched to the Oceania west catalogue. Although these catalogues were relatively small, this is significantly fewer than the 4.6 expected if they were members of the Oceania west population. However, if it is assumed that the New Zealand 'population' is in fact the eastern Australian population, it would be expected that approximately the same proportion, $p_{NZ\text{-}OW}$, of the whales sighted in New Zealand to have been seen in Oceania west as the proportion of the Oceania west whales that were seen in eastern Australia; i.e. $p_{NZ\text{-}OW} = 4/166 = {}_{POP\text{-}SITE}/13$. On this basis, 0.3 matches would be expected between the NZ and OW catalogues. That no matches were found is consistent with this.

Of the 13 whales sighted in New Zealand, none were matched to the Oceania east catalogue. This is fewer but not significantly fewer than the 2 expected if they were members of the Oceania east population.

DISCUSSION

The result of the comparison between the New Zealand and eastern Australian populations, is consistent with the hypothesis that the whales observed in New Zealand are from the eastern Australian population.

While there is evidently appreciable interchange between the eastern Australian and the Oceania west populations and between the Oceania east and Oceania west populations, the results presented herein support that these are discrete populations. While there may be some interchange between the eastern Australian and the Oceania east populations, the evidence from these data suggests that these populations are discrete.

While there may be some interchange between the Oceania west and New Zealand populations the evidence from these data suggests that these populations are discrete. The failure to find significance in the comparison between New Zealand and Oceania east (Table 4), may be largely due to the small size of the New Zealand catalogue and the relative small proportion of the Oceania east population in the Oceania east catalogue. However, there is weak evidence in these data indicating that New Zealand and Oceania east are discrete populations.

Movements of humpback whales through New Zealand waters

Dawbin (1956) reported that northbound humpback whales travelling from Antarctic feeding areas approached New Zealand from various directions suggesting widespread lateral dispersion whilst in the Antarctic waters. The northward migration followed three main pathways through New Zealand waters (see Fig. 2). One stream moved along the eastern coastline and was deflected to the northeast, before rounding the northeastern tip and resuming their northerly migration. Another stream passed to the southwest of the South Island through Foveaux Strait and a separate but significant stream passed through Cook Strait between the North and South Island (Dawbin, 1956; 1966).

We speculate that northbound migrating humpback whales travelling from the eastern region of the Area V feeding areas, with site fidelity to the eastern Australian (E (i)) breeding grounds, are likely to pass to the south of the South Island of New Zealand and/or through the Foveaux and Cook Strait from east to west, rather than travel up along the

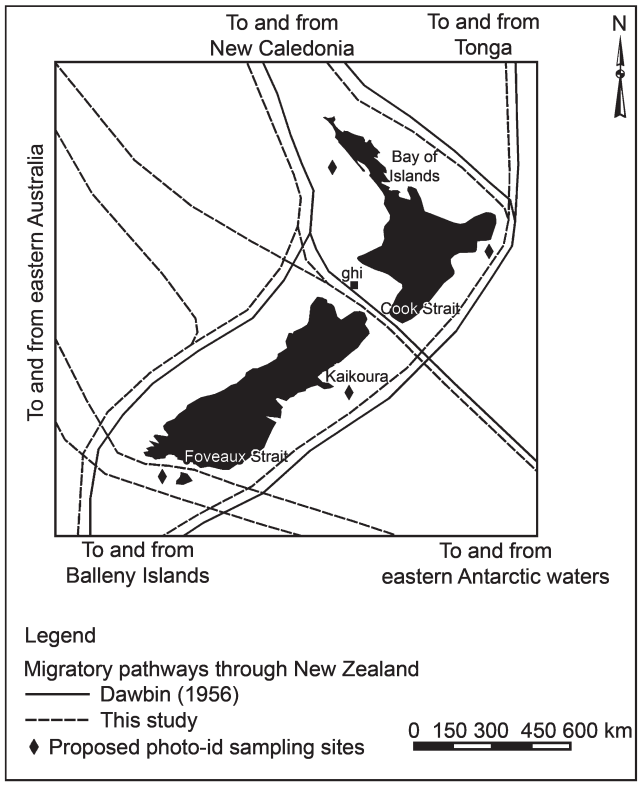

Fig. 2. The migratory pathways and migratory destinations described in (Dawbin, 1956) and the hypothesised migratory pathways and migratory destinations described in this study are shown in solid and broken lines respectively. The additional proposed photo-id sampling sites are shown as diamond shapes. The square symbol marked (g), (h) and (i) are the Cook Straits samples reported in South Pacific Whale Research Consortium (2007).

northeastern coastline of New Zealand. This is supported by the telemetry information in Gales *et al.* (2009).

In contrast, humpback whales with site-fidelity to the New Caledonia (E (ii)) and Tonga (E (iii)) breeding grounds are likely to pass northwards along the eastern coastline of the North Island of New Zealand and after clearing the northern tip of New Zealand, before resuming their migration to New Caledonia (E (ii)) on a northwesterly track, or to the Tongan Islands (E (iii)) on a northeasterly track along the Tongan trench. Two humpback whales sighted in Kaikoura during the northward migration, were also photographed in New Caledonia and Tonga, which suggests this may be the case (Constantine *et al.*, 2006). This is supported by the telemetry data in Garrigue *et al.* (2010).

Dawbin (1956) reported that southbound migrating humpback whales approached New Zealand from the north in narrowly focused pathways. The major proportion of the migration arrived along the western coastline of the North and South Islands, were deflected to the southwest until they rounded the southern tip of the South Island and continued their southern migration to Antarctic waters. Some southbound humpback whales passed around the northeastern tip of the North Island (Dawbin, 1956; 1966). This was the case with a humpback whale sighted in New Caledonia, which was also sighted in New Zealand at the Bay of Islands (NE of North Island) during the southern migration (Constantine *et al.*, 2006). An even smaller proportion of the migration, move from west to east through the Cook Strait and Foveaux Strait (Dawbin, 1956).

Humpback whales travelling directly from eastern Australia are likely to approach the western coastline of New Zealand from the east, whereas those migrating from New Caledonia and Tonga would be travelling from the north. Consequently humpback whales from eastern Australia would more likely arrive at, or towards the southern end of, the western coastline of the South Island of New Zealand.

Photo-identification sampling on the southeastern coast of New Zealand and in Cook Strait may therefore represent a sampling bias. Selecting at least three additional sampling sites for systematic photo-identification of humpback whales in New Zealand waters could provide data to determine the destinations of humpback whales passing through the northern waters of New Zealand. These sampling sites could include a site within the Foveaux Strait, a site on the northeastern coast of the North Island, a site on the northwestern coast of the North Island, and a site on the southeastern coast of the South Island, while continuing concurrent sampling in the Cook Strait.

Migration to breeding grounds north of New Zealand

Dawbin (1964) found Discovery mark matches between eastern Australia and Foveaux Strait, at the southern tip of New Zealand and Cook Strait located between the North and South Islands of New Zealand. He stated that the recapture rates of humpbacks marked off eastern Australia and in waters near New Zealand and Norfolk Island indicated that there was significant segregation between groups that migrated along the eastern coast of Australia and those that migrate past islands further east.

Differentiation between eastern Australian (E (i)), New Caledonia (E (ii)) and Tonga (E (iii)) animals has been substantiated by recent genetic and photo-identification studies (Anderson and Brasseur, 2007; Anderson *et al.*, 2010; Garrigue *et al.*, 2011; Garrigue *et al.*, 2006; Olavarria *et al.*, 2006a; Olavarria *et al.*, 2007; Olavarria *et al.*, 2006b; South Pacific Whale Research Consortium *et al.*, 2007). Over 800 sightings of humpback whales have been reported in New Zealand waters between 1970 and 2007 (Nadine Gibbs, pers. comm.). The majority of sightings were made on the southeast coast of New Zealand off Kaikoura and during systematic surveys conducted in Cook Strait (Constantine *et al.*, 2006; Gibbs and Childerhouse, 2000).

Comparisons of the New Zealand and eastern Australian catalogues for the period 1999–2004, reported herein, resulted in three matches with eastern Australia. All three matches were sighted in the Cook Strait during the early northbound migration and in Hervey Bay during the late southbound migration, two of the matches occurred within the same season (Garrigue *et al.*, 2011). Previous matches between New Caledonia, eastern Australia and New Zealand have been reported (Garrigue *et al.*, 2002; Garrigue *et al.*, 2000) and more recent comparisons of the New Zealand and Oceania catalogues have reported matches between New Caledonia, Tonga and New Zealand (Constantine *et al.*, 2006).

The results reported in this paper confirm that many humpback whales are migrating from Antarctic feeding areas through New Zealand waters to the eastern Australian (E (i)) breeding grounds. Whilst there is some evidence of humpback whales travelling through New Zealand waters to the New Caledonia (E (ii)) breeding grounds to the northwest, and the Tongan (E (iii)) breeding grounds to the northeast of New Zealand, further systematic sampling, at different locations around the northern coastline of New Zealand, is required to fully substantiate the destinations of humpbacks whales travelling through New Zealand waters.

Effect of exploitation and recovery on Pacific migratory destinations

Commercial whaling including some illegal post-war whaling is estimated to have reduced the Area V humpback whale population to 500 individuals or less by the early sixties (Chittleborough, 1965; Clapham *et al.*, 2009). Dawbin (1964) noted that the great decline in humpback numbers between 1959 and 1962 paralleled simultaneous decreases of humpback whales observed in many other South Pacific localities, such as the Chesterfields, Vanuatu and Fiji. Jackson *et al.* (2008) estimated that the humpback whale pre-exploitation abundance for eastern Australia and Oceania ranged from around 26,400–31,400 and 16,000–23,000 respectively. These results are similar to the most recent modelling exercise undertaken by the Scientific Committee who estimated pre-exploitation abundance at around 21,600–29,000 (90% credibility interval) for Breeding Stock E(i) and 11,000–19,600 (90% credibility interval) for Breeding Stock O (IWC, In press).

The humpback population from the eastern Australian (E (i)) breeding grounds has increased over the last fifty years was independently estimated to be around 7,000–8,000 in 2004 (Noad *et al.*, 2011; Paton *et al.*, 2011). The IWC Scientific Committee estimated the 2012 population to be

14,700–18,000 (90% credibility interval) during the modelling exercise referred to above (IWC, In press).

In contrast population levels in Oceania are relatively low. An overall estimate of the humpback population in Oceania by 2004 was 3,827 (CV, 0.12) individuals, with 472 in New Caledonia (E (ii)) and 2,311 in Tonga (E (iii)) (South Pacific Whale Research Consortium *et al.*, 2006). The IWC Scientific Committee estimated the 2012 population to be 4,500–6,000 (90% credibility interval) during the modelling exercise referred to above (IWC, In press). However, it noted that the complexities of eastern Oceania with respect to stock structure and trend information required further investigation.

There is little evidence of humpback whale population recovery in Vanuatu, Fiji and Norfolk Island, and no evidence of recovery at the Chesterfields in the Coral Sea (Jackson *et al.*, 2008; South Pacific Whale Research Consortium *et al.*, 2006). Whilst numbers of humpback whales have been observed in New Zealand waters in recent years, no abundance estimate is available for the humpback whales migrating past New Zealand (Constantine *et al.*, 2006; Gibbs and Childerhouse, 2000).

Clapham and Zerbini (2006) have suggested that social aggregation among the surviving Oceania humpback whales (i.e. that whales that once went to now-depleted breeding grounds changed their migratory destination to eastern Australia) may provide an explanation of why the eastern Australian (E (i)) group has recorded relatively earlier and stronger population increase than has been seen in New Caledonia (E (ii)) and Tonga (E (iii)) and why little recovery has been observed in Fiji and no recovery observed in the Chesterfields (see Clapham and Zerbini, (2006) for a discussion of the humpback 'Social Aggregation' Hypothesis).

Further research

Accumulation and comparison of photo-identification data, together with genetic and satellite tagging data obtained across the breadth of the Area V feeding area, would greatly improve our understanding of the level and rate of intermingling among humpback whales from different breeding groups while in Antarctic waters. Data on individual humpback whales, passing through New Zealand waters to breeding grounds in eastern Australia and the western Pacific, offers the opportunity to document and quantify temporary and/or permanent immigration between existing breeding grounds and to monitor and assess recovery of humpback whales in formerly occupied breeding grounds in Oceania.

Conclusions

The data herein supports earlier research that, although low levels of intermingling occur between eastern Australia (E (i)) and Oceania west (E (ii)) breeding ground populations and, Oceania west (E (ii)) and Oceania east (E (iii) and F) breeding ground populations, these populations are discrete breeding populations.

Although based on a small sample size from New Zealand, the results presented here confirm that eastern Australian humpback whales are travelling through southern New Zealand waters en-route from Antarctic feeding areas.

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Mixed-stock analysis of humpback whales (*Megaptera novaeangliae*) on Antarctic feeding grounds

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ABSTRACT

In understanding the impact of commercial whaling, it is important to estimate the mixing of low latitude breeding populations on Antarctic feeding grounds, particularly the endangered humpback whale populations of Oceania. This paper estimates the degree of genetic differentiation among the putative populations of Oceania (New Caledonia, Tonga, the Cook Islands and French Polynesia) and Australia (western Australia and eastern Australia) using ten microsatellite loci and mtDNA, assesses the power of the data for a mixed-stock analysis, determines ways to improve statistical power for future studies and estimates the population composition of Antarctic samples collected in 2010 south of New Zealand and eastern Australia. A large proportion of individuals could not be assigned to a population of origin (> 52%) using a posterior probability threshold of > 0.90. The mixed-stock analysis simulations however, produced accurate results with humpback whales reapportioned to their population of origin above the 90% threshold for western Australia, New Caledonia and Oceania grouped using a combined mtDNA and microsatellite dataset. Removing the Cook Islands, considered a transient region for humpback whales, from the simulation analysis increased the ability to reapportion Tonga from 86% to 89% and French Polynesia from 89% to 92%. Breeding ground sample size was found to be a factor influencing the accuracy of population reapportionment whereas increasing the mixture or feeding ground sample size improved the precision of results. The mixed-stock analysis of our Antarctic samples revealed substantial contributions from both eastern Australia (53.2%, 6.8% SE) and New Caledonia (43.7%, 5.5% SE) [with Oceania contributing 46.8% (5.9% SE)] but not western Australia. Despite the need for more samples to improve estimates of population allocation, our study strengthens the emerging genetic and non-genetic evidence that Antarctic waters south of New Zealand and eastern Australia are used by humpback whales from both eastern Australia and the more vulnerable breeding population of New Caledonia, representing Oceania.

KEYWORDS: HUMPBACK WHALE; CONSERVATION; FEEDING GROUNDS; GENETICS; MIGRATION; SOUTHERN OCEAN; ANTARCTIC

INTRODUCTION

In conservation and resource management there is often a requirement to assess how breeding populations are impacted either through deliberate or accidental removals. Management tends to focus on breeding units but for migratory species, exploitation or mortality often occurs in other parts of the range. In cases where only a single population is impacted this can be relatively straight forward, but the situation can become complicated when removals occur where populations mix. The assessment then requires an understanding of the degree of mixing and the relative impact on each population contributing to a mix, referred to as mixed-stock analysis. The classic example of this is the impact of pelagic fishing on salmon populations that exhibit natal philopatry but following smoltification return to the ocean where the mixing of genetically distinct stocks occurs simultaneously with commercial exploitation (e.g. Beacham *et al.,* 2011; Beacham *et al.,* 2008; Cadrin *et al.,* 2005; Olsen *et al.,* 2000; Utter and Ryman, 1993; Waples *et al.,* 1993). Under such conditions, the development of a mixed stock analysis model has been useful in minimising the risk of overexploiting less productive stocks in the mixed stock fishery.

During the era of industrial whaling in the Southern Hemisphere, > 2,000,000 whales were killed, driving some populations to near extinction (Clapham and Baker, 2002). The waters of Antarctica were heavily targeted because many baleen whale populations migrate to and mix in these krill-rich high-latitude waters during the summer. They subsequently return to their low-latitude breeding and calving grounds in the winter. Based on catch records corrected for illegal Soviet whaling, some 200,000 humpback whales were killed by pelagic whaling operations around Antarctica after 1900 (Allison, 2010; Clapham and Baker, 2002), driving a massive population decline (from an estimated pre-whaling population of 125,000) of this species.

The impact of whaling and the recovery of whale populations is a key focus of the International Whaling

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Commission (IWC) Scientific Committee. This Committee takes estimates of historical population abundance and trends and combines them with estimates of catches and population dynamic models to predict recovery rates. The models require an ability to accurately allocate catch to a source breeding population, estimates of biological parameters such as population structure, and abundance estimates, all of which are subject to considerable uncertainty (Baker and Clapham, 2004; Jackson *et al.,* 2008).

For whales hunted in the Southern Ocean, where the mixing of two or more breeding populations is suspected, the application of population dynamic models is particularly problematic. First pass attempts to allocate catches to a source population have been made using individual catch data collated and coded by the IWC from commercial whaling operations in Antarctic waters (Allison, 2010). For example, the first model (denoted 'Naïve') assumed that the breeding populations corresponded to a single feeding area along arbitrary lines of longitude (Areas I–VI) (IWC, 1998; Mackintosh, 1942;1965). As new information has emerged on the mixing of populations on the feeding grounds (Anderson *et al.,* 2010; Franklin *et al.,* 2008; Gales *et al.,* 2009; Steel *et al.,* 2008), alternative catch allocation models have been developed to include areas of mixing where whales are expected to be equally drawn from adjacent populations (e.g. IWC, 2010).

To date, assessments have been completed for several humpback whale breeding populations thought to have both simple and complex relationships between feeding areas and breeding grounds, e.g. those whales that winter in the south-western Atlantic (Zerbini *et al.,* 2006) and the south-eastern Pacific around Columbia, Panama and Ecuador (Johnston *et al.,* 2011) versus those that winter along the west and east coast of South Africa (IWC, 2009; 2011; 2012). The humpback whales that breed off eastern Australia and around the low latitude island groups of the South Pacific defined as 'Oceania', however present major challenges. This is largely due to uncertainties about both the population structure on the breeding grounds and the mixing of these populations in Antarctic waters.

As a further complication, recovery for the eastern Australian and Oceania populations has been variable. While the humpback whales migrating along eastern Australia have shown a high annual rate of population increase (10–11% Noad *et al.,* 2011), Oceania humpback whales are yet to show signs of recovery (Childerhouse and Gibbs, 2006; Gibbs *et al.,* 2006; Paton *et al.,* 2006). This lack of recovery has prompted the relisting of the population as Endangered on the IUCN Redlist (Childerhouse *et al.,* 2008; IWC, 1998). The IWC Scientific Committee have (IWC, 2011) therefore recommended an assessment of the mixing between eastern Australia and Oceania in Antarctic feeding Area V (130°E–170°W – south of New Zealand and eastern Australia), as well as eastern Australia and western Australia in Antarctic feeding Area IV (80–130°E – south of western Australia).

In light of the uncertainty about the population structure of the humpback whales of Australia and the South Pacific, many different structure hypotheses have been proposed for consideration (IWC, 2006; 2011). The present study examines different hypotheses that deal with this uncertainty by keeping the low latitude island groups of Oceania either separated or combined. Hypothesis 1 proposes a population structure where Oceania is sub-divided into four populations including New Caledonia, Tonga, Cook Islands and French Polynesia, with eastern Australia also considered a demographically independent population. This hypothesis was ranked 'medium' in plausibility as a realistic biological model during an IWC Scientific Committee workshop on the Comprehensive Assessment of Southern Hemisphere Humpback Whales, based on available biological evidence (Garrigue *et al.,* 2011; IWC, 2006; Olavarría *et al.,* 2007). Hypothesis 2 combines New Caledonia, Tonga and French Polynesia to represent the 'combined' Oceania population, while retaining eastern Australia as a separate population and eliminating the Cook Islands. This hypothesis was proposed for 'priority' consideration in the comprehensive assessment as a simple but plausible population structure scenario to deal with the limitations of catch allocation, which excludes the Cook Islands as it lacks a viable abundance estimate and is considered a transitory region as opposed to a true population (Garrigue *et al.,* 2002; Hauser *et al.,* 2010; IWC, 2011; Jackson *et al.,* 2006; Jackson *et al.,* 2009). Although these hypotheses include groupings that do not necessarily represent the true population structure, they can be used in catch allocation scenarios for population modelling (IWC, 2011).

Population genetic analysis has the potential to test these two hypotheses. Furthermore, genetic analysis can also assist in determining the degree of mixing of Australian and Oceania humpback whale populations on their feeding grounds. Population-level genetic methods hold promise for these tasks, i.e. using genetic information to ascertain population membership of groups of individuals (Manel *et al.,* 2005). Mixed-stock analysis uses allele frequencies in all potential contributing (baseline) populations and maximum likelihood or Bayesian methods to estimate proportional contributions of each population to a mixture (Pella and Milner, 1987). Here, the question of interest is not the population origin of individual whales in a feeding ground mixture, but rather the population composition of a feeding ground mixture and how it changes in space and time.

Several studies of humpback whales have employed maternally inherited mitochondrial DNA (mtDNA) in mixed-stock analysis to estimate population mixing within Antarctic feeding areas (Albertson-Gibb *et al.,* 2008; Pastene *et al.,* 2011; Pastene *et al.,* 2013), the last being most comprehensive as it includes over 1,000 high latitude samples. However, no study to date has combined mtDNA and nuclear markers to investigate humpback whale population allocation on the feeding grounds nor assessed statistical power to conduct a mixed-stock analysis. The present study draws on the most comprehensive dataset of mtDNA and nuclear microsatellite markers presently available for humpback whales of Australia and Oceania. The dataset stems from a large scale collaborative effort between two laboratories, with a total of more than 1,300 samples obtained over eleven years (Fig. 1). This extensive dataset provides us with an unprecedented opportunity to investigate the mixing of humpback whales on the feeding grounds.

Specific objectives of the present study were to: (1) assess the patterns and extent of genetic differentiation among the

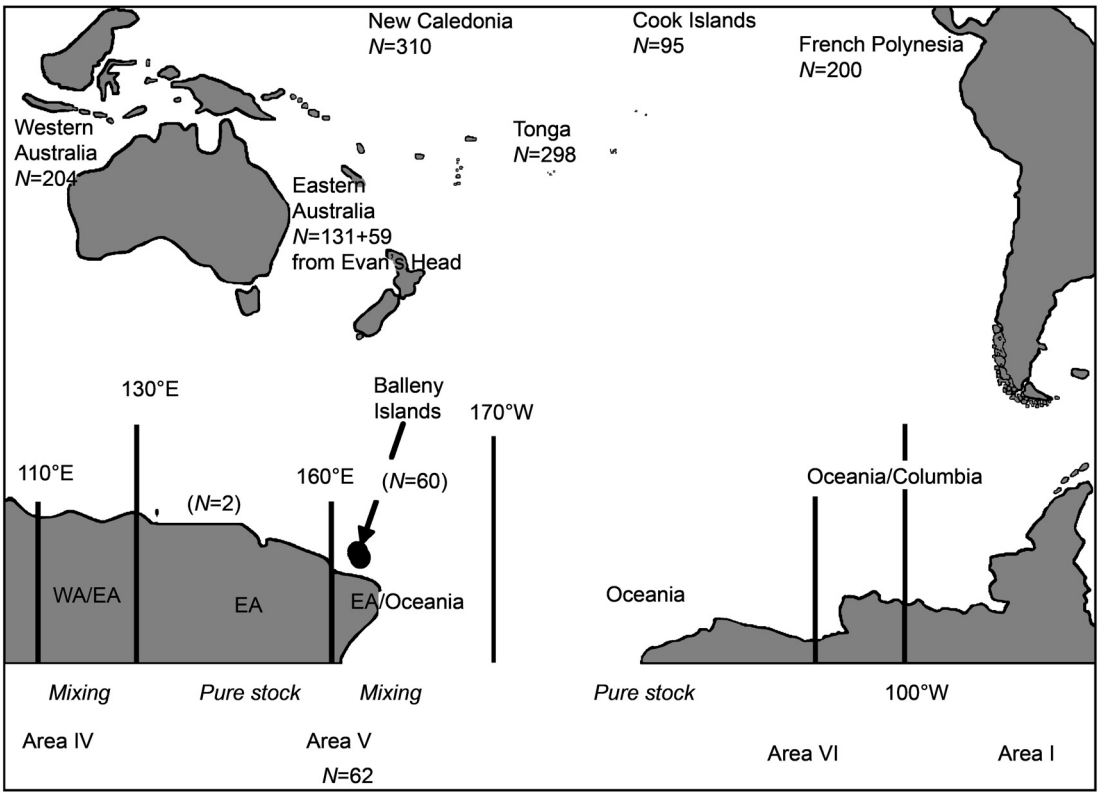

Fig. 1. Australian and Oceania humpback whale breeding/migratory populations and their associated feeding areas (Area IV, V, VI and I) divided into 'Pure Stock' and 'Mixing' areas (IWC, 2009). We also include the number of individuals sampled from each region (N) with Area V samples divided into Area VW ($N = 2$) and Area VE ($N = 60$). 'Oceania' combines New Caledonia, Tonga and French Polynesia in a population structure hypothesis proposed for the Comprehensive Assessment of Southern Hemisphere humpback whales (IWC 2006). WA = western Australia; EA = eastern Australia.

populations; (2) apply a series of simulations to evaluate the power of the microsatellite and mtDNA datasets for mixed-stock analysis given available sample size and the patterns of genetic divergence among populations under the two hypotheses on population structure; (3) extend the simulations to determine ways in which we can improve the accuracy and precision of mixed-stock analyses for these priority populations for future studies; and (4) estimate the population composition of Antarctic Area V samples collected during the Australia/New Zealand Antarctic Whale Expedition (AWE) in 2010, and interpret the findings in light of the simulation outcomes.

METHODS

The sample collection

Antarctic Area V sampling

Skin biopsy samples from 64 animals were collected from humpback whales in Antarctic feeding Area V (130°E–170°W), south of New Zealand and eastern Australia (where the mixing of breeding populations is expected) during a six week Australian–New Zealand Expedition (AWE) conducted in February and March 2010. The majority of samples were collected from adult whales between 162˚E and 179˚E around the Balleny Islands (specific sampling locations are available from the authors). Samples were obtained using a biopsy dart propelled by a modified .22 calibre rifle and stored in 70% ethanol at –80˚C. All pods were sampled opportunistically with every effort made to sample all individuals within a pod, weather and time permitting.

Seven additional samples collected during the IWC's IDCR/SOWER surveys[13] of Antarctic Area V from 1999–2004 were also included in the sample dataset, with five samples from Area VE and two samples from Area VW (Table 1; Fig. 1) (described in Albertson-Gibb *et al.,* 2008; Steel *et al.,* 2008).

Source data

Mixed-stock analysis assumes that all potential populations contributing to a mixture have been sampled. For the source dataset, we included six breeding/migratory populations which are likely to mix in Antarctic feeding Area IV or V both frequently and sporadically (Albertson-Gibb *et al.,* 2008; Chittleborough, 1965; Gales *et al.,* 2009; Steel *et al.,* 2008; Steel *et al.,* 2011): western Australia, eastern Australia and Oceania (New Caledonia, Tonga, Cook Islands and French Polynesia). Oceania samples were obtained by members of the South Pacific Whale Research Consortium during synoptic surveys dating back to 1999 (described in Constantine *et al.,* 2014). Australian samples were collected off Exmouth (Western Australia), Tasmania and Eden (NSW) between 2006 and 2008 (described in Schmitt *et al.,* 2014). An additional 59 samples from eastern Australia were collected off Evan's Head (NSW), 560km north of Eden and were included in the second mixed stock analysis of the Area V samples (see METHODS section III).

See Table 1 for a summary of the sample details. Fig. 1 provides a map of the sampling locations and the feeding areas.

[13] *http://iwc.int/SOWER*

Table 1

Samples from individual whales (assumed from unique genotypes) genotyped at ten microsatellite loci and sequenced at the mtDNA control region for Antarctic feeding Area V and the six source populations. M = males; F = females; ? = unknown.

		N							
			Sex				Sex		
Region	Sampling period	Microsatellites	M	F	?	mtDNA	M	F	?
Antarctica Area V	1999–2010	**62**	31	31	–	**62**	31	31	–
Western Australia									
Exmouth	2007	204	116	88	–	189	107	82	–
Eastern Australia		190	127	62	1	180	141	59	–
Eden	2008	61	47	14	–	57	44	13	–
Tasmania	2006–08	70	34	36	–	66	31	35	–
*Evans Head**	2009	59	46	12	1	57	66	11	–
Total Australia		**394**	243	150	1	**369**	248	141	–
New Caledonia	1999–2005	310	172	123	15	299	170	121	8
Tonga	1999–2005	298	196	97	5	292	193	95	4
Cook Islands	1999–2005	95	47	42	6	91	46	42	3
French Polynesia	1999–2007	200	100	83	17	190	93	81	16
Total Oceania		**903**	515	345	43	**872**	502	339	31
Total		**1,359**	789	526	44	**1,303**	781	511	31

*Evans Head samples only used in the mixed-stock analysis of Antarctica Area V samples.

Molecular genetic analysis

The DNA extraction, sex-typing, microsatellite genotyping and mtDNA sequencing have been described fully elsewhere. See Schmitt *et al*. (2014) for the Australian samples, and Constantine *et al.* (2014) for the samples from Oceania. Note that due to minor differences in the laboratory procedures, it was necessary to standardise the allele sizes for the microsatellite loci before the datasets could be combined. The standardisation was achieved by re-analysis of 22 reference samples drawn from the Constantine *et al*. (2014) study for which DNA was re-extracted and genotyped by the methods of Schmitt *et al.* (2014). The lack of unresolvable discrepancies between the datasets allowed us to combine them for all subsequent analyses. The final combined microsatellite dataset consisted of ten loci genotyped for 335 samples from Australia (plus 59 samples from Evans Head), 903 from Oceania and 62 from Antarctic Area V (Table 1).

For the mtDNA analysis, DNA sequences from the control region were truncated and aligned with a 470bp consensus region starting at position six of the reference humpback whale control region sequence (GenBank X72202: see Baker and Medrano-Gonzalez, 2002; Olavarría *et al.,* 2007). In total, 312 sequences from the Australian samples, 872 from Oceania and 62 from Antarctic Area V were used in all subsequent analyses (Table 1), with 57 sequences from the Evan's Head samples used in the mixed-stock analysis estimation.

Statistical analysis

Genetic structure

For an initial evaluation of the two hypotheses for population structure; hypothesis 1 (H1) where the Oceania populations are considered separately, and hypothesis 2 (H2) where New Caledonia, Tonga and French Polynesia are combined (IWC, 2006; 2011; Jackson *et al.,* 2006), genetic differentiation was calculated among each population pair for both scenarios using an Analysis of Molecular Variance (AMOVA; Excoffier *et al.,* 1992) as implemented in GenAlEx 6.5 (Peakall and Smouse, 2006; 2012) with statistical testing by random permutation (999 permutations). For microsatellite data, an estimate of F_{ST} (infinite allele model) was calculated as in Weir and Cockerham (1984), Peakall *et al*. (1995) and Michalakis and Excoffier (1996). Given the high variability of microsatellite markers, Jost's D_{EST} (Jost, 2008; Meirmans and Hedrick, 2011), an unbiased estimator of divergence, was also calculated using a modified version of the R package DEMEtics V0.8.0 (Jueterbock *et al.,* 2010), with statistical testing by bootstrapping with 1,000 permutations. Compared with F_{ST}, D_{EST} partitions diversity based on the effective number of alleles rather than on the expected diversity to give an unbiased estimation of divergence (Jost, 2008). For mtDNA data, an AMOVA was performed at both the nucleotide and haplotype level. For these analyses, genetic distance matrices were constructed using individual pairwise differences at all polymorphic nucleotide sites (following Excoffier *et al.*, 1992), or haplotype differences among all individuals (Nei, 1987). In keeping with the common practice in similar studies we use the notation F_{ST} for haplotype differentiation and Φ_{ST} for nucleotide differentiation (Olavarria *et al.,* 2006; Olavarría *et al.,* 2007; Rosenbaum *et al.,* 2009). For all marker sets we also estimated Shannon's Mutual Information index, ${}^{S}H_{UA}$ among population pairs as offered in GenAlEx 6.5 (Sherwin *et al.,* 2006). This analysis provides a G-test of allele frequency differences, but with tests of significance performed by random permutation rather than by the more conservative chi-square.

Simulations

This is the first study to attempt a mixed stock analysis of Antarctic Area V humpback whale samples using both mtDNA and microsatellite markers. The assembled genetic data are the most comprehensive presently available for putative source populations, although the sampling of the potential source population is not uniform across the study system. Computer simulations were used to assess our ability to estimate mixing on the feeding grounds.

In these simulations, the source data are analogous to a predictive model. A high degree of correct apportionment (see below for thresholds) would suggest that the level of genetic differentiation is sufficient to distinguish the populations in a mixture. The term 'confidence' comprises two components: accuracy and precision. 'Accuracy' in these simulations is defined as the agreement between the simulated value and the expected value, and 'precision' refers to the repeatability of the simulated value as measured by a confidence interval (i.e. the smaller the confidence interval, the more precise the value). The square root of the mean square error (RMSE) is also reported in evaluating the resolution of the source datasets for a mixed-stock analysis which incorporates both the standard deviation and bias (Estimate–Expected) of an estimate.

Three factors are known to be important for effectively estimating mixture proportions using mixed-stock analysis: the degree of differentiation among source populations and stocks, adequate sampling of all contributing source populations and a sufficient number of genetic markers (Epifanio *et al.,* 1995; Kalinowski, 2004; Pella and Milner, 1987). These factors are considered below.

EVALUATING THE RESOLUTION OF SOURCE DATASETS FOR A MIXED-STOCK ANALYSIS

For the mixed-stock analysis, the program SPAM, v. 3.7 (Alaska Department of Fish and Game, 2003; Debevec *et al.,* 2000) was used as it is currently the only mixed-stock simulation software that can accommodate both microsatellite and mtDNA data combined. SPAM employs a maximum likelihood approach, with allele frequency distributions modelled using the Rannala-Mountain posterior (Rannala and Mountain, 1997). This approach allows for the estimation of allele frequencies for loci with many low-frequency alleles that can cause bias and/or imprecision in stock-composition estimates.

The 100% simulation feature in SPAM was used to assess the ability of mixed-stock analysis to accurately reapportion populations, assuming there is no mixing. This approach simulates a sample composed of 100% of each population from the source data and then attempts to reapportion simulated individuals to their population of origin. The simulation uses bootstrap resampling of allele frequencies from the source data based on a user nominated sample size of the 'pure stock'. This provides an initial benchmark with which to test the statistical power of our datasets for mixed-stock analysis and is a widely reported method in demonstrating the apportion accuracy for genetic stock identification applications (e.g. Beacham *et al.,* 2006; Smith *et al.,* 2005).

The simulations were performed on three separate datasets: microsatellites, mtDNA, and microsatellites + mtDNA combined. All 100% sample reapportioning simulations were conducted with 40 simulated individuals per iteration and 1000 bootstrap resamplings were used to calculate all mean proportional contribution estimates with 95% symmetric bootstrap confidence intervals. The sample size of 40 was chosen as a conservative sample number that might be collected on a six week voyage in the Southern Ocean. A population was considered identifiable if 90% or more of the simulated 'pure stock' was correctly identified to have originated from within the population (e.g. as demonstrated by Albertson-Gibb *et al.,* 2008; Anderson *et al.,* 2008; Hess *et al.,* 2011; Smith *et al.,* 2005; VanDeHey *et al.,* 2010).

It is well established that sampling from populations, particularly when sample sizes are small, can lead to bias in allele frequency estimation where the sample allele frequencies differ by more than the real (unknown) allele frequencies of the populations being sampled (Anderson *et al.,* 2008). This in turn leads to an over inflation of F_{ST} which may yield overly optimistic conclusions about the accuracy of a mixed-stock analysis. For example, Anderson *et al.* (2008) showed that for co-dominant genetic markers, raw F_{ST} is inflated by a magnitude of approximately $1/(2S)$, where S is the population sample size.

Therefore, in a further test of the ability of mixed-stock analysis to accurately reapportion populations, mixed-stock outcomes were evaluated using the 100% simulation feature in SPAM for 'mtDNA only test sample sets' under H1 in which the degree of genetic differentiation (F_{ST}) among the populations was on average less than observed for the real data. To obtain these test sample sets, customised routines in GenAlEx 6.5 (Peakall and Smouse, 2012) were used that drew on the simulation routines described in Banks and Peakall (2012). In brief, test sample sets of $N = 200$ for each of the six source populations were obtained by randomly drawing mtDNA haplotypes from respective population haplotype frequency distributions. To reduce pairwise F_{ST} values relative to the original data, haplotypes that were drawn from the baseline haplotype frequency distribution of the combined populations at defined rates (effectively simulating 'migration') were incorporated. Subsequent AMOVA analyses confirmed that this approach had the desired outcome of reducing average pairwise F_{ST} values, while at the same time broadly retaining the pairwise patterns of population genetic structure (See Appendix Table 4 for details). The performance of five-test sample sets for each of the three new levels of F_{ST} were then evaluated for each source population as described above.

IMPROVING THE RESOLUTION OF OUR SOURCE DATASETS FOR MIXED-STOCK ANALYSIS

A mixed-stock analysis combining microsatellites + mtDNA for the grouped Oceania populations (H2) correctly assigned the greater proportion of samples and therefore was used in subsequent mixed-stock analyses. The influence of source data sample size on the ability of mixed-stock analysis to accurately reapportion a 100% sample of each putative population was examined by changing the number of samples in the source dataset to $N \geq 200$, 250, 300 and 400 for all populations (e.g. any population with less than 200 individuals in the source dataset would be increased to $N = 200$ and any population with $N \geq 200$ would remain at the current sample size) and the 100% simulation was repeated in SPAM using 40 simulated individuals and 1,000 bootstrap resamplings. When simulating an increase in source population sample sizes, the original baseline allele frequency was used to generate new individuals and therefore was not taken into account the increased likelihood of rare alleles appearing if larger sample sizes were available. Despite the bias associated with sampling error (Anderson *et al.,* 2008), the result will help determine whether the

differences in sample size between populations have a strong influence on the ability to identify each population in a mixture. Larger baseline samples are expected to increase accuracy in population identification (Beacham *et al.,* 2011; Kalinowski, 2004).

Given extensive sampling in the Southern Ocean can be both expensive and time consuming, it is also useful to determine whether feeding ground sample size is important for an accurate mixed-stock analysis. Different sample sizes of a 'pure stock' were simulated, representing samples on the feeding grounds, to determine the minimum number of samples required to confidently reapportion one population from its neighbouring population, as likely to occur in a feeding ground mixture (i.e. western Australia and eastern Australia; Oceania and eastern Australia). Using the 100% simulation feature in SPAM, various feeding ground sample sizes (i.e. N = 40, 65, 80, 120, 160, 200, 280, 400) were simulated and mean correct assignment of all individuals compared to their population of origin. By plotting these estimates for one population from each potential mixture and identifying the inflection point where the mean correct assignment begins to stabilise, the minimum sample size required for that given level of accuracy can be determined.

The Antarctic feeding grounds are likely to be a mixture of neighbouring humpback whale breeding populations (e.g. 50% from western Australia and 50% from eastern Australia; 60% from eastern Australia and 40% from Oceania; 10% from western Australia, 50% from eastern Australia and 40% from Oceania). By simulating realistic population mixtures with user defined proportions in SPAM, the degree of confidence in the source dataset to determine the proportion of humpback whales assigned to each population in a mixture can be assessed. Predicted precision and accuracy was assessed from the difference between predicted and observed population proportions. An error rate of ≤10% outside the predicted proportion was used to imply confidence in the source data in predicting stock contribution in a mixture (VanDeHey *et al.,* 2010). Two possible mixture combinations of N = 40 with expected proportional contributions varying from 0.0 to 1.0 were simulated. The influence of the sample size of the source data and the number of simulated individuals (mixture or feeding ground sample size) on our ability to estimate different population contributions in the two mixtures was investigated by repeating the analysis using a population sample size of $N \geq$ 200 and a mixture sample size of N = 160 based on results from previous analyses.

Mixed-stock estimation of the 62 individual samples collected from Antarctic feeding Area V

The program SPAM and the source data was used to calculate maximum likelihood estimates of humpback whale population contributions (with Oceania populations grouped and not grouped) to the Antarctic feeding Area V samples using all three genetic marker sets and 10,000 bootstrap re-samplings. Based on the outcome of the mixed-stock analysis simulations (see below), the estimation both with and without the 59 samples from Evan's Head in eastern Australia was carried out. It was decided not to conduct an individual assignment as most individual whales from the source data could not be assigned to a population of origin.

RESULTS

The data set consisted of 1,309 individuals, including microsatellite data for 1,300 samples, and mtDNA sequences for 1,246 samples. Summary genetic data for each microsatellite locus as well as variability in the mtDNA control region for all samples are presented in Appendix Tables 1 and 2. There was only one case out of the 80 tests (10 loci × 8 datasets) for which significant departure from Hardy-Weinberg equilibrium expectations was detected at $P < 0.01$ (Appendix Table 1). There was some evidence for a non-random association of alleles between EV14 and rw4-10, and EV37and GT23 for New Caledonia but not elsewhere. The sex ratio was significantly biased towards males (743 males to 514 females, $\chi^2 = 54.6$, $P < 0.0001$) for all sampling locations with the exception of the Cook Islands (47 males to 42 females, $\chi^2 = 0.3$, $P = 0.60$) (Table 1).

Statistical analysis

Genetic structure

The patterns of genetic diversity for the Oceania population sub-divided (H1) versus grouped (H2) were examined.

Under H1, genetic differentiation was weak but significant (microsatellites: F_{ST} = 0.004, P = 0.001; D_{EST} = 0.004, P = 0.035, mtDNA: haplotype level F_{ST} = 0.018, P = 0.001; nucleotide level Φ_{ST} = 0.025, P = 0.001). Pairwise comparisons for the ten microsatellite loci detected no significant difference between Antarctic Area V and eastern Australia (infinite allele model of mutation F_{ST} and Jost's D_{EST} = 0, $P > 0.05$), and Antarctic Area V and New Caledonia (F_{ST} and $D_{EST} < 0.005$, $P > 0.05$). Using the D_{EST} index there was also no significant structure detected between the Cook Islands and New Caledonia, Tonga, and French Polynesia respectively ($P > 0.05$) (Table 2a). For mtDNA there was low but significant structure detected at the haplotype level between all comparisons except Antarctic Area V and eastern Australia, and French Polynesia and the Cook Islands ($P > 0.05$). At the nucleotide level twelve pairwise comparisons were significantly different ($P < 0.05$) and nine were not including Antarctic Area V and eastern Australia, New Caledonia, Tonga and the Cook Islands respectively ($P > 0.05$) (Table 3a).

With the Oceania populations grouped (H2), genetic differentiation was similarly weak but significant across the entire dataset, but with a substantial increase in D_{EST} (microsatellites: D_{EST} = 0.017, P = 0.001, mtDNA: haplotype level F_{ST} = 0.012, P = 0.001; nucleotide level: Φ_{ST} = 0.020, P = 0.001). Pairwise genetic differentiation was weak but significant between all comparsions (P = 0.001) except Antarctic Area V and eastern Australia for all statistics, and Antarctic Area V and Oceania for Φ_{ST} (Tables 2b and 3b).

The Shannon's *Mutual Information Index* supported the AMOVA results but also found no significant difference in allele frequencies between Tonga and the Cook Islands (${}^{S}H_{UA}$ = 0.009, $P > 0.05$) and the Cook Islands and French Polynesia for the ten microsatellite markers (${}^{S}H_{UA}$ = 0.012, $P > 0.05$) (Appendix Table 3).

Simulations

EVALUATING THE RESOLUTION OF SOURCE DATASETS FOR A MIXED-STOCK ANALYSIS

Overall, the mtDNA alone reapportions a 'pure stock' with a slightly greater accuracy than did the combined and

Table 2

Pairwise F_{ST} and D_{EST} values among source populations and Antarctic feeding Area V under: (a) H1; and (b) H2 based on ten microsatellite loci. F_{ST} values are given below the diagonal and D_{EST} values are given above the diagonal. Significant *P*-values ($P < 0.05$ after sequential Bonferroni correction) for F_{ST} , based on statistical testing of 999 random permutations and for D_{EST}, based on 1,000 bootstrap resamplings, are shown in **bold**. Area V = Antarctic feeding Area V; WA = western Australia; EA = eastern Australia; NC = New Caledonia; TG = Tonga; CI = Cook Islands; FP = French Polynesia.

Population	Area V	WA	EA	NC	TG	CI	FP
(a) H1							
Area V		**0.028**	0.000	0.004	**0.019**	0.020	**0.035**
WA	**0.006**		**0.031**	**0.024**	**0.023**	**0.026**	**0.026**
EA	0.000	**0.005**		**0.014**	**0.023**	**0.020**	**0.023**
NC	0.002	**0.006**	**0.003**		**0.009**	0.008	**0.022**
TG	**0.016**	**0.014**	**0.015**	**0.013**		0.000	**0.007**
CI	**0.007**	**0.010**	**0.009**	**0.004**	**0.013**		0.000
FP	**0.008**	**0.005**	**0.005**	**0.005**	**0.009**	**0.004**	

Population	Area V	WA	EA	Oceania
(b) H2				
Area V		**0.028**	0.000	**0.013**
WA	**0.006**		**0.031**	**0.021**
EA	0.000	**0.005**		**0.016**
Oceania	**0.005**	**0.01**	**0.01**	

Table 3

Pairwise F_{ST} and Φ_{ST} values among source populations and Antarctic feeding Area V under: (a) H1; and (b) H2 based on mitochondrial DNA control region sequences. F_{ST} values are given below the diagonal and Φ_{ST} values are given above the diagonal. Significant *P*-values ($P < 0.05$ after sequential Bonferroni correction) based on statistical testing of 999 random permutations are shown in **bold**. Area V = Antarctic feeding Area V; WA = western Australia; EA = eastern Australia; NC = New Caledonia; TG = Tonga; CI = Cook Islands; FP = French Polynesia.

Population	Area V	WA	EA	NC	TG	CI	FP
(a) H1							
Area V		**0.02**	0.001	0.003	0.005	0.018	**0.05**
WA	**0.016**		**0.042**	**0.017**	**0.022**	**0.045**	**0.082**
EA	0.002	**0.015**		**0.021**	0.012	0.012	**0.036**
NC	**0.005**	**0.016**	**0.010**		0.005	**0.019**	**0.042**
TG	**0.015**	**0.016**	**0.010**	**0.009**		0.007	**0.035**
CI	**0.033**	**0.031**	**0.025**	**0.030**	**0.010**		0.005
FP	**0.037**	**0.034**	**0.031**	**0.031**	**0.017**	0.003	

Population	Area V	WA	EA	Oceania
(b) H2				
Area V		**0.024**	0.001	0.006
WA	**0.016**		**0.042**	**0.027**
EA	0.002	**0.02**		**0.013**
Oceania	**0.010**	**0.02**	**0.010**	

microsatellite datasets (Fig. 2). Furthermore, the patterns of high population reapportionment for the mtDNA dataset under H1 were largely maintained across the 15 'test sample sets' in which the average pairwise F_{ST} values were reduced (see Appendix Fig. 1), relative to the original data set used in the simulations shown in Fig. 2, particularly those populations that achieved a correct reapportionment above the 90% threshold. The combined mtDNA + microsatellite dataset however, showed a consistent trend of more precise estimates, characterised by smaller Coefficient of Variation, CV (e.g. for populations grouped under H2, mtDNA mean $CV = 0.06$; mtDNA + microsatellites mean CV = 0.05) with a lower RMSE for all populations except eastern Australia and the Cook Islands (e.g. for populations grouped under H1, EA: mtDNA RMSE = 0.113, mtDNA + microsatellites RMSE = 0.135, CI: mtDNA RMSE = 0.315, mtDNA + microsatellites RMSE = 0.352). Overall, confidence in reapportioning a 'pure stock' was highest when populations were grouped as for H2. Under this grouping, mixed stock apportionment was correct 90% or more of the time for mtDNA and the combined marker set with the exception of eastern Australia (average ~ 94%). By contrast when populations were grouped as for H1, correct reapportionment was lower than the 90% threshold (between 77.2% to 86.7%, with the exception of western Australia, eastern Australia and French Polynesia for mtDNA, and western Australia and New Caledonia for the combined marker set). Given the improved confidence under the H2 groupings and consistent trend of improved precision (lower confidence intervals and RMSE), all subsequent simulations were carried out using the combined marker set and grouped as for H2 (with Oceania populations combined).

IMPROVING THE RESOLUTION OF OUR SOURCE DATASETS FOR MIXED-STOCK ANALYSIS

The cost involved in obtaining whale samples is high. Simulations allowed us to evaluate the potential benefits of increasing sample size from putative breeding populations and

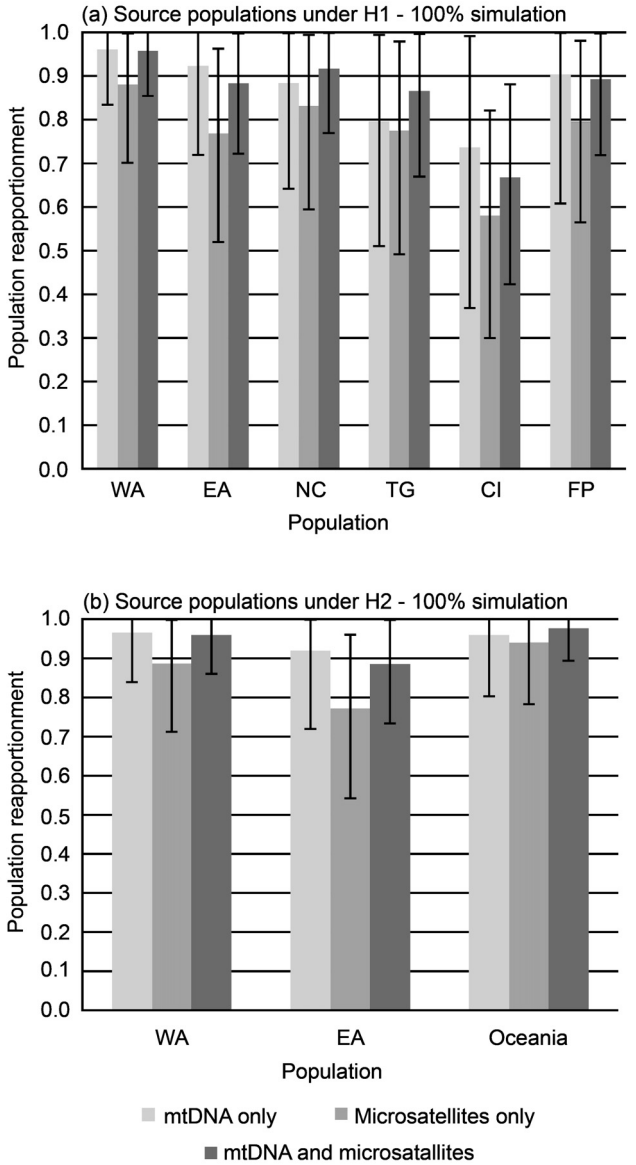

Fig. 2. Results of 100% simulations for humpback whale populations under (a) H1 and (b) H2. The program SPAM was used to simulate a 'pure stock' (N = 40) consisting of 100% of each source population. We then assessed the ability of mixed stock analysis to correctly estimate the reapportionment of each population using mitochondrial DNA (mtDNA) control region sequences, ten microsatellite loci, and mtDNA + microsatellites combined. We expect to see 100% of the correct population. Error bars represent 95% confidence intervals. WA = western Australia; EA = eastern Australia; NC = New Caledonia; TG = Tonga; CI = Cook Islands; FP = French Polynesia.

on the feeding grounds under the assumptions that present allele frequencies are representative of the source populations.

Increasing the simulated sample size for eastern Australia had the greatest effect on our ability to reapportion a 'pure stock' using mixed-stock analysis, increasing the mean correct assignment in the 100% sample reapportioning simulations to over 93.9% (an increase of 5.4%, Fig. 3). Accuracy and precision of assignment improved only marginally for western Australia and eastern Australia when sample sizes were increased from ≥ 250 to ≥ 400 (WA by 1.7% and EA by 3.1% overall).

The number of simulated individuals, representing feeding ground individuals, had minimal impact on the accuracy of reapportioning a 'pure stock' using mixed-stock analysis, although precision increased (Figs 4a and b). Confidence

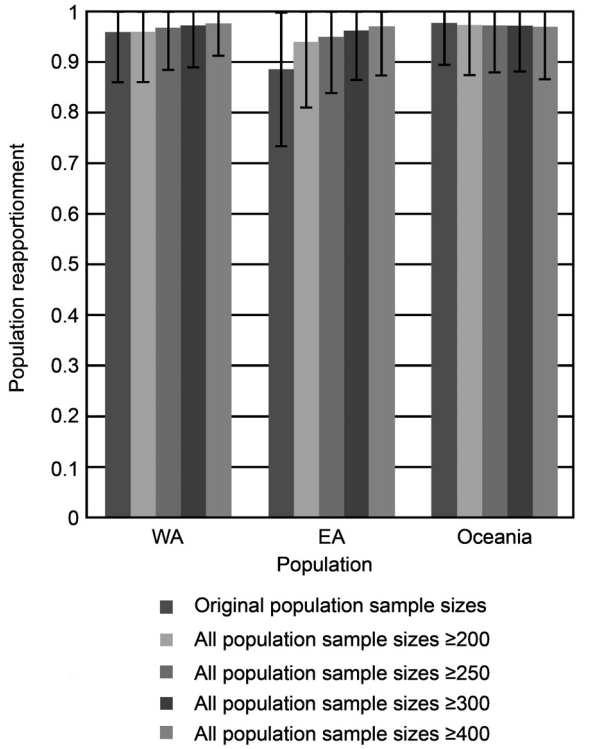

Fig. 3. The effect of increasing population sample size on the genetic distinctiveness of populations under H2 for the combined mtDNA + microsatellite dataset using the 100% simulation analysis in SPAM and a simulation sample size of N = 40. Error bars represent 95% confidence intervals.

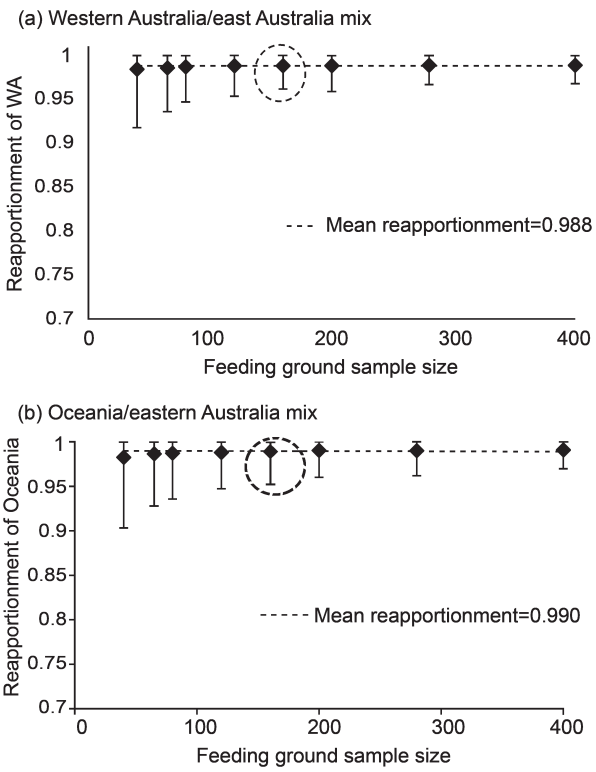

Fig. 4. Mean reapportionment for (a) western Australian humpback whales in a western Australia/eastern Australia mix, and (b) Oceania humpback whales in a Oceania/eastern Australia mix, simulated as a function of feeding ground (mixture) sample size using the 100% simulation feature in the program SPAM and the combined microsatellite and mtDNA control region dataset. Error bars represent 95% confidence intervals. The horizontal line represents where the mean correct assignment begins to stabilize. In both figures the dashed circle encompasses the feeding ground sample size where the mean reapportionment matches the horizontal line value and confidence intervals begin to stabilize (N = 160).

intervals around the mean correct assignment begin to stabilise at a sample size of 160 for both feeding area mixes.

In simulating mixtures of different proportions using our original sample sizes and a mixture sample size of $N = 40$, the differences between expected and estimated proportions for both feeding ground mixes were all within the 10% threshold error rate (3.4 to 3.6%) for identity except when eastern Australia was at an expected proportion of 90% (11.3%, Figs 5a and b). Confidence intervals however, were all outside the 10% threshold error rate and at their largest for a 50:50 mixture.

When sample size was increased from 131 to 200 for eastern Australia, the accuracy of proportion estimates increased for both mixtures. Differences between the expected and estimated proportions of western Australia (and likewise for eastern Australia) were reduced by an average of 0.9% (all differences within 1.8%) while for eastern Australia (and likewise Oceania) the differences were reduced by an average of 3.0% (all differences within 6.3%) with estimates improving by as much as 5% for expected proportions of 50–90% (Figs 5c and d). Increasing the source data sample size had little effect on confidence intervals.

When mixture sample size was also increased to $N = 160$, confidence intervals were reduced by half and were within the 10% threshold error rate for all expected proportions for both feeding area mixtures (Figs 5e and f).

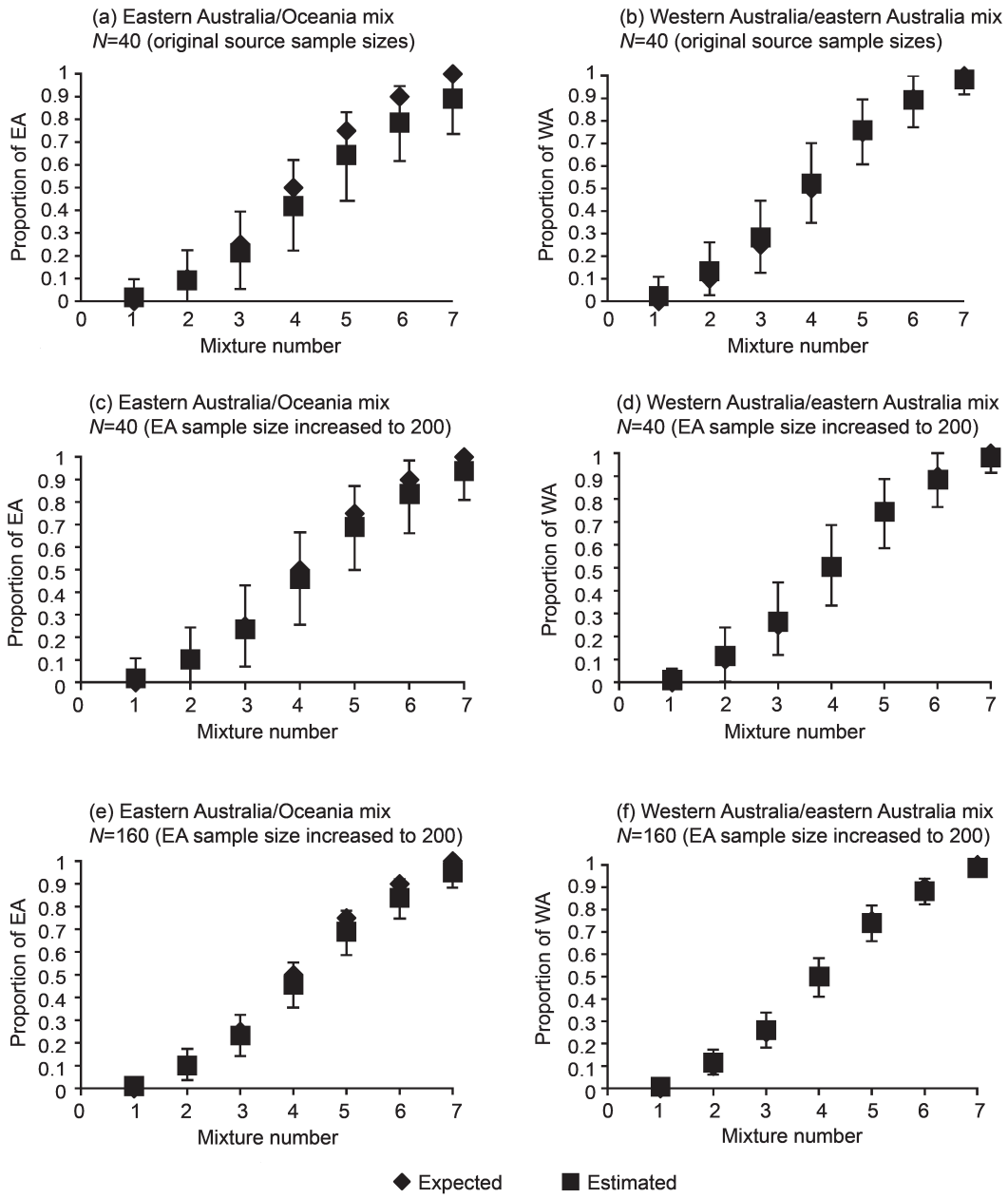

Fig. 5. Results of simulated mixture analyses for two humpback whale feeding ground mixtures; eastern Australia/Oceania and western Australia/eastern Australia. We used the program SPAM to simulate mixtures with expected proportional contributions varying from 0.0 to 1.0 (e.g. mixture 1 = 0% eastern Australia/100% Oceania; 0% western Australia/100% eastern Australia). We then performed mixed stock analysis, calculated maximum likelihood estimates of the proportional contributions in each simulated mixture, and compared estimated values to the true expected proportions using the combined microsatellite + mtDNA control region datasets. (a) and (b) used original population sample sizes and a mixture sample size of $N = 40$; (c) and (d) used population sample sizes ≥ 200 and a mixture sample size of $N = 40$; (e) and (f) used population sample sizes ≥ 200 and a mixture sample of $N = 160$.

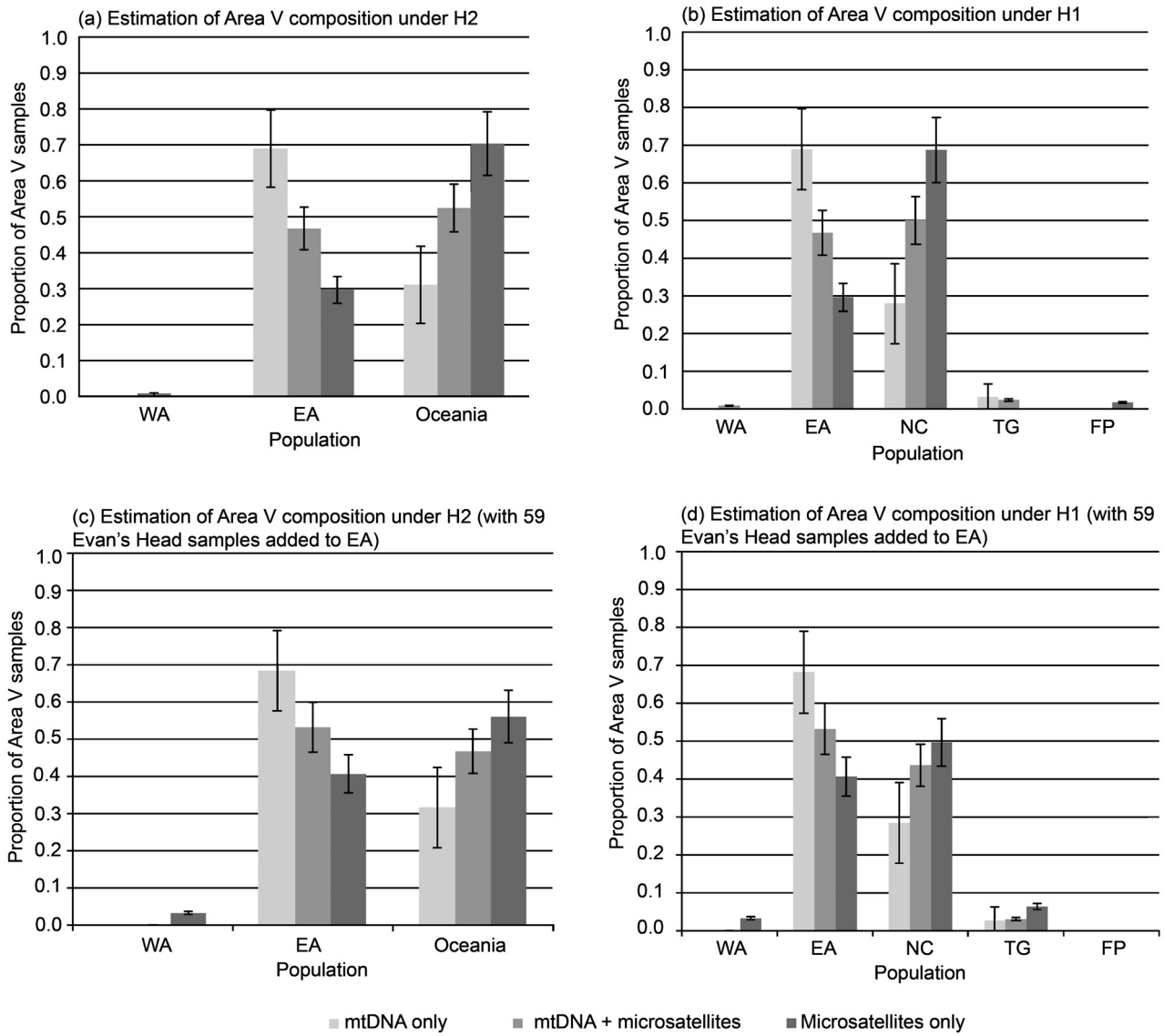

Fig. 6. SPAM maximum likelihood estimates of humpback whale feeding Area V composition (N = 62) under H1 (b) and (d) and H2 (a) and (c) using all three genetic marker sets. Error bars represent jackknife standard errors. (a) and (b) show estimates using source data and (c) and (d) show estimates using source data with eastern Australia supplemented by 59 Evan's Head samples.

Mixed-stock estimation of the 62 individual samples collected from Antarctic feeding Area V

With populations grouped as for H2, eastern Australia accounted for 46.8% (SE = 5.9%), Oceania accounted for 52.4% (SE = 6.7%) and western Australia for 0.8% (SE = 0.1%) of the 62 Antarctic feeding Area V samples using the combined mtDNA + microsatellite dataset. Eastern Australia accounted for as much as 68.9% (SE = 10.8%) using the mtDNA only dataset (Oceania: 31.1%, SE = 10.8%) but only 29.6% (SE = 3.7%) using the microsatellite dataset (Oceania: 70.4%, SE = 8.9%) with no contribution from western Australia (Fig. 6a).

Although signals in the above simulations appear to favour a grouping of populations in Oceania, under H1, three populations for mtDNA and two for the combined dataset performed above the 90% threshold in the 100% sample reapportioning simulations. Based on this result, a mixed-stock analysis was also carried out with Oceania as separate populations. In this case, contributions from Oceania to the Antarctic samples were found to be predominantly drawn from New Caledonia across all three marker sets (combined: 50.0%, SE = 6.4%; mtDNA: 27.9%, SE = 10.6%; microsatellites: 68.7%, SE = 8.6%) with close to negligible contributions from Tonga (Fig. 6b).

At the beginning of the simulation study, the 59 samples from Evan's Head (eastern Australia) were not available, and were therefore not included in the simulations. As increasing the number of samples from eastern Australia was found to improve the accuracy of population allocation estimates, the mixed-stock analysis for the Area V samples with these additional 59 samples was repeated. An AMOVA analysis between the three eastern Australian sampling locations found no significant differentiation for either the microsatellite (F_{ST} = 0.000, P = 0.5; D_{EST} = 0.000, P = 0.5) or the mtDNA (F_{ST} = 0.003, P = 0.2; Φ_{ST} = 0.000, P = 0.5) datasets, thereby justifying the pooling of the data. The addition of these 59 samples had little effect on apportionment for the Area V samples using the mtDNA data only however, the estimated contribution of eastern Australia for both microsatellite datasets increased, while the contribution of New Caledonia and Oceania as a whole decreased (combined: EA, 53.2%, SE = 6.8%; NC, 43.7%,

SE = 5.5%; Oceania, 46.8%, SE = 5.9%; microsatellites: EA, 40.6%, SE = 5.1%; NC = 49.6%, SE = 6.3%; Oceania = 56.1%, SE = 7.1%) (Figs 6c and d).

DISCUSSION

This study combined genetic analysis of mtDNA and microsatellite DNA data and simulations to explore the role of differentiation among source populations, as well as source and feeding ground sample size in effectively identifying pure samples and estimating mixture proportions. Consistent with other humpback whale studies in the Southern Hemisphere, weak but significant differentiation was detected between populations (e.g. Olavarría *et al.,* 2007; Rosenbaum *et al.,* 2009; Schmitt *et al.,* 2014). In cases such as this where differentiation is low, simulations are particularly important to evaluate the statistical power given the available genetic markers and the sample size. The discussion below examines the strengths and limitations of our current datasets for drawing conclusions about population allocations on the feeding grounds. Recommendations on sampling gaps and adjustments that can be implemented to ensure robust estimates are provided.

Genetic structure

This is the first study to assess the patterns of genetic differentiation at nuclear loci across the populations of Australia and Oceania. The degree of differentiation among pairwise comparisons was consistently low for both marker sets (microsatellites: H1 D_{EST} from 0.000 to 0.035, H2 D_{EST} from 0.000 to 0.031; mtDNA: H1 F_{ST} from 0.002 to 0.037, H2 F_{ST} from 0.002 to 0.016; Table 2 and 3). Differentiation was particularly weak among the ungrouped populations of Oceania (H1), with a D_{EST} of only 0.009 between New Caledonia and Tonga, 0.000 between Tonga, the Cook Islands and French Polynesia and 0.009 between Tonga and French Polynesia (mtDNA F_{ST} = 0.009, 0.010, 0.003 and 0.017 respectively). In spite of this result, differentiation between New Caledonia, Tonga and French Polynesia was found to be significant for both markers across all statistics ($P < 0.05$), suggesting demographic independence among these breeding grounds. These results are consistent with recent findings based on multi-state measurements of genotype exchange within the ungrouped populations of Oceania and between these populations and eastern Australia i.e. eastern Australia may not be more isolated from Oceania than animals within Oceania are from one another (Jackson *et al.,* 2012).

Feasibility of a mixed stock analysis

The ability to confidently reapportion the populations of Australia and Oceania using a mixed-stock analysis was influenced by the choice of genetic markers and the degree of differentiation. The 100% sample reapportioning simulation results suggest that the ten microsatellite loci alone did not allow accurate reapportion of each population using a 90% identity threshold, and may therefore give a poor estimate of population apportionment on the feeding grounds. This finding is likely to have been influenced by the low differentiation at the microsatellite loci. Although the mtDNA control region dataset alone could accurately discriminate among most populations at the 90% identity threshold and a mixture sample size of 40, the combined mtDNA + microsatellite dataset could do so with a greater precision (smaller confidence intervals and RMSE). Given that the increase in precision was not substantial however, mtDNA control region sequences alone may be sufficient for mixed-stock analysis in humpback whales. Furthermore, the levels of population reapportionment under H1 were largely maintained for the mtDNA data even when pairwise F_{ST} values were reduced in the 'test sample sets'. Collectively, these results are consistent with the highly discriminatory nature of mtDNA due to their haploid nature and uniparental inheritance which are expected to result in a larger genetic drift compared to nuclear loci and a smaller effective population size (e.g. Avise, 1995; Sunnucks, 2000). Although nuclear loci can provide greater resolution in discriminating between populations due to the variable nature of some markers (Angers and Bernatchez, 1998; Selkoe and Toonen, 2006), the AMOVA results in this study suggest that the ten microsatellite loci may add little to the discriminatory power of mtDNA. This result may also be a direct consequence of male-driven gene flow which, given the male-bias sex ratios in our datasets, would act to reduce structure between the breeding populations and, in turn, impact the accuracy of the feeding ground mixed-stock analysis. However, a previous study focused on Australian humpback whales found little evidence to support male biased dispersal (Schmitt *et al.,* 2014) and there is still debate over whether the male biased sex ratio is an artefact of behaviour or sampling (Brown *et al.,* 1995). Therefore, given this and the low differentiation that characterises Oceania and Australian humpback whales at the nuclear level, combining both marker types may not necessarily improve the ability to estimate the mixture contributions of populations on the feeding grounds.

The 100% sample reapportioning simulations showed that western Australia, eastern Australia, New Caledonia and French Polynesia could be reapportioned above the 90% threshold for either the mtDNA or combined dataset using original sample sizes and a simulation sample size of 40. The lack of power to reapportion Tonga and the Cook Islands is likely to be a consequence of the interplay between the smaller sample size of the Cook Islands and the weak differentiation between them. Yet when the Cook Islands was removed from the simulation analysis, the ability to reapportion Tonga increased from 86% to 89% and French Polynesia increased from 89% to 92% using the combined mtDNA + microsatellite dataset (data not shown). This result and the lack of significant differentiation between Tonga, the Cook Islands and French Polynesia, is consistent with the suggestion that the Cook Islands aggregation is transient (Garrigue *et al.,* 2002; Hauser *et al.,* 2010).

Improving the accuracy and precision of mixed-stock analyses

The sample size of the source populations was found to influence the accuracy of the predicted population identification with feeding ground sample size impacting the precision of each estimate. For example, a moderate increase in the sample size of eastern Australia from 131 to 200 had the greatest effect on our ability to reapportion the population, increasing the accuracy from 88.5% to 93.9%; above the 90% threshold for identity. Increasing the sample size of eastern

Australia and the feeding ground mixture also produced estimates and confidence intervals within the stringency threshold for all expected proportions for both feeding area mixtures. Indeed a moderate increase in source sample size has been found to have greater gains in the statistical power of the data than moderate increases in the number of nuclear loci (up to 20 loci; 8–33 alleles each), particularly when F_{ST} is low (< 0.01) and the average correct assignment to a population is greater than 80% (Hess *et al.,* 2011; Kalinowski, 2005; Morin *et al.,* 2009). However, given that the increase in source sample sizes did not take into account the increased likelihood of rare alleles appearing, these results should be interpreted with caution. Therefore for this study we can say that increasing the sample size of eastern Australia will improve the accuracy of apportioning these populations on the Antarctic feeding grounds but cannot determine with sufficient certainty the specific number of samples required.

Simulation limitations

There are several ways in which our analyses may bias estimates of simulation performance for all three marker sets.

SPAM has been found to overestimate the predicted accuracy and precision of mixed-stock analysis by resampling from the baseline with replacement, particularly for closely related populations (Anderson *et al.,* 2008). Different types of simulation software have attempted to address this problem (Anderson *et al.,* 2008; Banks and Eichert, 2000; Piry *et al.,* 2004) but there is still no software available yielding unbiased estimates of genetic stock identification that can accommodate combined mtDNA and nuclear data. Preliminary analyses using the 100% sample reapportioning simulation feature in ONCOR which attempts to reduce this bias (Anderson *et al.,* 2008) and the microsatellite data only, produced similar estimates when mean correct assignment was greater than 90% (e.g. SPAM estimate for Oceania under H2 = 94.1%; ONCOR estimate = 92.4%). However, when the SPAM estimates dipped below 80–85%, the ONCOR estimates dropped below 70% (e.g. SPAM estimate for New Caledonia under H1 = 83.2%; ONCOR estimate = 67.5%). Nonetheless, it is uncertain what effect sampling the baseline with replacement might have on mtDNA or combined mtDNA and nuclear data. Despite the bias associated with SPAM, our results provide information on the relative accuracy and precision of marker types, and the effect increasing marker number and sample size has on genetic stock identification in humpback whales.

It should also be noted that all mixed-stock analysis simulations assume that the source samples and allele frequency estimates are representative of the populations present in the mixture and, therefore, do not take account of unrepresentative baseline sampling or omitted source populations. Presently there is no way to systematically account for the possibility of individuals from unsampled populations in the mixture, although computer intensive models have attempted to address this issue (e.g. Smouse *et al.,* 1990).

Estimates of both nuclear allele frequencies and mtDNA haplotype frequencies are inevitably a biased estimate of the true global but unknowable frequencies. This bias has the potential to lead to underestimation of genetic differentiation despite implicit corrections for sample size in F-statistics estimation via the methods of Weir and Cockerham (1984), or the Analysis of Molecular Variance framework (Excoffier *et al.,* 1992). Simulation and estimation results should therefore be interpreted with a degree of caution.

Population composition of Area V samples

Our simulations offer important clues about the degree of confidence that can be expected in estimating the population apportionment of Australia and Oceania humpback whales on the Antarctic feeding grounds using a mixed-stock analysis. It is evident that these estimates are influenced by the genetic distinctiveness among source populations, choice of genetic markers, and both source and mixture sample sizes.

Notwithstanding the value of increasing sample sizes, the simulations indicate that our mtDNA and combined mtDNA + microsatellite datasets have the potential to provide estimates that are close to satisfying the 90% stringency threshold for both hypotheses of population structure.

In light of these simulations, what can be safely concluded about the population mixture of the Antarctic Area V sample? Two important insights emerge from the simulations. The first is that the contribution of western Australia is small to negligible. We have a high degree of confidence in this conclusion given both the small mixed-stock analysis estimated error (Figs 6a to d) and the outcomes of the simulations that predict close agreement between estimated and expected proportion mixtures when the contribution from western Australia is low (Fig. 5b). The second insight is that both eastern Australia and Oceania (largely represented by New Caledonia) make substantial contributions to the Area V sample. What is less certain is the exact apportionment of feeding Area V samples to these populations. This uncertainty arises from the discrepancy between the mixed-stock analysis estimates between the three different marker sets, and the error surrounding these estimates (Fig. 6a and b). The simulations also indicated the largest errors are predicted when there are more or less even contributions of eastern Australia and Oceania (Fig. 5a). With the addition of the 59 Evan's Head samples to eastern Australia however, the discrepancy between estimates for each dataset was reduced (Fig. 6c and d). Thus, while we can be confident that there is a substantial contribution of both populations to Antarctic feeding Area V, whether or not the contributions are equal will require more discriminatory genetic markers.

Collectively, these results add support to individual connection studies using Discovery tags, photo-identification and genotype matches, as well as satellite tags linking eastern Australia to Antarctic Area V (Constantine *et al.,* 2014; Dawbin, 1966; Franklin *et al.,* 2008; Gales *et al.,* 2009; Olavarria *et al.,* 2006; Rock, 2006). From the Antarctic Area V whales used in this study, Constantine *et al.* (2014) found the majority of fluke and genotype matches were to eastern Australia, with one match to New Caledonia and the New Zealand migratory corridor. Despite the low number of matches with Oceania, their result nonetheless implies that Area V is a region where mixing between eastern Australia and Oceania occurs. Their study also corroborates our findings of a negligible contribution from western Australia in Area V, with no matches found. This is consistent with the results of Discovery tag recoveries, implying humpback whales breeding in western Australia are more likely to mix

with those of eastern Australia east of 115°E in Antarctic Area IV (Chittleborough, 1965; Dawbin, 1966).

Our findings are broadly consistent with the mixed-stock analysis study of Pastene *et al.,* (2013). That study, which also focused on the Australian and Pacific region, used only mitochondrial data from a greater number of feeding ground samples but fewer samples from the breeding grounds (1,057 vs 1,297). The mixed-stock analysis from the study indicated a very high proportion of eastern Australian and New Caledonian whales allocated to Area V whereas breeding grounds further east or west were not represented or were at very low frequencies. However, by sector the analyses indicated a high proportion of New Caledonian whales in Area VE ($N = 61$; ~0.84) whereas our study, (using combined marker data) suggested approximately equal proportions allocated to eastern Australia and New Caledonian whales ($N = 62$). Interestingly, our analyses of mitochondrial data alone showed a greater discrepancy with the Pastene *et al*., (2013) study despite using an identical marker (~0.84 NC vs ~0.3 NC). This discrepancy may simply be a consequence of substructure within feeding grounds and the localised nature of the sampling in this study. However, as per our simulations it remains difficult to estimate mixing proportions in this sector. Such difficulties were recognised by the IWC Scientific Committee during the recent in-depth assessment of breeding stocks D, E and F (IWC, 2014; Annex H) and 'significant differences between the high latitude catch allocations that best fitted a three stock population model and the results of a mixed stock analysis' were noted. Consequently IWC (2014) recommended *inter alia* further studies to examine the influence of sample sizes from the breeding grounds in mixed-stock analyses. Our study will contribute to addressing this recommendation.

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APPENDIX

Appendix Table 1

Genetic diversity in humpback whales sampled from Antarctic feeding Area V, the six source populations, and the Evan's Head data from eastern Australia genotyped at ten loci. *N* = number of genotyped individuals per locus, *Na* = number of alleles, *Ho* = observed heterozygosity, *He* = expected heterozygosity, and HW = deviation from Hardy-Weinberg equilibrium (p-value); significant at $P < 0.01$ (standard errors in parentheses).

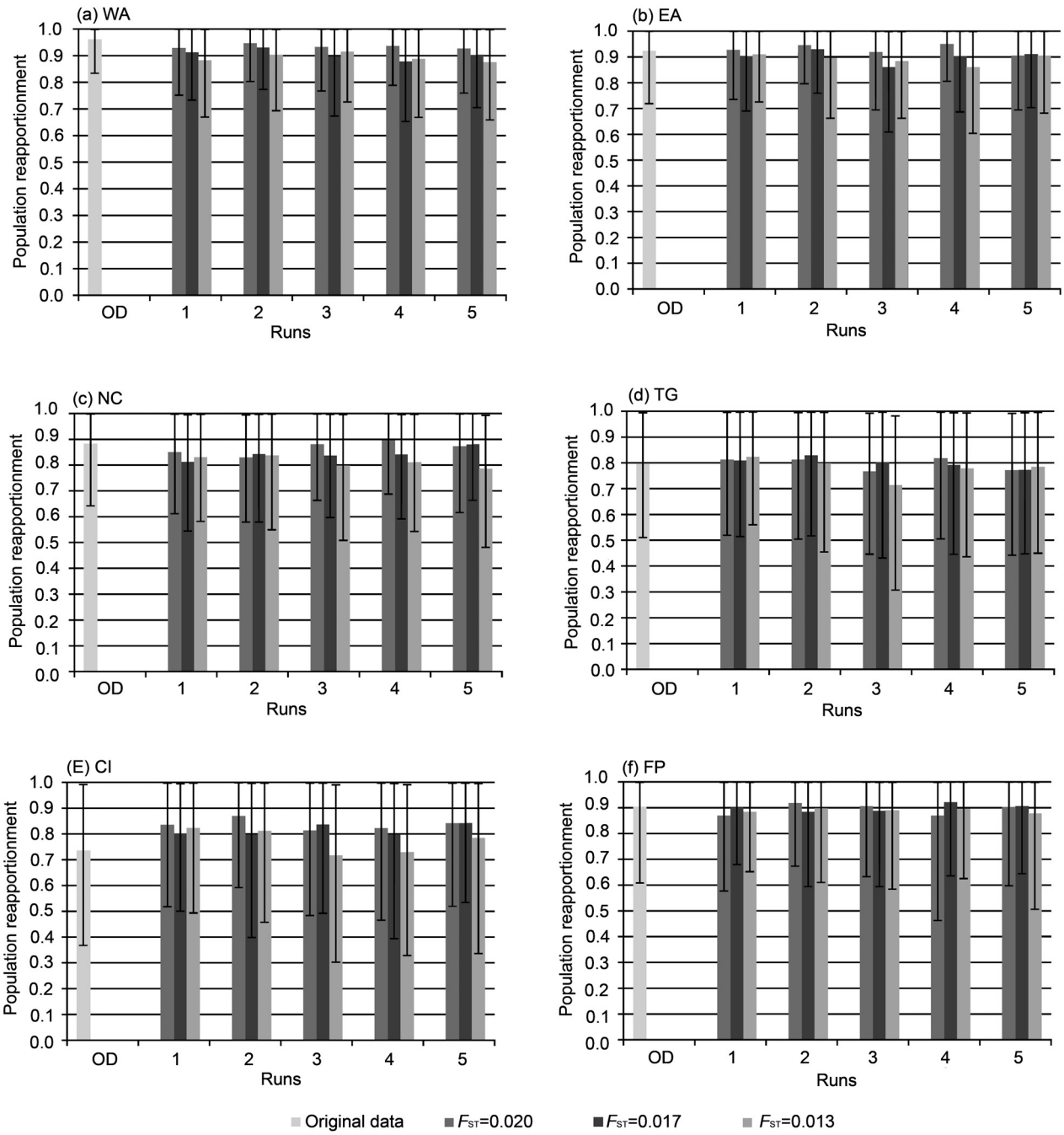
	Antarctic Area V					Western Australia				Eastern Australia				Evan's Head (eastern Australia)				New Caledonia				Tonga				Cook Islands				French Polynesia			
Locus	*N*	*Na*	*Ho*	*He*	HW	*N*	*Na*	*Ho*	*He*	HW	*N*	*Na*	*Ho*	*He*	HW	*N*	*Na*	*Ho*	*He*	HW	*N*	*Na*	*Ho*	*He*	HW	*N*	*Na*	*Ho*	*He*	HW	*N*	*Na*	*Ho*	*He*	HW
Ev14	62	9	0.758	0.723	0.426	203	8	0.754	0.778	0.458	131	9	0.725	0.748	0.742	59	11	0.729	0.757	0.367	309	9	0.725	0.729	0.558	188	10	0.766	0.773	0.344	94	9	0.830	0.798	0.120	189	9	0.735	0.761	0.014
Ev37	62	16	0.935	0.909	0.372	202	19	0.931	0.904	0.322	131	19	0.916	0.913	0.360	59	15	0.898	0.910	0.043	292	21	0.932	0.925	0.910	288	19	0.913	0.921	0.025	90	17	0.867	0.921	0.011	199	19	0.920	0.909	0.761
Ev96	62	13	0.823	0.852	0.049	202	12	0.876	0.869	0.688	131	13	0.863	0.848	0.867	59	12	0.915	0.864	0.641	310	13	0.910	0.880	0.375	292	12	0.839	0.878	0.303	87	12	0.770	0.864	0.039	183	12	0.869	0.867	0.309
GATA417	58	15	0.862	0.883	0.420	203	15	0.911	0.903	0.741	131	15	0.870	0.890	0.631	59	13	0.898	0.877	0.043	275	18	0.931	0.904	0.378	294	21	0.925	0.909	0.935	75	17	0.920	0.898	0.790	197	21	0.873	0.905	0.590
GT211	62	9	0.758	0.787	0.868	203	10	0.803	0.836	0.033	130	10	0.785	0.820	0.675	59	9	0.644	0.849	0.024	310	10	0.852	0.831	0.425	290	10	0.824	0.825	0.637	94	10	0.840	0.816	0.869	199	9	0.804	0.823	0.437
GT23	62	8	0.823	0.759	0.492	204	9	0.838	0.821	0.618	131	9	0.763	0.797	0.185	59	8	0.797	0.792	0.410	309	9	0.822	0.790	0.883	292	9	0.818	0.795	0.226	95	9	0.811	0.778	0.771	196	9	0.806	0.811	0.265
rw4-10	59	10	0.932	0.835	0.819	203	12	0.877	0.854	0.798	131	12	0.786	0.831	0.582	59	10	0.847	0.825	0.123	307	11	0.834	0.844	0.144	292	13	0.795	0.824	0.289	77	12	0.805	0.813	0.938	196	11	0.801	0.822	0.941
Ev1	62	4	0.452	0.565	0.006	203	4	0.567	0.526	0.428	130	4	0.523	0.552	0.429	59	4	0.694	0.581	0.434	300	4	0.500	0.506	0.057	288	4	0.479	0.480	0.244	94	4	0.511	0.501	0.624	193	4	0.430	0.455	0.510
Ev94	62	10	0.823	0.801	0.182	202	9	0.827	0.809	0.357	130	9	0.792	0.807	0.760	59	8	0.780	0.831	0.081	309	10	0.848	0.807	0.461	293	9	0.775	0.805	0.194	90	9	0.711	0.813	0.020	192	9	0.802	0.803	0.034
GT575	61	14	0.803	0.783	0.703	203	16	0.788	0.804	0.292	130	14	0.815	0.811	0.824	59	11	0.847	0.819	0.578	308	15	0.828	0.814	0.417	292	15	0.815	0.833	0.391	95	12	0.758	0.817	0.300	197	14	0.838	0.806	0.688
All loci	61.2	10.8	0.80	0.79	0.43	202.8	11.4	0.82	0.81	0.47	130.6	11.4	0.78	0.80	0.61	59	10.1	0.81	0.81	0.27	302.9	12.0	0.82	0.80	0.46	280.9	12.2	0.80	0.80	0.36	89.1	11.1	0.78	0.80	0.45	194.1	11.7	0.79	0.80	0.46
		(0.5)	*(1.2)*	*(0.04)*	*(0.03)*	*(0.10)*	*(0.20)*	*(1.4)*	*(0.03)*	*(0.03)*	*(0.08)*	*(0.2)*	*(1.3)*	*(0.03)*	*(0.03)*	*(0.07)*	*(0.0)*	*(2.9)*	*(0.09)*	*(0.09)*	*(0.08)*	*(3.6)*	*(1.6)*	*(0.04)*	*(0.04)*	*(0.09)*	*(10.3)*	*(1.6)*	*(0.04)*	*(0.04)*	*(0.08)*	*(2.3)*	*(1.2)*	*(0.04)*	*(0.04)*	*(0.12)*	*(1.6)*	*(1.6)*	*(0.04)*	*(0.04)*	*(0.10)*

*Of the 13,590 genotypes in total we failed to genotype 384, with only two of 1,359 individuals missing genotypes from three or more loci and no individuals missing data from more than four of ten loci.

Appendix Table 2

Variability in the mtDNA control region of humpback whales sampled from Antarctic feeding Area V, the source populations, and Evan's Head (eastern Australia) (h = haplotype diversity and π = nucleotide diversity). Area V = Antarctic feeding Area V; WA = western Australia; EA = eastern Australia; NC = New Caledonia; TG = Tonga; CI = Cook Islands; FP = French Polynesia.

	Region/population	No. of haplotypes	No. of unique haplotypes	$h \pm$ SD	$\pi \pm$ SD
Antarctica	Area V	30	3	0.969 ± 0.008	0.141 ± 0.072
	WA	56	23	0.971 ± 0.004	0.132 ± 0.067
	EA	40	4	0.966 ± 0.005	0.126 ± 0.065
	NC	64	9	0.973 ± 0.002	0.138 ± 0.070
	TG	53	4	0.964 ± 0.003	0.136 ± 0.069
	CI	29	1	0.925 ± 0.016	0.125 ± 0.065
	FP	30	3	0.919 ± 0.010	0.114 ± 0.059
	Oceania	80	30	0.986 ± 0.009	0.133 ± 0.067
Evan's Head	EA	27	1	0.946 ± 0.018	0.199 ± 0.103
Total		114	48	0.973 ± 0.002	0.133 ± 0.067



Appendix Fig. 1 Results of 100% simulations conducted in the program SPAM comparing 'mtDNA only test sample sets' with our original mtDNA only dataset under H1 for (a) western Australia, (b) eastern Australia, (c) New Caledonia, (d) Tonga, (e) Cook Islands and (f) French Polynesia. With the 'mtDNA only test sample sets' the degree of genetic differentiation (F_{ST}) among the populations was on average similar or less than observed for the real data (F_{ST} = 0.020, F_{ST} = 0.017, F_{ST} = 0.013; original mtDNA only dataset, F_{ST} = 0.018) over five simulated runs. In SPAM we simulated a 'pure stock' (N = 40) consisting of 100% of each source population. We then assessed the ability of mixed stock analysis to correctly estimate the reapportionment of each population. We expect to see 100% of the correct population. Error bars represent 95% confidence intervals.

Appendix Table 3a

Pairwise comparisons of allele frequency differences (Shannons mutual information index, *sHua*) among source populations and Antarctic feeding Area V under: (a) H1; and (b) H2 based on ten microsatellite loci. Significant p-values ($P < 0.05$ after sequential Bonferroni correction) based on statistical testing of 999 random permutations are shown in **bold**. Area V = Antarctic feeding Area V; WA = western Australia; EA = eastern Australia; NC = New Caledonia; TG = Tonga; CI = Cook Islands; FP = French Polynesia.

Population	Area V	WA	EA	NC	TG	CI
(a) H1						
WA	**0.020**					
EA	0.012	**0.023**				
NC	0.010	**0.017**	**0.013**			
TG	**0.012**	**0.019**	**0.017**	**0.010**		
CI	**0.027**	**0.023**	**0.024**	**0.013**	0.009	
FP	**0.021**	**0.026**	**0.024**	**0.019**	**0.012**	0.012

Population	Area V	WA	EA
(b) H2			
WA	**0.020**		
EA	0.012	**0.023**	
Oceania	**0.005**	**0.011**	**0.008**

Appendix Table 3b

Pairwise comparisons of haplotype frequency differences (Shannons mutual information index, *sHua*) among source populations and Antarctic feeding Area V under: (a) H1; and (b) H2 based on mitochondrial DNA control region sequences. Significant p-values ($P < 0.05$ after sequential Bonferroni correction) based on statistical testing of 999 random permutations are shown in **bold**. Area V = Antarctic feeding Area V; WA = western Australia; EA = eastern Australia; NC = New Caledonia; TG = Tonga; CI= Cook Islands; FP = French Polynesia.

Population	Area V	WA	EA	NC	TG	CI
(a) H1						
WA	**0.367**					
EA	0.165	**0.378**				
NC	**0.149**	**0.374**	**0.193**			
TG	**0.321**	**0.376**	**0.255**	**0.215**		
CI	**0.430**	**0.375**	**0.369**	**0.246**	0.089	
FP	**0.370**	**0.434**	**0.397**	**0.319**	**0.168**	**0.112**

Population	Area V	WA	EA
(b) H2			
WA	**0.367**		
EA	0.165	**0.378**	
Oceania	**0.091**	**0.254**	**0.127**

Appendix Table 4

Average pairwise F_{ST} values among source populations and Antarctic feeding Area V under H1 for the 'mtDNA only test sample sets', where genetic differentiation among the seven regions was on average similar or less than observed for the real data. Pairwise F_{ST} comparisons are shown for a total, average F_{ST} of: (a) 0.020; (b) 0.017; and (c) 0.013 across five simulation runs. Area V = Antarctic feeding Area V; WA = western Australia; EA = eastern Australia; NC = New Caledonia; TG = Tonga; CI = Cook Islands; FP = French Polynesia.

Population	Area V	WA	EA	NC	TG	CI
(a) F_{ST} = 0.020						
WA	0.019					
EA	0.011	0.016				
NC	0.011	0.014	0.012			
TG	0.018	0.015	0.013	0.010		
CI	0.035	0.028	0.027	0.026	0.012	
FP	0.038	0.032	0.032	0.029	0.018	0.007
(b) F_{ST} = 0.017						
WA	0.017					
EA	0.008	0.014				
NC	0.009	0.013	0.010			
TG	0.018	0.013	0.011	0.011		
CI	0.029	0.024	0.020	0.024	0.009	
FP	0.030	0.024	0.024	0.022	0.014	0.007
(c) F_{ST} = 0.013						
WA	0.014					
EA	0.006	0.012				
NC	0.008	0.011	0.008			
TG	0.012	0.012	0.008	0.005		
CI	0.020	0.018	0.015	0.014	0.006	
FP	0.025	0.022	0.020	0.018	0.013	0.004

Method for estimating sperm whale abundance from an acoustic strip transect survey with a two-element towed hydrophone

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ABSTRACT

A method for estimating sperm whale abundance in an acoustic line-transect survey with a two-element hydrophone is described. The analysis starts from the point where a set of click trains have been identified by an analyst. Using likelihood methods, a description is given of the estimation from each click train of (i) whale positions from the bearing patterns of click trains, (ii) most likely numbers of whales in aggregations and (iii) a radial detection function based on the times of detected clicks and the estimated position. The method uses the complete set of allowable arrangements of these click trains into different numbers of whales. The number of arrangements is potentially very large yet can be computed because many click train combinations are not permissible, e.g. overlapping click trains cannot be from the same whale. It is suggested that the method could work well over perpendicular distances where the detection function is near-certain i.e. a strip transect survey. The method is applied to survey data from the western Mediterranean. Simulations based on the estimated radial detection function support a strip width of 5km. Some shortcomings and areas for further development are discussed.

KEYWORDS: ABUNDANCE ESTIMATE; SURVEY–ACOUSTIC; ACOUSTICS

INTRODUCTION

Sperm whales (*Physeter macrocephalus*) produce a series of loud regular clicks when diving, and these 'click trains' are of similar long duration to the dives themselves. These characteristics make the species unusually amenable to acoustic survey methods.

Acoustic line transect surveys to estimate sperm whale abundance have been successfully carried out where the whales disperse widely and are encountered more-or-less in solitude, e.g. Antarctica (Leaper *et al.,* 2000) and between the Faroe and Shetland Islands (Hastie *et al.*, 2003). However, at most temperate latitudes, adult females and younger animals tend to form aggregations. Counting the number of whales is then more challenging.

In their acoustic/visual line-transect surveys, Barlow and Taylor (2005) used visual methods for estimating aggregation size. This required interrupting the acoustic survey, and making visual counts, which are themselves difficult. Hiby and Lovell (1989) developed a method for point transect acoustic surveys of sperm whales, but it is not clear how it performs as aggregation size becomes large. Some recent acoustic line-transect surveys (e.g. Swift *et al.,* 2009) have used target-motion analysis together with expert manual analysis of click characteristics to identify click trains and count the animals in aggregations, a process that is time-consuming and has some element of subjectivity.

The work presented here attempts to count aggregated sperm whales in uninterrupted ('passing mode') acoustic line-transect surveys with an explicit and objective analysis.

In an acoustic survey for sperm whales not all clicks are detected, particularly at greater ranges, and there are periods of prolonged silence (often 10–20 minutes) when the whales do not vocalise much, which correspond more-or-less to the surfacing of the whales. The long silences between the click trains mean that it is not necessarily clear which trains are produced by which animals, and therefore how many animals are present. Fig. 1 shows the positions of some whales relative to a passing survey vessel, at the times that clicks were made. One problem for the surveyors is that the location of the clicks (and the whales) is not actually known and must be estimated. Another problem is estimating the number of sperm whales present from a set of click trains. Within the strip in Fig. 1 (upper solid grey line), between two and five whales may have been present, depending on which click trains were produced by which animals. In reality the number of animals and click trains could be

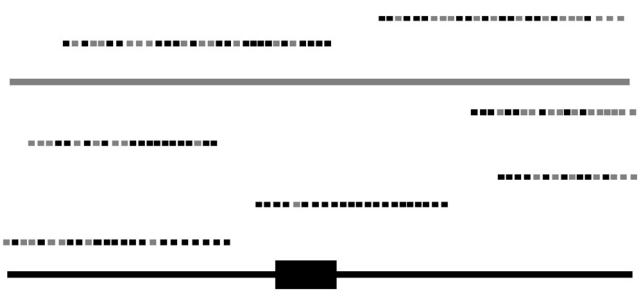

Fig. 1. Imaginary example of an unknown number of stationary whales making clicks as a boat (solid rectangle) passes by on a survey trackline (solid black line). Relative to the boat, the whales appear to be moving, and the illustration shows the positions of the whales in the surface plane at the moments they click (dots). Filled dots indicate clicks that are detected by the surveyors and grey dots that were not. Sperm whale clicks are typically produced in trains with longer silences in between. The number of clicks produced has been greatly reduced for the purposes of illustration. As radial distance from the boat increases, the probability of detecting a click is level or falls, and as perpendicular distance from the trackline increases, the probability of detecting a passing whale is level or falls. In this paper, a strip width is inferred within which it is supposed all whales will be detected (solid grey line).

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Table 1

Main parameters and data.

Data	
$\underline{\tau} = (\tau_1, \tau_2, ..., \tau_K)$	Detection times of clicks in a train.
$\underline{\delta t} = (\delta t_1, \delta t_2, ... \delta t_K)$	Measured time-of-arrival differences at hydrophone pair at detection times.
$\underline{b} = (b_1, b_2, ... b_K)$	Estimated bearings at those detection times.
$b(\tau)_k^{(j)}$	The kth bearing b_k detected at the kth time τ_k for click train j.
$\underline{b}(\underline{\tau})^{(j)}$	The bearings $\underline{b}$ detected at times $\underline{\tau}$ for click train j.
$[\tau]_m$	The mth detection period after resampling at a lower frequency $1/\Delta$.
$b[\tau]_m$	Average of the bearings detected during the mth detection time.
Constant/known parameters	
Δ	Lower frequency sampling period.
c	Click rate of a whale that is in a clicking state.
$\underline{\eta} = (a, b, \rho)$	Vocalisation cycle parameters.
w_y	Strip half-width.
w_r	Radial detection limit.
u	Speed of sound in seawater.
d	Separation of hydrophone elements.
m	The minimum number of sampling intervals containing click detections required for an animal to be detected
Estimated parameters	
$\underline{X} = (x_0, y_0, v_x, v_y)$	Initial state vector , where (x_0,y_0) = starting position, (v_x,v_y)=velocity of whale relative to survey vessel.
$\underline{X}(t) = (x(t), y(t), v_x(t), v_y(t))$	Dynamical state vector.
$\underline{X}(t)^{(i)}$	The dynamical state vector for the ith click train or combination of click trains.
n_i	Number of whales in aggregation i within the strip half-width w_y.
σ^2_k	Variance of the kth bearing in a sequence of bearings.
N	Total abundance of whales in the survey region.

considerably more numerous than in this example. Some animals may be missed altogether if their clicks go undetected, and this must be taken account of in the estimate of abundance. In this paper, a strip width is inferred within which it is supposed all whales are detected, to allow analysis as a strip transect survey. For reference, the data and parameters used in the analysis are summarised in Table 1.

1. DATA

In the case of a two-element hydrophone where the axis of the elements is parallel to the survey transect, the basic data are:

times of detections of clicks $\underline{\tau} = (\tau_1,\tau_2,\ldots)$ at one hydrophone element; and

time-of-arrival differences of clicks between the two elements $\delta t = (\delta t_1,\delta t_2,\ldots)$.

A sequence of bearings can then be estimated $\underline{b} = (b(\tau)_1,b(\tau)_2,\ldots b(\tau)_K)$ in which $b(\tau)_k$ is the bearing b_k detected at time τ_k with time-of-arrival difference δt_k using

$$\hat{b}(\tau)_k = \cos^{-1}\left(\frac{\delta t_k \times u}{d}\right) \tag{1}$$

where u is the speed of sound in water and d is the distance between the hydrophones.

This estimate is accurate in the 'far field', i.e. accurate at distances much greater than the separation of the hydrophone elements.

The data are ordinarily collected by digital equipment sampling at a 'high' rate, the sampling rate of the digitising equipment (e.g. often 48kHz), and the times of this high-frequency data are treated here as continuous. Because of the resulting high precision, the caret is dropped in the notation for b from here on.

Later in this paper the data are effectively resampled at a low frequency $1/\Delta$, with an average of the bearings taken over each sampling period Δ. The reasons for doing so are to:

(1) approximate normally distributed errors (as discussed in the development of eqn. 9);

(2) reduce the computational load when forming the allowable combinations of click trains (see section 3).

Using square brackets we can indicate resampled time as

$$[t] = floor\left(\frac{t}{\Delta}\right) \tag{2}$$

and similarly we can write the mth resampled detection time as

$$[\tau_m] = floor\left(\frac{\tau_k}{\Delta}\right) \tag{3}$$

with corresponding average bearing of

$$b[\tau_m] = \overline{b(\tau_k)}, \Delta[\tau_m] \le \tau_k < \Delta[\tau_m + 1] \tag{4}$$

and we can denote the whole sequence of resampled detection times as $[\underline{\tau}]$, and corresponding sequence of average bearings as $\underline{b}[\underline{\tau}]$.

2. ESTIMATE OF POSITION OF WHALE FROM A SINGLE CLICK TRAIN

2.1 Maximum Likelihood Estimation

The aim here is to find an estimate of whale position from the sequence of bearings of detected clicks. It is important to stress the assumption that the whales are at the surface. In fact they are often at depth. For example a whale at 1000m depth directly below the hydrophone will be assumed to be at the surface at a perpendicular distance of 1000m.

Following Nardone *et al*. (1984) we can define an initial state vector as:

$$\underline{X} = (x_0,\ \ y_0,\ \ v_x,\ \ v_y) \tag{5}$$

where (x_0, y_0) is the initial position of the whale relative to the boat, in directions parallel and perpendicular to the trackline respectively

and (v_x, v_y) is the velocity of the whale relative to the boat, assumed constant.

This determines a dynamical state vector at time t of

$$\underline{X}(t) = (v_x t + x_0,\ \ v_y t + y_0,\ \ v_x,\ \ v_y) \tag{6}$$

The parameters of $\underline{X}(t)$ are given by $\underline{X}$ (eqn. 5).

Given $\underline{X}$, we have estimates of the bearing to the whale at time t of:

$$\beta(t) = \tan^{-1}\left(\frac{v_y t + y_0}{v_x t + x_0}\right) \tag{7}$$

and a range at time t of:

$$r(t) = \left[\left(v_x t + x_0 \right)^2 + \left(v_y t + y_0 \right)^2 \right]^{1/2} \quad (8)$$

Nardone *et al.* (1984) give the likelihood of the initial state vector $\underline{X}$ with the observed data (bearings $\underline{b}$ detected at times $\underline{\tau}$), under the assumption of normally distributed bearing errors. With the present notation this is:

$$L_{\underline{b}|\underline{\tau}}(\underline{X}) = \frac{1}{((2\pi)^n \det(\underline{W}))^{1/2}} \exp\left(-\frac{1}{2} (\underline{b} - \beta(\underline{\tau}))^T \underline{W}^{-1} (\underline{b} - \beta(\underline{\tau})) \right) \quad (9)$$

where

$W = diag(\underline{\sigma}^2)$, in which $\sigma^2_k = \text{var}(b_k)$

The notation for the subscript $\underline{b}|\underline{\tau}$ is here intended to indicate that the times of detections $\underline{\tau}$ are given and there is no information at this stage about the process of signal production and detection which leads to these detection times.

The MLE estimates of $\underline{X}$ have an estimated covariance matrix given by (Nardone *et al.,* 1984):

$$\hat{S} = [A^T R^{-1} W^{-1} R^{-1} A]^{-1} \quad (10)$$

where

$$A = \begin{bmatrix} \cos\beta(0) & -\sin\beta(0) & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots \\ \cos\beta(\tau_k) & -\sin\beta(\tau_k) & \tau_k \cos\beta(\tau_k) & -\tau_k \sin\beta(\tau_k) \\ \vdots & \vdots & \vdots & \vdots \\ \cos\beta(\tau_K) & -\sin\beta(\tau_K) & \tau_K \cos\beta(\tau_K) & -\tau_K \sin\beta(\tau_K) \end{bmatrix}$$

$R = diag(\underline{r}^2)$in which $\underline{r}$ is the vector of range estimates, K is the total number of bearings in the sequence,

and with the time origin set here to the time of the first detection (τ_1).

Having an estimate of the covariance matrix provides information about the error structure of the locations. The two eigenvalues of the covariance matrix estimate the variances of the errors in the directions of its eigenvectors.

Note that if there are insufficient bearings in a sequence, then a positional estimate will be impossible or highly erroneous. If there are sufficient detection data available, and therefore sufficient bearings data, then a sampling period Δ can be introduced such that the bearings used in eqn. 9 are *average* bearings over each such period. By the Central Limit Theorem, if there are enough bearings over each Δ, then the average bearings will have normally distributed errors irrespective of the original distribution. This is the approach taken in this paper to satisfy the error assumptions of eqn. 9.

In the remainder of this paper a simpler situation is modelled, in which whales are assumed stationary and the vessel speed is constant and known (i.e. only x_0 and y_0 are free parameters in eqn. 5).

Example

An example of positional estimates of click trains made from real data using this approach is shown in Fig. 2. In this example the whales are assumed stationary, the boat moving in the x direction (along the transect) at speed s_x, (i.e. the state vector is $\underline{X} = [x_0, y_0, -s_x, 0]$) and a global estimate (i.e. for all click trains) of the variance of the bearings has been made from the data.

The ellipses around the location estimates (dots) are approximate error regions, using the eigenvalues of the estimated covariance matrix. Intuitively, the shape corresponds well with the crossings of the bearings.

3. ESTIMATE OF NUMBER OF WHALES IN AN AGGREGATION FROM MANY CLICK TRAINS

The more general and often realistic case of data from several whales present at once in an aggregation (e.g. Figs 1 and 2) is covered here. The approach used is based on the idea of generating all possible arrangements of click trains, that is, all the different ways click trains might be matched together as different whales. In this respect, it resembles the work by Hiby and Lovell (1998), which generated all possible arrangements of detections from a double-platform survey.

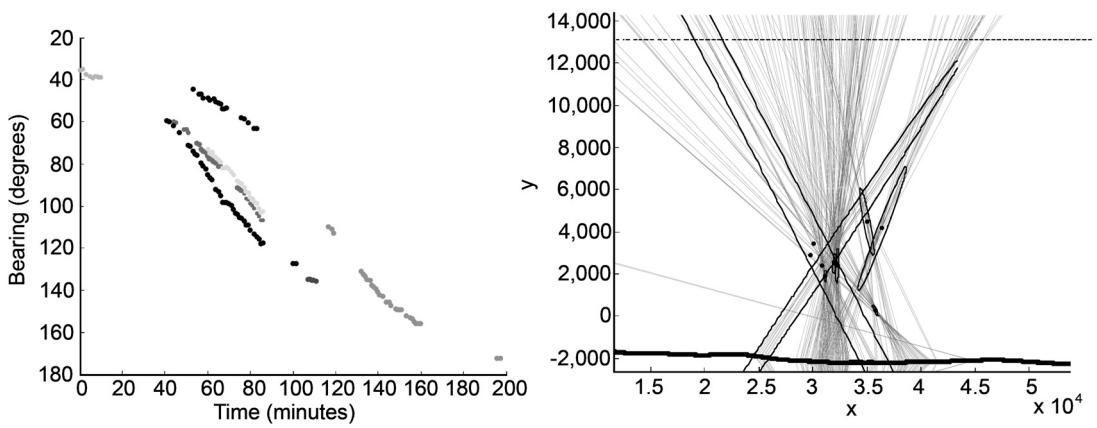

Fig. 2. Left: Bearing-time plot of received click trains. Here an analyst has grouped together clicks into eight different trains, but trains separated by prolonged silence cannot be matched together objectively. Right: Estimated positions of sources of click trains (single dots) with error ellipses. The boat track is shown along the x–axis and the measured bearings as grey lines.

3.1 Arrangements of click trains in an aggregation:
Define

T = {1, 2, …} to be the set of indices of the click trains, of size |T|.

and

S = {S_1, S_2, …} to be the set of allowable combinations of the elements of T, of size |S|.

G = {G_1, G_2, … } to be the set of possible arrangements of click trains, of size |G|. Each element of G is an arrangement: it is a set containing disjoint combinations of the elements of S, that is also exhaustive, in the sense that it contains every element of T.

In the present analysis, the number of possibilities is constrained; for example, simultaneous click trains cannot be from the same whale. The total number of possible subsets of T is $2^{|T|} - 1$, but the total number of allowable click train combinations is less (since some combinations are disallowed), so that:

$$|S| = \underline{1}^T \left(\underline{I} - \underline{A}_T\right)^{-1} \underline{1} \tag{11}$$

where

$\underline{1}$ is a column vector of ones,

$\underline{I}$ is the identity matrix, and

$\underline{A}_T$ is an adjacency matrix between click trains, that is, $a_{ij} = 1$ if T(i) followed by T(j) is potentially the same whale, and 0 otherwise.

Define Q as the (|G| × |S|) matrix in which

$$q_{ij} = \begin{cases} 1, & if\ S_j \in G_i \\ 0, & otherwise \end{cases}$$

Each row of Q represents an arrangement G_i, as defined above.

The number of whales in each arrangement is given by the (|G| × 1) vector:

$$\underline{w} = Q\underline{1} \ . \tag{12}$$

where $\underline{1}$ is a column vector of ones.

Example
Consider the imaginary case shown schematically in Fig. 3 containing 3 click trains.

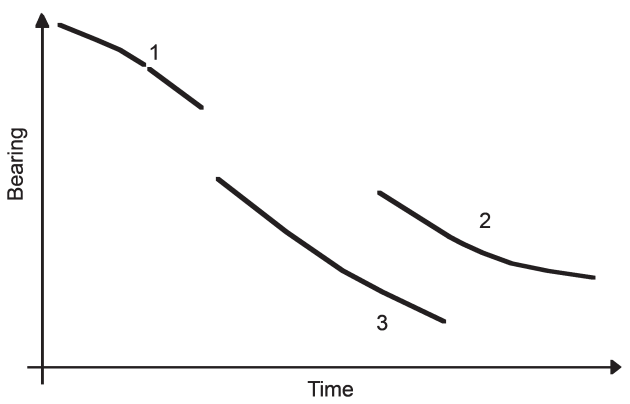

Fig. 3. Bearing-time plot for whale trains in the example. Trains 2 and 3 must be from different whales since they overlap in time.

In this case the various sets defined above are:

T = {1, 2, 3}

S = {{1, 3}, {1, 2}, 1, 2, 3}

G = {{{1, 3}, 2}, {{1, 2}, 3}, {1, 2, 3}}

so that |T| = 3, |S| = 5, |G| = 3

Note that S does not include the combinations {2,3} or {1,2,3} because click trains 2 and 3 overlapped in time and could not have come from the same whale. So the number of allowable click train combinations (|S| = 5 in this case) is less than the total number of possible subsets of T ($2^3 - 1 = 7$).

The adjacency matrix in this case is

$$A_T = \begin{pmatrix} 0 & 1 & 1 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

The lower triangle in the matrix is all 0 because the trains are sequenced in time (if train i follows j then j cannot follow i). The element at row 2 and column 3 is 0 because train 3 overlaps in time with train 2 and so cannot be from the same whale. Eqn. 11 gives |S| = 5 as expected.

The matrix of arrangements is:

$$Q = \begin{bmatrix} 1 & 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 & 1 \\ 0 & 0 & 1 & 1 & 1 \end{bmatrix}$$

and the number of whales over the arrangements is:

$$\underline{w} = Q\underline{1} = \begin{bmatrix} 2 \\ 2 \\ 3 \end{bmatrix}$$

3.2 Estimate of numbers of whales based on positional likelihood

Define l_j to be the likelihood associated with the jth click train combination S_j as given by eqn. 9. The vector of data is obtained by combining the data associated with the component click trains, the combined data being $\underline{b}[\tau]^{(j)} = \bigcup_{i \in S_j} \underline{b}[\tau]^{(i)}$ with the superscripts indicating the ith click train and the jth combination of click trains. The likelihood of the combined data is given by eqn. 9. Define $\underline{l}$ to be the (|S| × 1) vector of all these l_j, j = 1…|S|, i.e. a vector of the likelihoods for each click train combination:

$$l_j = L_{\underline{b}[\tau]^{(j)}}(\underline{X}^{(j)}) \tag{13}$$

The likelihood considered as a function of the number of detected whales n is given by:

$$L(n) = \sum_{w_i = n} \exp(\underline{q}_i \log \underline{l}) \tag{14}$$

where $\underline{q}_i$ denotes the ith row of the matrix Q.

The likelihood of any arrangement is from a model with a number of parameters that depends on the number of whales and their associated state vector $\underline{X}$. For example, in models in which the relative velocity of the whales is assumed constant and known, there are two free parameters for each whale. For models in which the whales have a constant

but unknown velocity, there are four free parameters for each whale. There may also be additional free parameters relating to the variances of the bearings, σ^2_k, if these are estimated.

When considering all the arrangements to estimate n using eqn. 14, the AIC statistic can be used to incorporate a penalty for the number of free parameters q:

$$AIC = -2\log L + 2q \tag{15}$$

If there are p free parameters for each whale, then combining eqns. 14 and 15 gives:

$$AIC(n) = -2\log L(n) + 2np \tag{16}$$

The estimate of the number of observed whales is the value of n corresponding to the minimum AIC.

4. MODEL OF VOCALISATION CYCLE

4.1 Model of alternating clicking/silent states

Sperm whale vocalisations are quite predictable and closely related to the dive cycle, which is itself quite regular partly because of the requirement that the whales breathe. Regular and fairly constant clicking occurs for most of the time that the whales are submerged and generally ceases when the whales are at the surface. The purpose of a model for what is the whales' 'intermittent availability' for detection (Laake and Borchers, 2004) is to estimate a detection function (see Estimate of a Radial Detection Function, below).

A mathematical model of sperm whale vocal behaviour can therefore be provided by an 'alternating renewal process' (Cox 1962). The whales alternate between a clicking state of duration T_c during dives and a silent state of duration T_s while at the surface. This gives the sequence $T_{c_1}, T_{s_1}, T_{c_2}, T_{s_2}, \ldots$ where the alternating silent or clicking periods T_s or T_c are independently and identically distributed.

The probability $\pi_c(t)$ that a whale is in a clicking state at time t, given that it was in a clicking state at time 0, can be derived analytically using Laplace transforms (Cox, 1962). If it is assumed that the statistical process started a long time ago (long before time 0), then this is termed an 'equilibrium' alternating renewal process. In the equilibrium renewal process, the observer is effectively starting to observe at a random moment during the clicking state. Alternatively, the 'ordinary' alternating renewal process gives the probability that the whale is in a clicking state given that it *entered* a clicking state at time 0.

Using Γ-distributions for the two probability density functions (pdfs) with positive integer shape parameter considerably simplifies the analysis. This restriction gives an Erlang distribution. The duration of the clicking state then has pdf given by

$$f(t,a,\rho) = \frac{\rho(\rho t)^{(a-1)}\exp(-\rho t)}{(a-1)!} \tag{17}$$

where a is the shape parameter (a positive integer), and ρ is the scale parameter. The duration of the silent state has a similar distribution, with positive integer shape parameter b. A further assumption made here is that the two Erlang distributions share the scale parameter ρ. Restricting the shape parameter to integer values still gives a wide family of distributions.

The parameters of both distributions can be collected together in a vector $\underline{\eta} = (a, b, \rho)$. In the analysis described in this paper, it is assumed that this parameter vector is fixed and homogenous throughout the population of whales being surveyed.

Assume that detection of a whale click is immediate and certain when it is made within some range (not yet specified). Suppose the whale passes abeam at time t_0, its closest approach to the survey vessel, and when detection is most certain. Then either the whale is already in a clicking state at time t_0; or it is in a silent state at time t_0 and enters a clicking state straightaway or more likely some time later.

In the first case, the clicking state is joined at a random moment in time (assuming the whale's vocalisations are unrelated to position of the survey vessel), and the first detected click is (nearly) immediate ($\tau_1 \approx t_0$). The probability of being in a clicking state from then is described by an 'equilibrium' renewal equation, with the Laplace transform (Cox, 1962) of:

$$\mathcal{L}\{\pi_c(t-\tau_1)\} = \tag{18}$$

$$\frac{a}{a+b} + \frac{\rho}{a}\left\{\frac{ab}{\rho(a+b)s} - \frac{\{(\rho+s)^a - \rho^a\}\{(\rho+s)^b - \rho^b\}}{s^2\{(\rho+s)^{a+b} - \rho^{a+b}\}}\right\}$$

In the second case, the whale is detected when it later *enters* a clicking state, so the first click detection is at $\tau_1 \geq t_0$. The probability of being in a clicking state after the first click is described by an 'ordinary' renewal equation with the Laplace transform:

$$\mathcal{L}\{\pi_c(t-\tau_1)\} = \frac{1-\rho^a/(\rho+s)^a}{s\{1-\rho^{a+b}/(\rho+s)^{a+b}\}} \tag{19}$$

These models are plotted in Fig. 4 using the empirical parameter values $\underline{\eta}$ estimated in the next section.

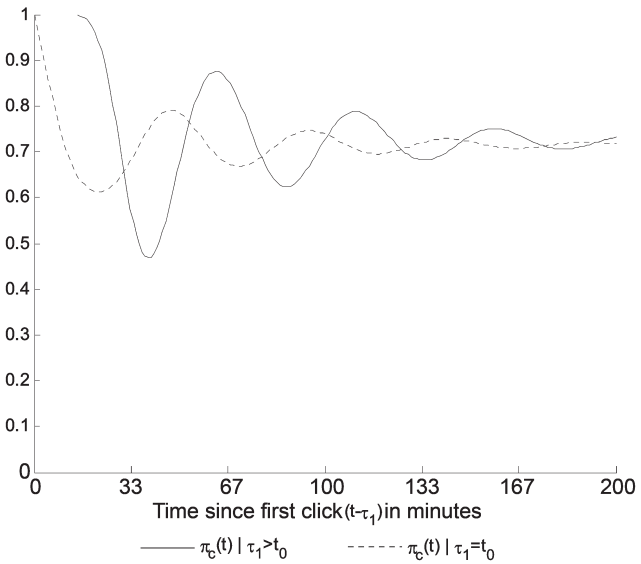

Fig. 4. Probability that a whale is clicking as a function of time since the first detected click at τ_1. It is assumed here that detection is certain and immediate if a whale is in a clicking state. If as the whale passes abeam at time t_0, the time of the first detection $\tau_1 = t_0$, then the observer has joined a clicking state at a random moment and an 'equilibrium' model is used. If $\tau_1 > t_0$, the observer has joined the beginning of a clicking state and an 'ordinary' model is used. See text and Fig. 5 for further details.

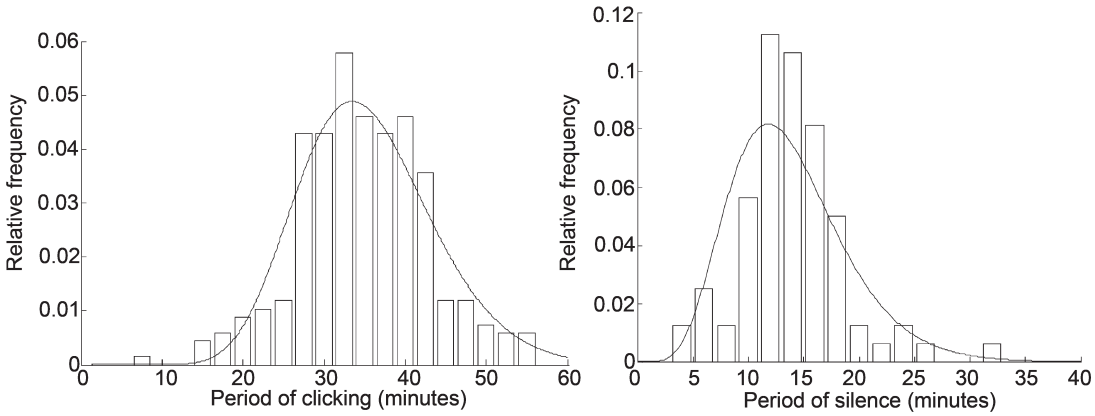

Fig. 5. Clicking and silent periods in minutes (data from Teloni, 2005) with fitted distributions.

4.2 Estimate of parameters from real data on durations of vocal and silent states

The results of fitting to empirical data from Teloni (2005) are shown in Fig. 5. These results were obtained by fitting gamma distributions and rounding the shape parameters, giving $\underline{\eta}$ = (17, 7, 0.5). The two distributions have means of 14 minutes (silent state) and 34 minutes (clicking state).

The fit of the model to these data is not particularly good; for example the data for the clicking periods seems more peaked than the model. However the data itself may be somewhat problematic, as it is not clear how click trains were matched in the original analysis, especially when intervals of silence were long. Under the circumstances the model seems a reasonable first approximation.

5. ESTIMATE OF A RADIAL DETECTION FUNCTION

Using the vocalisation cycle model of the previous section, we can go on to estimate the probability of detecting a clicking whale over a short time interval Δ.

Let h(r; $\underline{\phi}$) be a radial detection function for an individual sperm whale *click* produced at range *r*, with parameter vector $\underline{\phi}$. Assume that $h(0) = 1$, i.e. a click at radial distance 0 will definitely be detected.

Let c be the click rate, assumed constant, of a whale that is in a clicking state. The expected number of clicks in a sampling interval is then $c\Delta$.

Let $f(r; c, \underline{\phi}, \Delta)$ be the probability of detecting *at least one* click from a clicking whale at range *r* over a sampling period Δ. If there are negligible changes in $h(r)$ over a sampling period, then *f* will be:

$$f(r;\underline{\phi},c,\Delta) = 1-(1-h(r;\underline{\phi}))^{c\Delta} \qquad (20)$$

The constant parameters Δ and c are omitted as arguments from this point on.

To estimate the parameters $\underline{\phi}$ in eqn. 20, recall that:

(i) the estimated range to a whale as a function of time, given its position vector, is $r(\underline{X}(t))$ (eqn. 8); and

(ii) the probability $\pi_c(t)$ that a whale is in a clicking state at time t given that it was in a clicking state initially, was given in eqns 18 and 19.

For the observed detection times $[\underline{\tau}]$ in the click train of an *individual* animal passing by *given* $\underline{X}$ and whose vocalisation cycle vector $\underline{\eta}$ is also known, the likelihood of the detection parameters $\underline{\phi}$ is then:

$$L_{[\underline{\tau}]}(\underline{\phi}\,|\,\underline{X}) = \prod_{[t]=\varepsilon_1}^{\varepsilon_2} \left\{ f(r[t])\pi_c[t] \right\}^{\delta[t]} \left\{ 1-f(r[t])\pi_c[t] \right\}^{(1-\delta[t])} \qquad (21)$$

$$\text{where } \delta[t] = \begin{cases} 1 & if \quad [t] \in [\underline{\tau}] \\ 0 & if \quad [t] \notin [\underline{\tau}] \end{cases},$$

i.e. a binary variable indicating whether or not time $[t]$ was one of the detection times $[\underline{\tau}]$, and

ε_1, ε_2 are the times at which the whale is first and last within radial detection limit w_r.

When there is more than one whale, the likelihoods (eqn. 21) for each can be multiplied together.

6. ESTIMATE OF ABUNDANCE

This paper uses a strip transect approach to estimate abundance, i.e. where detection of whales is assumed to be certain within the strip (and detections beyond it are excluded). The smaller survey strip compared to that which might be used in distance sampling means a potential loss of precision in the analysis, but could allow:

(1) more objective identification of the click trains and the size of each aggregation, using a statistical rather than heuristic approach;

(2) more detailed justification of the detection function used; and

(3) a less labour intensive analysis.

The radial detection function from section 5 can be used to identify or test the strip size within which detection of a whale is certain. In section 7.5, simulations with some estimated (radial detection function, $\underline{\phi}$) and assumed (vocalisation cycle, $\underline{\eta}$) parameter values are carried out to support the strip half-width used.

If detection is certain, the total number of whales $\hat{n}$ within the survey strip of half-width w_y is the sum of $\hat{n}_i$ over all aggregations i. With appropriately random transects and

equal coverage probability, the estimate of the number of whales $\hat{N}$ in the entire survey area A is:

$$\hat{N} = \frac{A\hat{n}}{2Lw_y} \quad (22)$$

where L is the total survey line length. If the strip transect approach is valid (i.e. w_y is known) then the only uncertain element is $\hat{n}$. Lognormal-based confidence limits on $\hat{N}$ can be obtained using the survey transects as sampling units to estimate variance (Buckland *et al.*, 2001; Borchers *et al.*, 2002).

7. SOME SIMULATION RESULTS

A set of simulations were carried out to test various aspects of the method. These were not intended to provide comprehensive results and further investigations are needed. Some important common assumptions, also shared with the Mediterranean analysis in section 8, were:

(1) the whales are stationary;

(2) the boat motion is constant and known (v_x = 3 ms^{-1} and v_y = 0 ms^{-1});

(3) the 'far-field' approximation (eqn. 1) for the bearing from a hydrophone pair is adequate;

(4) whales click at a constant rate when in a clicking state (1.2 s^{-1});

(5) the bearings have the same errors, $\sigma_j^2 = \sigma^2$ for all j (in reality, errors increase as angles approach the hydrophone's axis); and

(6) the whale is at the surface (i.e. not diving)

7.1 Error structure of position estimates

Simulations were carried out in which the individual bearing errors were assumed to be independently and identically normally distributed with a known variance σ^2, which was then estimated in the simulations. In terms of the timing of the detected bearings, three example scenarios were examined, where the whale's clicks were detected (a) for 10 minutes abeam of the boat, (b) for 10 minutes ahead of the boat and (c) for periods given by the alternating model for the vocalisation cycle.

Examples of bearings and detection times from the latter two cases are illustrated in Fig. 6, along with some examples of the estimated positions and errors. (The results for case (a) are qualitatively similar to case (c) and are not shown). The true initial positions of the whale in cases (b) and (c) were (x_0,y_0) = (8,000, 5,000), and (x_0,y_0) = (900, 5,000) in case (a). The error structure (ellipses), as determined from the estimated covariance matrix are in agreement.

The results of the simulations are shown in Table 2. In these examples where bearing errors are constant, estimation

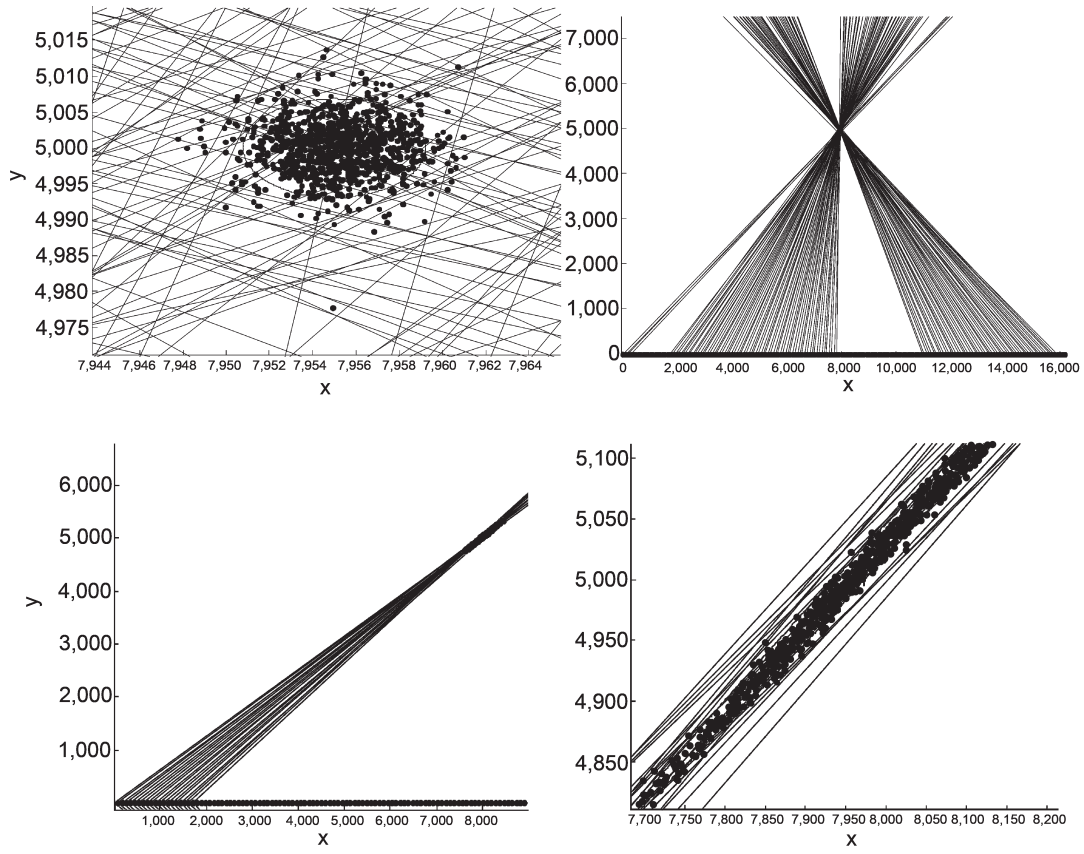

Fig. 6. Illustration of simulations of the estimation of a stationary whale's position from the detected bearings, as a boat passes by on a transect left-to-right along the x-axis at known speed. For clarity, the bearings from a single simulation run only are shown (grey lines). Position estimates of each simulation are shown as black dots. Ellipses are error regions based on the average of the estimated covariance matrices.

Top figures: A sequence of bearings made according to the vocalisation cycle model, and a close-up of the estimated positions.

Bottom figures: A 10 minute sequence of bearings detected when the whale is at some distance ahead of the boat.

Table 2

Results of simulations to estimate the position of a whale at known fixed position (see Fig. 6 for illustrations of these scenarios). 1,000 trials each. b( ) is the bias and sd( ) the standard deviation. For the burst scenarios (10-minute sequences) the total number of clicks detected 720 and number of bearings per sampling period n=36.

Position scenario	σ^2	Clicking	$\hat{b}(\sigma^2)$	$\hat{sd}(\sigma^2)$	$\hat{b}(x_0)$	$\hat{b}(y_0)$	$\hat{sd}(x_0)$	$\hat{sd}(x_0)$
Ahead	1	Burst	–0.04	0.31	36.4	146.8	24.2	103.6
Ahead	10	Burst	–0.54	3.2	53.0	449.1	36.6	317.6
Ahead	1	Model	0.14	0.27	0.16	2.20	0.03	3.7
Ahead	10	Model	1.09	2.57	–0.13	6.8	–1.0	10.79
Abeam	1	Burst	0.03	0.37	2.38	18.7	3.32	32.7
Abeam	10	Burst	–0.54	3.11	2.08	10.6	16.1	108.0

Table 3

Results of simulations to estimate number of whales n. |G| is the number of (valid) arrangements and |S| is the total number of (valid) train combinations. See text for further details. There were 50 simulations in each set.

n	Simulation set	Goodness-of-fit processing?	$\overline{\lvert G\rvert}$	sd(|G|)	max(|G|)	$\overline{\lvert S\rvert}$	sd(|S|)	max(|S|)	$\overline{n}$	sd(n)
6	1	n	21.8	57.9	281	10.9	4.8	25	6.08	0.34
8	2	n	1,288.0	451.2	2756	15.76	7.3	44	8.02	0.55
10	3	n	936.2	4,266.6	27,720	22.1	11.6	65	10.1	0.53
6	4	y	4.0	4.2	19	8.6	2.3	13	6.0	0.35
8	5	y	17.2	41.6	227	12.6	4.0	25	8.04	0.53
10	6	y	28.6	47.7	232	16.7	4.3	26	10.1	0.52

of σ^2 seems to be fairly accurate. There is a fairly low bias in the estimation of the (along-axis) position x_0. The bias in estimates of y_0 (perpendicular to axis) is higher than for x_0, but still quite accurate, except in the case of a burst of a click train ahead of the boat (b).

In summary, the estimates of position are accurate (low bias) and precise (low variance) when bearings are obtained at widely different angles, i.e. when whales go past the beam during a click sequence (a), or when a series of click sequences are obtained over a long period of time (c). However, when whales are only detected a long way ahead (or behind), bearings are nearly parallel and the errors are relatively large in the direction of the bearings.

7.2 Estimation of number of detected whales in an aggregation

Aggregations of whales of known size were simulated passing a survey vessel and the numbers of whales in the aggregations were estimated. The whales vocalised according to the model outlined in section 4 and the radial detection function had parameter values estimated from the Mediterranean survey (section 8). Various parameter values are shown in Table 4. As in the Mediterranean analysis, the variance of the bearings was estimated separately for each aggregation.

Table 4

Parameter values used in simulations to estimate whale numbers (section 7.2) and the Med. survey data (section 8). See text for further details.

Click rate when in a clicking state (c)	1.2 per sec.
Strip half-width (w_y)	5km
Radial detection limit (w_r)	15km
Vocalisation cycle parameters ($\underline{\eta}$)	(17, 7, 0.5)
Speed of sound in water (u)	1,500 m/s
Hydrophone separation (d)	3m
Minimum number of detections in a train (m)	10
Sampling period (Δ)	30 secs
Vessel velocity (v_x, v_y)	(3, 0) m/s
Whale velocity (s_x, s_y)	(0,0) m/s
Condition limit	1e8
Significance level for goodness-of-fit comparison (α)	1/1,000

7.3 Elimination of click train combinations

Trains or combinations of trains were eliminated (i.e. treated as undetected) if any of the following conditions applied:

(1) the number of detections in the train (i.e. number of sampling intervals containing detections) was less than the minimum number allowed;

(2) the lower limit of y was beyond w_y;

(3) the position-fitting routine failed to converge;

There were further criteria for combinations of trains only:

(4) A nearly-singular estimated covariance matrix (eqn. 10) was obtained, where the condition number of the matrix was larger than threshold. This removes unreliable location estimates.

To reduce the computational burden, before further processing a goodness-of-fit test compared the log-likelihood of a particular click train combination with the sum of the log-likelihoods of its s component click trains. Denoting these as $\log L_S$ and $\log L_T$ respectively, a statistic is calculated as $2(\log L_T - \log L_S)$. Since in these simulations the relative velocity of the boat is assumed known, there are only three free parameters for any click train combination (the position of the whale x_0 and y_0, and an estimate of the variance of bearings, assumed the same for all trains in the aggregation). L_T and L_S are associated with $2s + 1$ and 3 degrees of freedom respectively. The statistic was compared with a critical value of $\chi^2_{\alpha,2s-2}$, and click train combinations rejected if necessary; α was chosen to keep the rate of rejected combinations fairly low.

7.4 Simulation steps

Data were simulated in steps (1)–(4):

(1) generate $j = 1, \ldots, n$ whales with $\underline{X}^{(j)} = (x_0, y_0, v_x, v_y)$,

where $y_0 \sim \text{UNIF}(0, w_y)$
$x_0 = \sqrt{(w_r^2 - y^2)}$
v_x, v_y are known

(2) generate observed detection times $\underline{\tau}_i$ for each click train using $\underline{\eta}$, $\underline{\phi}$, $\underline{X}^{(j)}$;

(3) generate observed bearings $\underline{b}$ for each click train using $\underline{\tau}_i$, $\underline{X}^{(j)}$, $\underline{\sigma}^2$. Homogeneous bearing errors, $\sigma_i^2 = 1$ were assumed;

(4) click trains are separated into different whales when not meeting a joining criterion (details below). An example of some simulated data is shown in Fig. 7.

Estimates were simulated in the remaining steps:

(5) estimate $\underline{X}^{(i)}$ ($i = 1 \ldots |T|$) for each train using eqn. 9;

(6) eliminate trains in the set T that are invalid;

(7) form the adjacency matrix representing valid train combination pairs (some pairs are invalid e.g. if simultaneous);

(8) form the set S representing the allowable train combinations;

(9) eliminate train combinations in the set S that are invalid;

(10) estimate $\underline{X}^{(j)}$ ($j = 1 \ldots |S|$) for each combination of trains using eqn. 9;

(11) form the set G representing all the possible arrangements; and

(12) estimate $n|\{\underline{X}^{(j)}\}$ using eqn. 16

The results of the simulations are given in Table 3, and show that removing train combinations based on goodness-of-fit clearly reduces $|S|$, $|G|$, and therefore the computational load. There is a small positive bias in estimates of n.

7.5 Simulated distribution of perpendicular distances of detected whales

Simulation steps (1)–(4) of 7.4 were used to simulate click trains for single whales (other steps relating to combining ambiguous trains were omitted since these relate to aggregations of whales). Various parameter values used are shown in Table 4. The parameters $\underline{\phi}$ = (2171, 5.01) were those estimated in section 8. Trains were rejected if they satisfied any of the conditions outlined in section 7.2, i.e. they were treated as nondetections. In a trial with 1,000 runs, 999 were detected. The simulations appear to support the assumption of certain or near-certain detection of whales within the strip, i.e. $g(y) = 1$ from $y = 0$ to 5km.

8. APPLICATION TO A REAL SURVEY

The methods described here were applied to data acquired on a real survey of the southwestern Mediterranean. in 2004, described in Lewis *et al*. (In prep.). Click trains from the survey were identified and joined together by an analyst. In Lewis *et al*. (In prep.), the positions of the whales were estimated by the method described in this paper, and those positions were used to carry out a conventional distance sampling analysis. The alternative analysis given here avoids

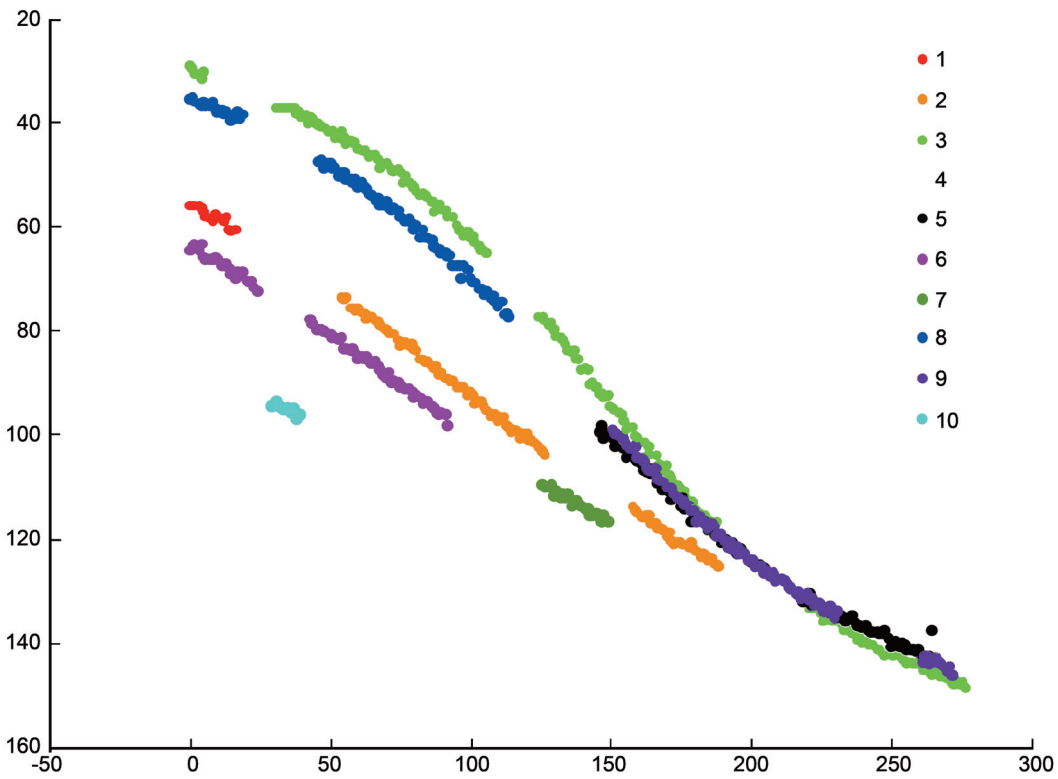

Fig. 7. Example bearing-time plot of simulated data. The simulated click trains, in this case from six vocalising whales, were broken apart if there was an interval of silence of more than the average period of silence, 14 minutes. This gave 10 click trains that required matching in order to estimate the number of whales present.

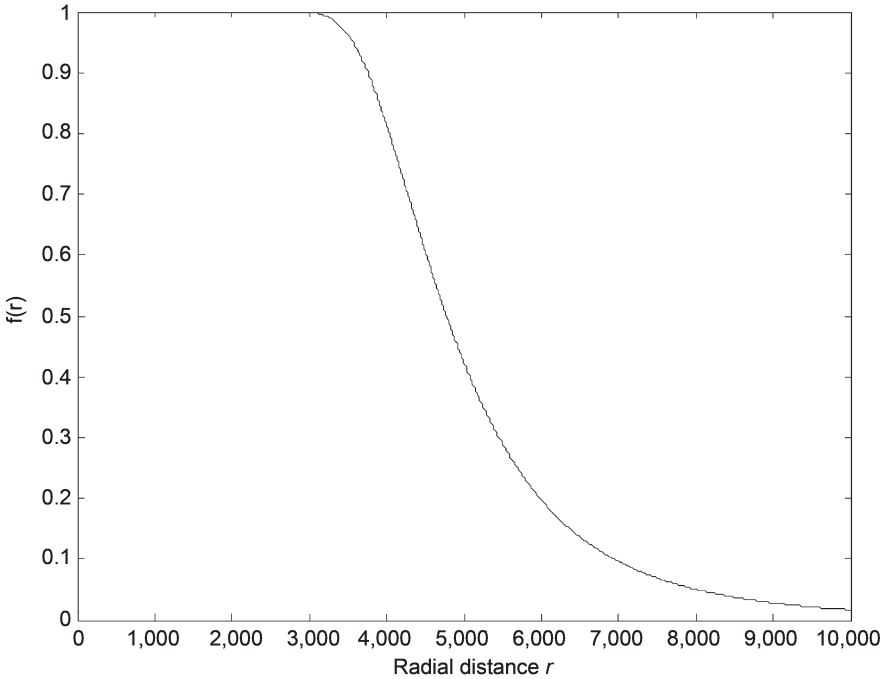

Fig. 8. Curve showing the estimated probability of detecting a whale at radial distance r (metres), clicking at rate c = 1.2 per sec, over a time period Δ = 30 seconds, using estimates for the Mediterranean. (See section 8).

subjective joining of click trains when separated by more than a certain interval (see below) and treats the survey as a strip transect.

The parameter values shared with the simulations in section 7.2 are shown in Table 4. Eliminations of click trains or click train combinations were as described in section 7.3. The click trains for the analysis were created by breaking up the click trains originally matched by the analyst. The criterion used was that any of the original trains separated by more than 2 minutes were treated as different trains. A further step in processing the data was a decision to choose the most likely side for any click train, based on eqn. 9.

After estimating the number of whales, only the arrangements corresponding to that number of whales are retained before estimating $\underline{\phi}$ as described in section 5. For this, the equilibrium vocalisation model (section 4) was used. This is justified by choosing a click randomly from a click train. For this, the click train made closest to the vessel, with the highest detection probability, is chosen. This is to minimise any consequences of missed detections.

The resulting abundance estimate for the entire survey region with 95% lognormal confidence limits was $\hat{N}$ = 652 (336, 1265). The estimated parameter $\underline{\phi}$ = (2171, 5.01)and the corresponding function $f(r;\underline{\phi},\Delta,c)$ is shown in Fig. 8.

DISCUSSION

The analysis approach outlined here is intended to allow line-transect surveys of aggregated sperm whales to be carried out without the need for visual estimates of the number of whales in aggregations, nor for analysts to make the more subjective links between click trains during analysis. By incorporating all (allowable) arrangements of click trains into the analysis the method attempts to draw more objective conclusions than would be obtained by a visual count of whales or a manual assessment of the number of whales in the acoustic data. Analysis still begins from a dataset made by an analyst grouping clicks together into trains. This prior process is labour-intensive, and would benefit from automation.

Stopping for visual estimation of whale numbers during an acoustic line-transect survey is worth avoiding where possible: it is time-consuming and can disrupt the survey and disturb the whales. It is also potentially inaccurate: for example, it is difficult to count dispersed whales visually, many of which will be asynchronously submerged for long periods; and when stopping there is a risk of counting whales that would otherwise have been located beyond the survey strip, or not counting whales that would otherwise have been within the survey strip.

Hiby and Lovell (1989) developed a method ('Cartwheels') for acoustic point transect surveys of sperm whales. One immediate advantage is that it is a much more concise analysis than that presented here. In addition, although based on a point transect approach, it is not necessary to interrupt the line transect survey in order to carry out point counts as long as the distance travelled by the vessel during the counts is small relative to the detection range (Gillespie, 1997). Using point transects at intervals means that some information from the survey is not used, but this may be acceptable in many contexts. Hiby and Lovell (1989) showed that the method is quite insensitive to clustering of the whales. The main drawback of the method, if any, is that it uses counts of whales within sectors (octants) of a circle, and it may be problematic to estimate these numbers reliably within large aggregations. Whitehead (2009) provided a more general discussion of this sort of approach.

Localisation

Given the large number of bearings expected from a passing sperm whale well within detection range, the accuracy of the

location estimate is potentially quite high, and the errors are quite well-defined (unlike the estimates of location made during conventional visual surveys). Nevertheless some disadvantages of the bearings-only solution remain, as identified below:

(1) The model still assumes that whales either are stationary or at least do not accelerate. The latter assumption is the more realistic but still a simplification. Movement of the whales is therefore a source of further error.

(2) Position estimates are produced in two dimensions (at the surface) that will be somewhat biased, as in reality the whales are often diving. One consequence of this is that some diving animals within the strip width might be treated as if they are beyond it, and not counted. This is unlikely to be problematic if the strip width is large enough (see Lewis *et al.*, In prep., for further discussion). Another is that the estimate of the number of whales, which is based on positional information, could be biased. This difficulty has not been explored in this paper.

(3) There is left-right ambiguity: two surface solutions are produced, one on each side. The ambiguity can be resolved if there are known accelerations of the receiving hydrophones, with measurements taken from, for example, boat GPS or heading sensors on the hydrophones. The Mediterranean survey (Lewis *et al.,* In prep.) used deliberate zigzagging of the survey vessel.

A general source of error for towed localisation systems is uncertainty about the position of the receivers (hydrophones) in the system, especially as the hydrophone cable weaves about in the water, or the vessel wanders from its course. These uncertainties could be reduced with improved accuracy of GPS systems in the survey vessel, 'inertial navigation' systems in the receivers, or sound sources of known location.

More elaborate acoustic detection systems with more (>2) hydrophone elements have been applied to sperm whales (e.g. Thode, 2005; Teloni, 2005) and can provide better, even instantaneous, estimates of location. If available, this kind of information would allow a simpler and more robust analysis of location than that used here. On the other hand, this hardware is harder to build and deploy, and is more expensive. Because there are typically long intervals of relative silence between trains, matching trains across these intervals would remain a problem, even if acoustically-derived locations were very accurate.

Vocalisation cycle modelling

The analysis described here assumes that a sperm whale clicks continuously when in a vocalising state, which is somewhat simplistic. Whales are not always completely silent when at the surface either (e.g. Wahlberg *et al.*, 2005), but it is assumed here that surface vocalisations are relatively rare. Further examination of the consequences of a failure to meet these assumptions is required.

In this paper, the model for the time-dependent vocalisation state probabilities (section 4) does not further consider the consequences of false negatives in this element of the analysis, i.e. where clicks are missed because detection is uncertain. Using a more limited strip half-width and, for any particular whale, using the closest click train to the survey boat to determine the vocalisation state clearly moderates any problem this may cause, but this is an area needing further investigation.

It is assumed here that the vocalisation parameter values $\underline{\eta}$ are known, corresponding to models fitted to data from the northwest Mediterranean from Teloni (2005). Three problems with this approach are that:

(1) the empirical data and/or the fit of the model to it could be improved (see section 4);

(2) the data used are (possibly) from a different population and a different behavioural context; and

(3) the parameter values are assumed homogenous throughout the population, whereas it is quite likely that there will be, for example, gender and age differences in diving and clicking behaviour.

Short click trains

Short click trains (trains with few bearings) are problematic in several ways:

(1) it may not be possible to localise them (maximisation of the likelihood fails);

(2) solutions may have large errors (if the bearings are nearing parallel);

(3) they quickly multiply the number of possible arrangements and the required computations; and

(4) it can be difficult to resolve the side-to-side ambiguity.

These issues have not been investigated in detail in this paper. Instead, short click trains and/or those with these characteristics were removed near the beginning of processing. Removing short trains should have relatively little effect on estimations of group size if, as seems likely, the remaining clicks from a whale enable a good location estimate.

A particular problem, if they are not removed, is that short click trains may not be correctly assigned to the correct side, and if this happens is likely to cause an upward bias in the estimates of aggregation size. Some potential technological solutions to side-to-side ambiguity have been mentioned above.

Assumption of certain detection

Part of the method outlined attempts to identify a perpendicular truncation distance w_y within which detection of whales is certain within the survey strip. Some supporting evidence for the value of w_y chosen in analysis of the Mediterranean survey (5km) has been given. Some estimates of the perpendicular detection function $g(y)$ from other surveys seem to be broadly consistent with this value (e.g. Lewis *et al.*, In prep.; Leaper *et al.*, 2000) and some are not (e.g. Hastie *et al.*, 2003, Barlow and Taylor, 2005), and background noise is likely to account for much of this variation. Acoustical considerations by Mellinger *et al.* (2003) with their particular setup support the idea of more-or-less certain instantaneous detection $h(r)$ of a clicking (diving) sperm whale to a range of about 5km. Ward *et al.*

(2012) state 'all vocalizing sperm whales within a 3.8km radius of a hydrophone are assumed to be detected', this being the average spacing of their static hydrophones, but they do not discuss the detection limits beyond there.

The strip transect approach does not utilise the extended detection functions used in distance sampling, which offer increased survey coverage and sample sizes, and have a lot of theoretical and applied support (Borchers *et al*., 2002, Buckland *et al.*, 2001). An advantage of the strip transect is that it is not necessary to simultaneously estimate numbers of whales and detection functions, since if the strip width used is justifiable, only the former task need be carried out. To put it another way, estimating the numbers of whales from the observed click trains when detection is also uncertain seems difficult and can be avoided with strip transects. A practical advantage is that it reduces the number of detected whales in aggregations that need to be counted, so making the required computations more feasible.

The estimated radial detection function $f(r)$ and simulated perpendicular detection function $g(y)$ given here have some empirical grounding, though aspects of it such as the constant click rate are certainly very simplistic. It seems likely that further information on the instantaneous radial click detection function $h(r)$ for sperm whales will be obtained in the future using multi-hydrophone systems and DTAGs.

CONCLUSION

A method is outlined for acoustically surveying sperm whales with a two-element hydrophone system even when animals are aggregated. The method attempts to identify a perpendicular truncation distance within which acoustic detection of animals is certain, and count the whales within it using the detected clicks. Topics for further examination or development include: automated formation of the initial click trains; removal of short click trains; the effect of violation of the surface assumption, and more detailed modelling of click rates.

ACKNOWLEDGEMENTS

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The relation of coastal geomorphology to larger mass strandings of odontocetes around Australia

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ABSTRACT

Sites of larger live mass strandings (10 to 250 individuals) for five selected odontocete (toothed whale) species around Australia are examined to see if they have any characteristics or properties which might be related to the strandings. Bays are the significant coastal unit in the 66 events reported over a 100 year period; only three events were not within bays but on open sandy coastlines. Species, species adult size and bay size do not appear to be factors in these larger stranding events. The reason for the association of bays with larger mass strandings is not obvious. Many of the bays have simple planform and uncomplicated bathymetry. However, they share some properties previously associated with strandings that are a consequence of the processes of bay formation. Coastal locations other than particular types of bays do not necessarily have all of these properties, potentially explaining why these bays dominate the Australian mass stranding record. A chain of geomorphological, physical, and biological factors can be constructed to explain the role of the bays in mass strandings. Regardless of this possible explanation, there is an observed correlation of particular site properties with larger live mass strandings about Australia which might be expected to have predictive power in indicating potential mass stranding sites. This is particularly apparent when key properties of stranding sites are defined and compared in terms of simple quantitative thresholds. The sites of herd strandings around New Zealand generally exhibit the expected properties.

KEYWORDS: AUSTRALASIA; AUSTRALIA; STRANDINGS; ODONTOCETE; PACIFIC OCEAN; SOUTHERN HEMISPHERE; TRENDS

INTRODUCTION

There are a wide variety of potential reasons for mass strandings of cetaceans (e.g see the review by Perrin and Geraci, 2009) including behavioural characteristics, disease, military sonar, and fishing activities but the focus of the present paper is whether or not live mass strandings are influenced by stranding site characteristics. Australian stranding sites for five selected odontocete (toothed whale) species were charted to examine this question, particularly sites of 'larger' live strandings (10+ animals, see below) and sites where strandings have occurred repeatedly. Continental scale spatial and seasonal stranding patterns for the five odontocete species are compared with Ziphiidae (beaked whale) and baleen strandings in Hamilton and Lindsay (2014).

DATA AND METHODS

Definitions used in this paper

Coincidental strandings of two or more cetaceans, alive or dead, excluding mother-calf pairs, are considered unusual and are commonly referred to as 'mass strandings', although there is no consensus definition as to how close strandings have to be in time and space to be considered related. D'Amico *et al.* (2009) define an 'atypical' mass stranding as two or more animals stranded within six days of each other and within a range of 74km, excluding mother-calf pairs. Such definitions are broad and potentially may lead to false categorisation of unrelated events as mass strandings in addition to correct categorisations.

A further confounding factor when examining potential causes is that the stranding of numbers of live and dead animals may have unrelated causes. For example, the drifting of incapacitated cetaceans into shore due to prevailing conditions may in some cases result in strandings being categorised as mass strandings (implying common cause), whereas a number of animals may have arrived at the stranding site within a few days simply by chance.

To provide unequivocal examples of mass strandings, the present paper initially considers only live strandings of ten or more animals. Such events are also often better publicised and documented, enabling details to be more easily verified. Dolphins and porpoises were excluded from the analysis as these smaller odontocetes are often resident or semi-resident in harbours, bays, and coastal areas, so may not have the stranding patterns of other odontocetes (Brabyn, 1990).

Australian data

Strandings database

A database was constructed by Hamilton and Lindsay (2014) of stranding records for five cetaceans chosen (Table 1) as being broadly representative of odontocete whale species, other than small coastal species (see above), found stranded in Australian waters (Fig. 1). Dolphins and porpoises sometimes stranded together with the five species, but are not included in the counts of animals. The five species were chosen as sometimes having large numbers of animals in a stranding (tens to hundreds) and a range of maximum adult sizes. This was to examine possible differences in stranding behaviour caused by size e.g. agility in shallower waters, habitat/feeding behaviour and efficiency and acoustic frequency of vocalisations.

The five species are from two separate families, Physeteridae and Delphinidae; all are socially cohesive and can occur in large, relatively stable groups. The primary source for the database are records from the Commonwealth of Australia (2010) repository.

Stranding records in the database for the selected species date back to 1868 for the sperm whale, and extend up to 2010 (143 years). Strandings of 10+ animals date from 1911 to 2009

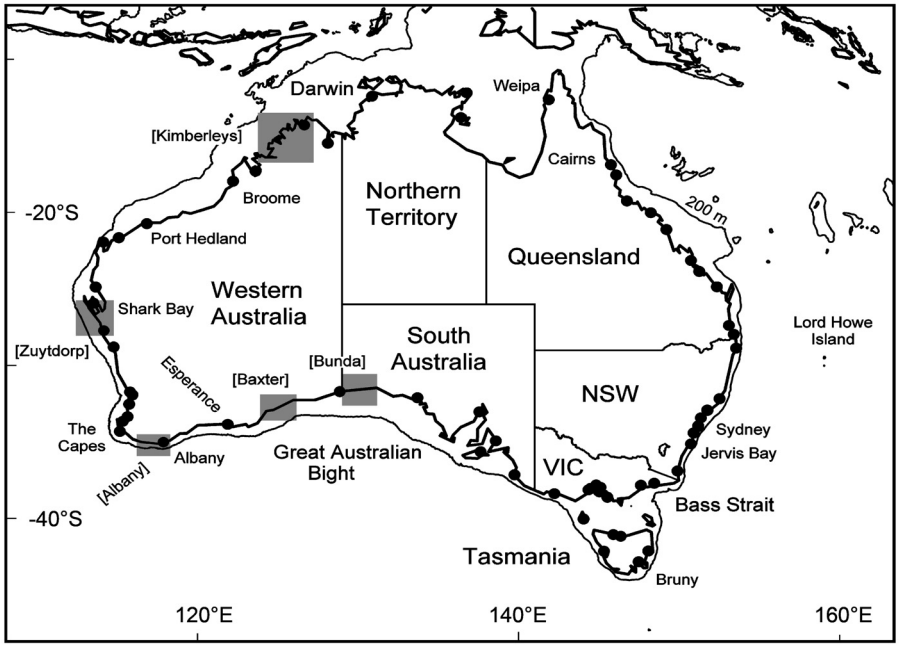

Fig. 1. The Australian coastline, Australian states, and selected population centres. Sea cliffs and rocky areas in Western Australia are outlined with rectangles and named in square brackets, for example [Baxter]. Cliff locations are adapted from Reader's Digest (1983) and Sharples *et al*. (2009).

Table 1

Five odontocete species considered in this study and number of larger stranding events of 10+ live animals (Hamilton and Lindsay, 2014) for which sufficient data on location are available. Numbers in brackets are the total number of strandings with two or more animals (including mother-calf pairs).

Species	Adult male length	Number of live[1] larger events (total 2+)	Maximum number in a single event
Physeteridae			
Sperm whale (*Physeter macrocephalus*)	*Ca* 18m	16 (27)	65
Delphinidae			
Killer whale (*Orcinus orca*)	*Ca* 9m	1 (2)	13
Long-finned pilot whale (*Globicephala melas*)	*Ca* 6.5m	32 (46)	200
False killer whale (*Pseudorca crassidens*)	*Ca* 5.5m	16 (20)	250
Melon-headed whale (*Peponocephala electra*)	*Ca* 2.8m	1 (3)	51
Total		66 (98)	

[1]Includes two cases where the animals were found dead but it was highly likely they had stranded alive.

(99 years), and more events have occurred since which are not included in the analysis. The data are temporally uneven, but this should not affect a spatial examination provided there are no temporal trends in either distribution of strandings or bias in reporting. Beaked whale (Ziphiid) strandings were also compiled and are discussed in Hamilton and Lindsay (2014). There were 35 beaked whale strandings of two or more individuals, with a maximum of 6 individuals in any one event. Not all beaked whale strandings are live events.

Stranding site properties

A range of relatively simple properties have been considered as a first step in determining whether or not sites of larger mass strandings have physical characteristics in common. Coastline configurations (primarily reported as bays or beaches in the database), bathymetric trends, slopes and sediments are basic properties used to describe the near shore environment. Quantitative measures of these and other parameters were collated where possible to enable comparisons between sites (e.g. see Table 2).

A bay is defined as a body of water partially enclosed by the inward curving of the land, with a wide mouth allowing access to the sea. This broad definition can be refined by classing bay geomorphology as one of three types:

(1) a headland and a gently curving planform;

(2) relatively deeply indented into the coastline with a headland often not prominent or absent; or

(3) either of the above two types with additional complexity such as that caused by interior coastline configuration (e.g. Cloudy Bay) or the presence of islands (Marion Bay).

Bay complexity may also arise due to the presence of reefs and irregular bathymetry within bays. Perkins Bay, for example, has extensive shallow sand bars, islands and channels in the southwest and west.

Type 1 bays are formally known as 'headland-bays' (Fig. 2). A headland-bay is a geomorphological unit where the harder more resistant headland controls the bay shape through eroding effects of diffracted and refracted swell waves on the adjacent downswell coastline. An archetypal headland-bay has only one headland, and a long, curving bay with a characteristic shape, often modelled as a log-spiral or

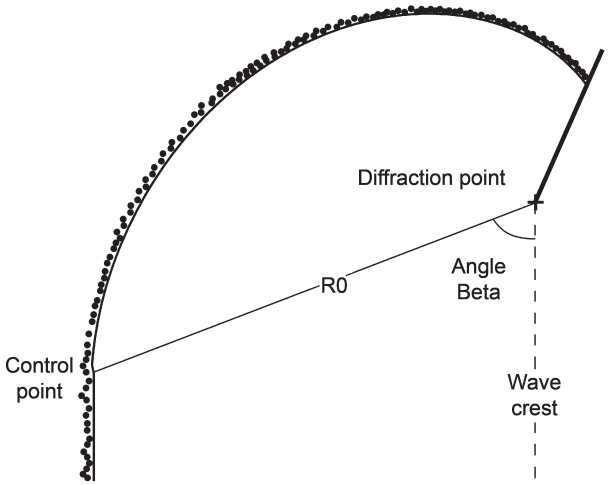

Fig. 2. Schematic of headland-bay geometry. Swell direction is from right to left. Distance R0 and angle Beta define the bay shape. Line R0 extends from the Diffraction point (usually a headland) to the point on the coastline where the beach shape changes from curved to straight. Beta is the angle between the dominant swell and line R0 (Moreno and Kraus, 1999).

zeta spiral (Moreno and Kraus, 1999). They are also termed zetaform, log-spiral, half-heart, or crenulate bays (Krumbein, 1944). Particular Australian examples are Geographe Bay, Ocean Beach, and Wreck Bay (Fig. 3). Modelling and observation indicate the log-spiral bay shape forms in response to the dominant swell direction in order to reduce wave action in the bay compared to other shapes (Silvester and Ho, 1972). The term 'hooked bay' is also used in the literature, but does not necessarily refer to a log-spiral shape or imply that a headland is present. The term headland-bay is used in the present paper to indicate that a headland is present and that this headland played a part in creating the shape of the bay.

Many of the bays have a headland at one or both ends. Bay width was measured from headland to beach end for the single headland case (Fig. 2), and headland to headland when two were present. Bay indentation distance was measured as the maximum value from shore perpendicular to the line specifying the bay width. Indentation ratio was computed as the ratio of bay width to bay indentation distance. We observed that a ratio of bay width to bay indentation of 2:1 could broadly be used to separate archetypal *log-spiral headland-bays* (ratio greater than 2) from *indented bays* (ratio less than 2). An indentation ratio >2 does not automatically specify a log-spiral bay (see Green Point and Treachery Beach (Fig. 3) which are rectangular bays), but a ratio <2 normally means that it is not a classic log-spiral bay, although it may still have significant log-spiral character. Twenty of the 35 sites (57%) have ratios >2, 12 of 35 (34%) have ratios <2 and the ratio was not able to be defined for three cases (9%) (Gunnamatta and Petrel Point in Victoria, and Crowdy Head in New South Wales).

Classification of sites in this paper

Table 2 summarises all of the sites considered bays referred to in the text by classification as follows:

CI: bay with indented character also with additional coastline or bathymetric complexity;

H: log-spiral headland-bay;

HC: log-spiral headland-bay with additional coastline or bathymetric complexity;

HI: log-spiral headland-bay with indented character;

I: indented bays without prominent headlands.

A beach is a coastal deposit of mobile material, often of sand size particles, in dynamic interplay with waves and currents. Royal Australian Navy (RAN) Hydrographic Office nautical charts were used to examine the morphology of stranding sites and to obtain descriptions of the seabed. All 18 sites for which RAN seabed indicators were available had

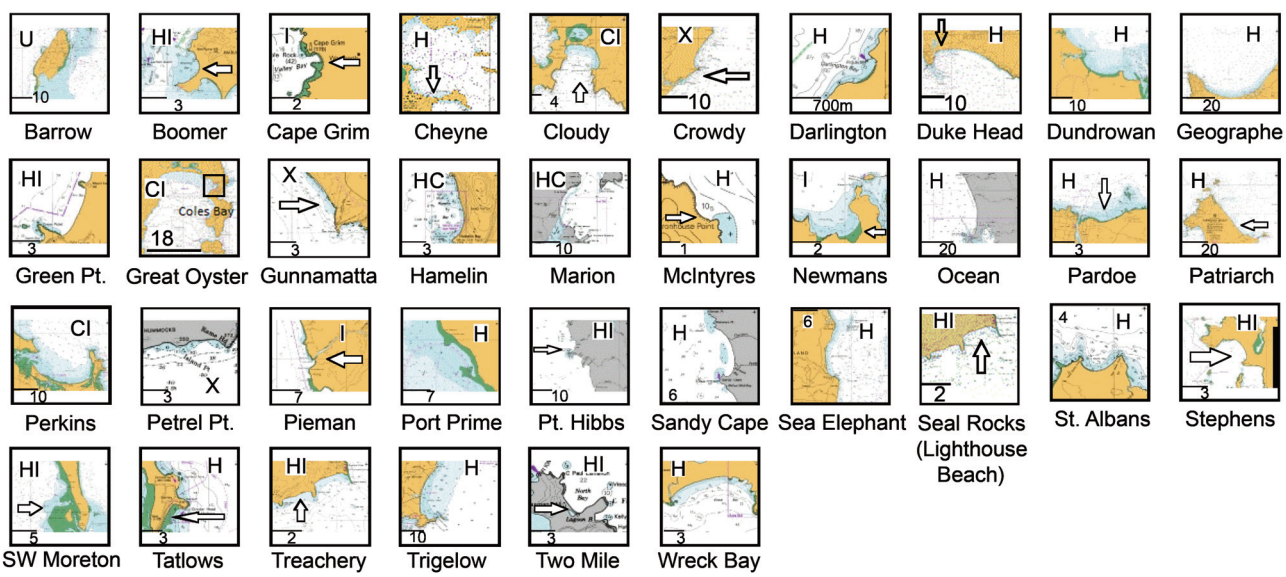

Fig. 3. Planforms of Australian sites of mass strandings of 10+ individuals. The actual stranding site on Barrow Island is unknown, but it is recorded as being in the bay at the south of the island. Symbols: H shows a log-spiral headland-bay, HI shows a log-spiral headland-bay with indented character, I shows an indented bay, U means the exact stranding site (on Barrow Island) is unknown. For HC (one site) and CI (two sites) the H and I have the meanings already given, and the C denotes additional coastline or bathymetric complexity. X shows coastline configurations which are not bays (three cases). Map scales (km) differ for the thumbnails.

dominantly sandy seabed, sometimes noted as fine sand. The descriptions were obtained by visual and tactile examination of fresh, wet samples. Hamilton (1999) has shown they are generally reliable indicators of sandy sediments with respect to the Udden-Wentworth sediment grain size and classification scheme (Wentworth, 1922). Sands have grain size diameter from 0.065–2mm. The divisions are: 0.065–0.125mm (very fine); 0.125–0.25mm (fine); 0.25–0.5mm (medium); 0.5–1mm (coarse); and 1–2mm (very coarse). Particles of diameter less than 0.065mm (e.g. silts and clays) are collectively termed muds and particles with diameter greater than 2mm (termed gravel) range from granules to boulders.

Bathymetric cross-sections were constructed from the RAN bathymetry charts for shore perpendicular transects (generally perpendicular to trends of depth contours). More transects were constructed for sites with larger geographical dimensions. These sections showed that sites tend to have either two or three regions of near constant seabed slope, with slopes decreasing with distance from the shore. With respect to Lowest Astronomical Tide (LAT) these are: nearshore slopes at 0–10m (an extension of the lower beach face in the wave or surf zone); a second slope from 10–20m (a transition zone for wave influence); and a third slope from 20–40m (with lesser seabed wave action than inshore areas).

Beach slope generally increases with grain size (Wiegel, 1965). This dependence is a function of sediment size, density, shape and wave exposure, particularly the higher wave energy available to move coarser sediment landward in times of storms and other major events. Fine sand beaches generally have slopes of about 1°, coarse sand and gravel beaches have slopes of 4 to 17°, and shingle beaches can attain slopes over 30° (Gilluly *et al.*, 1975).

Two techniques are often used to measure beach slopes (Jennings and Schulmeister, 2000). The first measures 'beachface slope' as an average from the top of the highest storm berm to low tide. Grain size is averaged over this distance. The second measures 'active profile slope' as the average from high tide to low tide on the day of survey, with average grain size assessed in the swash zone. Beachface slope can be higher than active profile slope because the coarsest material can be marooned above high tide level for long periods. These two slope measures would usually be higher than slopes at 0–10m LAT. The two measurements of beach slope describe different aspects of the environment and ideally both measures or beach profiles would be obtained together with offshore bathymetry profiles and slopes. Cetaceans venturing inshore will experience offshore seabed slopes before they encounter beach slopes.

Data from New Zealand

Properties of sites of New Zealand 'herd' strandings, defined as 2+ animals, excluding mother-calf pairs, were analysed by Brabyn (1990) and Brabyn and McLean (1992).

RESULTS

Australia

The 66 live larger mass strandings considered here occurred at 35 different sites (Tasmania 21, Western Australia 5, New South Wales 4, Victoria 2, Queensland 2, South Australia 1) spanning the width of the Australian continent south of 25°S (Fig. 4 and Table 2). The sites cover a wide latitude and longitude range of inhabited and uninhabited coasts with different geographic aspects, geomorphology, oceanography and scale. Therefore, we believe that any reporting bias caused by proximity to towns and settlements resulting in particular locations being over represented is unlikely to affect the broad conclusions.

Twelve of the 35 sites (34%) had more than one stranding of 10+ individuals. If smaller (1–9 animals) strandings of sperm whales, long-finned pilot whales, and beaked whales are included, then 20 of the 35 locations have more than one stranding event. The repetition of both large and small stranding events at sites with strandings of 10+ individuals suggests that site properties may be related to the strandings, not coincidence or other factors. Repeat stranding sites may thus be archetypes for characteristics of stranding sites, if such archetypes exist.

Morphology of stranding sites (see Table 2)

Thirty-two of the 35 sites (with 63 of the 66 events) refer to bays (Table 2 and Fig. 3). Bay widths ranged from 600m to 64km. Three sites, each with one live mass stranding event, depart from this general pattern: the coastline at Petrel Point (Victoria) has only a relatively slight indentation, while Gunnamatta Beach (Victoria) and Crowdy Head (NSW) are associated with a long almost straight coastline, not a bay. At least 28 of the 32 bays have a headland or headland-equivalent, as do Gunnamatta Beach and Crowdy Head. Headland-equivalents are formed more by the configuration of shallow bathymetry than coastline configuration, examples being Pardoe Beach (Tasmania) and Port Prime (South Australia). Sites without prominent or protruding headlands are the indented Cape Grim Bay, Cloudy Bay (although it has interior headlands), Great Oyster Bay, and Pieman Heads, all in Tasmania, and each has one 10+ stranding event.

A large proportion of the bays (at least 26 of 32) were visually assessed by the authors as having significant log-spiral character (those labelled H, HC, HI) (Table 2, Fig. 3). These account for 50 of 66 (76%) of strandings of 10+ individuals. The 18 more classically shaped or archetypal of these 26 bays (those classed H, HC) incorporate 40 of the 66 events (60%).

There are three rectangular bays (Green Point (Marrawah), Lighthouse Beach, Treachery Beach) that have an indentation ratio and bathymetric configuration matching the bays with a gently curving planform. They have been classified here as headland-bays with indented character.

Five bays have complexity in coastline configurations or bathymetry (Cloudy, Great Oyster, Hamelin, Marion and Perkins bays). Hamelin Bay is a sandy headland bay with interior reef structures. Cloudy, Great Oyster and Perkins bays are indented (classified as CI in Table 2 and Fig. 3). Cloudy Bay has several interior bays and headlands. The western side of Perkins Bay is made up of sandbanks, islands, and channels. Marion Bay (classified as HC in Table 2 and Fig. 3) is a zetaform headland-bay with complexity in coastline configuration to its north caused by a large island near the coast. Cloudy Bay and Great Oyster Bay have 1 strandings of 10+ individuals, Homelin Bay has 2, Marion Bay has 4 and Perkins Bay has 8 (Fig. 3). 'Classic' log-spiral

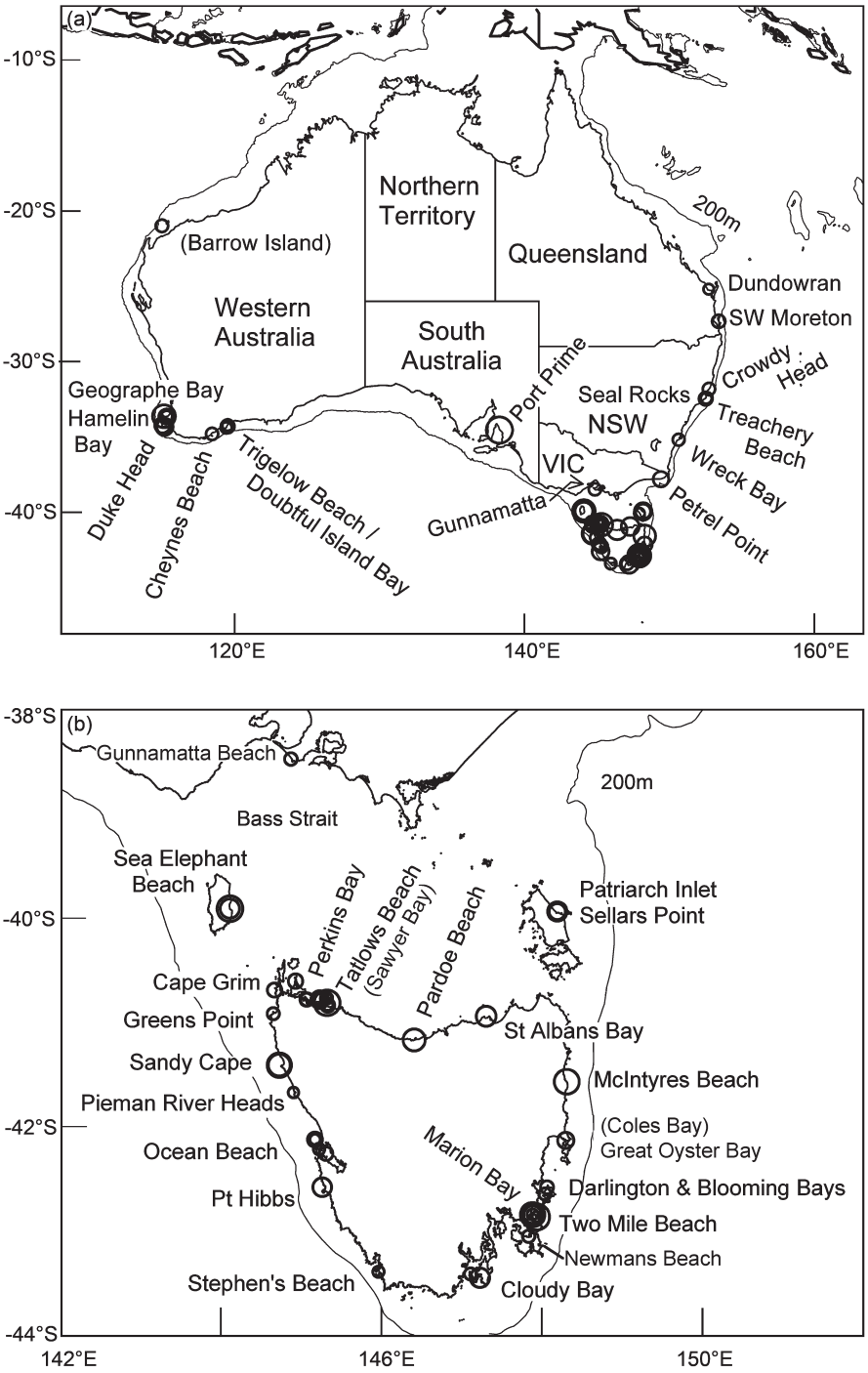

Fig. 4. Distribution of strandings of ten or more individuals for false killer, killer, long-finned pilot, melon-headed, and sperm whales. The maximum in a stranding is 250. (a) Australia; (b) Tasmania.

headland-bays have a maximum of five events at both Ocean Beach (Tasmania) and Trigelow Beach (Western Australia).

Of the 19 events with 100+ individuals in a stranding (see Table 2), 12 were in log-spiral headland-bays (H in Fig. 3), 2 were in log-spiral headland-bays with indented character (HI), none were in an indented bay (class I), and 5 were in three bays with complex character (Cloudy, Perkins, Marion Bays). Cloudy and Perkins bays (CI) each had one stranding of 100+ individuals, and Marion Bay (CH) has three.

Seabed sediments and gradients

As noted under methods, the 18 sites for which seabed type indicators are shown on RAN Hydrographic Office nautical charts all had dominantly sandy seabeds, sometimes noted as fine sand. However, as discussed below, there are three examples of mass strandings in rocky locations within bays in Tasmania.

From the RAN bathymetry charts, many of the sites tend to have either two or three regions of near constant seabed slope, with slopes decreasing with distance from the shore. Only 4 of 92 seabed slopes calculated for 29 of the 35 sites (some at different locations within the same bay) had slopes greater than 1°, all were for 0–10m, with 1.6 and 1.7° at Treachery Beach and Two Mile bays, and 1.9° at Crowdy Head. The outer slopes were usually less than 0.5°. Slope calculations for 0–10m represent a broad average, as sand

Table 2

Summary of the information on Australian sites with good position information with live large mass strandings with 10 or more animals per event (for details see text). *The position of the Barrow Island site is unknown. It is shown because it is the northernmost site, but it is not included in analyses. **Key:** Type: CI = bay with indented character and additional coastline or bathymetric complexity; H = log-spiral headland-bay; HC = log-spiral headland-bay with additional coastline or bathymetric complexity; HI = log-spiral headland-bay with indented character; I = indented bays without prominent headlands; and X = not bays. IR = Indentation ratio. Slope: N1 = nearshore; N2 = intermediate; N3 = offshore. Substrate: fS = fine sand, M = mud, MS = mud and sand, R = rocky, S = sand, SSh = sand with shell fragments. Large events: number of live events with 10+ animals (number with 100+ animals in parentheses). Small events: number of events (live and dead) of 1–9 animals for long fin pilot and sperm whales only. Beaked whales: number of beaked whale stranding events (of 1 or more animals).

Site	State	AUS chart	Type	Width (km)	IR	Slope (degrees)			Substrate if known	Large events	Small events	Beaked whales
						N1	N2	N3				
**Barrow Island*	*WA*	*742*	*?*	–	–	–	–	–	–	*1**	–	–
Boomer Bay	Tas	170	HI	3.8	2.1	0.3				1		
Cape Grim	Tas	790	I	0.6	0.8		0.4	0.2	R	1	2	
Cheyne Beach	WA	110	H	1.1	2.1	0.3	1.1	1.5		1	1	1
(in Frenchmans Bay)			*(I)*	*(5.6)*	*(1.8)*	–	–	–				
Cloudy Bay	Tas	795	CI	5.4	0.9	–	0.7	0.2		1 (1)	1	6
Crowdy Head	NSW	811	X	X	X	1.9	1.1	0.1	S	1	1	
Darlington	Tas	170	H	0.8	2.4	1.2	0.5	0.3		1		
Duke Head	WA	757	–	–	–	0.14	0.06		S	2(1)	1	
(Flinders Bay)			H	31.5	2.1	–	–					
Dundowran	Qld	817	H	21	2.9	0.06			S	1		
Geographe Bay	WA	755	H	63	2.6	0.2	0.08	0.07	S	4(1)		1
Great Oyster Bay	Tas	766	CI	18	0.7	0.2	0.1	0.1		1		1
Greens Point	Tas	791	HI	2.9	1.9	–	–	–		1		1
Gunnamatta	Vic	150	X	X	X	0.8	0.6	0.4	fS	1		
Hamelin Bay	WA	756	HC	7.3	2.2	0.24	0.2		S	2		
Marion Bay	Tas	169	HC	14.8	2.3	0.5	0.2			4 (3)	1	2
McIntyres Beach	Tas	766	H	1.7	2.8	0.5	0.5	0.3		1(1)	2	1
Newmans Beach	Tas	171	I	1.7	1.1	0.24	0.08		M, S	1		
Ocean Beach	Tas	353	H	18.5	2.7	0.4	0.2	0.5	S	5	7	6
Pardoe Beach	Tas	164	H	4.7	2.5	0.4	0.3	0.2	S	1(1)		
Patriarch Inlet and Sellars Point	Tas	800	H	21	3.7	0.14	0.07	0.05	S	2(1)	1	1
Perkins Bay	Tas	790	CI	18	1.5	0.17	0.03		fS, S	8 (1)	3	1
Petrel Point	Vic	359	X	X	X	0.8	1.3	2	S, SSh	1		
Pieman River Heads	Tas	791	I	2	1.7	–	–	–		1		1
Port Prime	SA	781	H	7.6	1.7	0.07	0.2	0.04	S	1(1)		
Point Hibbs	Tas	353	HI	5	1.9	0.3	0.07	0.07	R	1(1)		
Sandy Cape	Tas	353	H	10.6	3.5	–	–	–	R	2(2)		1
Sea Elephant Beach	Tas	789	H	10.4	2.7	0.5	0.1	0.13	SSh	2(2)		
Seal Rocks (Lighthouse Beach)	NSW	219	HI	2.2	2.4	1.3	0.9	0.6		1		
St Albans Bay	Tas	798	H	5.6	1.8	0.4	0.35	0.12	S	1(1)		
Stephen's Beach	Tas	176	HI	3.3	1.7					1		
SW Moreton	Qld	236	HI	5.7	2.5	0.2	0.9	0.1	MS, S	1(1)		
Tatlows Beach (Sawyer Bay)	Tas	790	H	18.8	2.7	0.2	0.2	0.1		5(1)	1	3
Treachery Beach	NSW	219	HI	2.2	3.8	1.7	1.1		SSh	1		
Trigelow Beach	WA	337	H	23.6	2.5	0.2	0.1	0.03		5	2	
Two Mile Beach	Tas	169	HI	4.6	1.6	1.6	1.0	0.7		2(1)	1	1
Wreck Bay	NSW	807	H	8.9	2.5	0.3	0.25	0.3	S	1		
Number of sites:			**35**					**Number of larger events:**		**66(20)**		

bars and smaller features do not appear on charts. However, slope estimations are consistent in trends across all sites. Slopes for waters deeper than 10m are usually well defined.

Australian repeat stranding sites

If site properties influence live mass strandings, then sites where strandings have occurred more than once may have similar properties, irrespective of numbers in a stranding. To investigate this, strandings of 1–9 animals, both live and dead, for beaked, sperm and long-finned pilot whales were examined. There are about 100 sites in the database that have two or more such stranding events. However, restricting the search to well-documented sites and reports, 15 locations were found to have three or more strandings events of 1–9 animals, all of which were bays (Fig. 5 and Table 3).

South Australia had only one event (Port Prime) with 10+ animals, but several repeat stranding sites. Streaky Bay (with 6 events) is an indented headland-bay with complexity in planform in the south and shallow sand ridges. Anxious Bay (3 events) has headland-bay structure in both north and south. Coffin Bay (7 events) is an indented headland-bay with coastline and bathymetric complexity in the south. The Coorong (with 21 events) is a wide sandy headland-bay open to the southwest. Kangaroo Island acts to extend the action of the headland. Port Fairy (3 or more events) is a log-spiral headland-bay, with a secondary headland. D'Estrees Bay (3 events) is a log-spiral headland-bay on Kangaroo Island. Rivoli Bay (5 events) is a twin headland-bay.

For Tasmania, in addition to the eight repeat sites for large events (see Table 2), there were three additional repeat sites that included no large events. Adventure Bay (5 events, none of 10+) is a log-spiral headland-bay with a secondary headland. The log-spiral shape is interrupted by more resistant material northwest of the primary southern

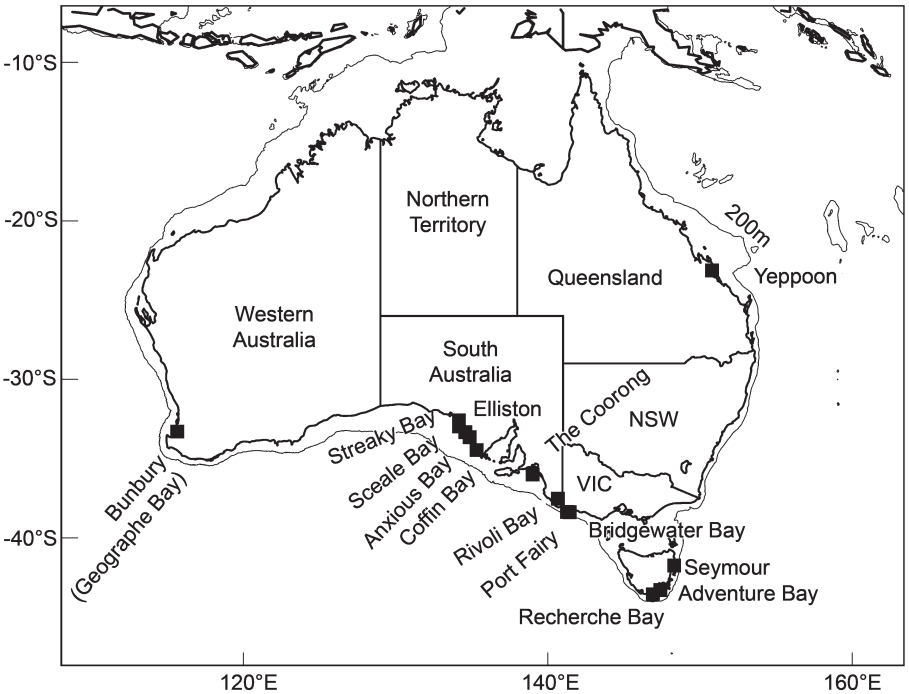

Fig. 5. Location of Australian sites with good position information with three or more smaller strandings (1–9 animals, alive or dead, including mother-calf pairs), and no events with 10+ animals in a stranding. For beaked whales, long-finned pilot whales, and sperm whales only

Table 3

Summary of the information on Australian sites with good position information with three or more smaller strandings (1–9 animals, alive or dead, including mother-calf pairs), and no events with 10+ animals in a stranding. For beaked whales, long-finned pilot whales (LFP), and sperm whales only. For key to column headings and symbols see Table 2.

Site	State	AUS chart	Type	Width (km)	IR	Slope (degrees)			Substrate if known	Number of events		
						N1	N2	N3		Sperm	LFP	Beaked whale
Adventure Bay	Tas	173	HI	1.9	1.9	1.1	0.4	0.1	S		1	2
Anxious Bay	SA	121	HI	58	2.5	1.2	0.5	0.1				4
Bridgewater Bay	Vic	140	HI	12	2.4	0.4	0.2	0.5		1	1	2
Bunbury	WA	115	H	9.3	3.9	1.6	0.4	0.5	S			3
Coffin Bay	SA	342	HC	31	2.3	0.1	0.3	0.1	fS, MS, S	1	3	5
Coorong	SA	347	H	283	2.3	0.3	0.4	0.1	fS, S, SSh	9	3	9
D'Estrees Bay	SA	346	H	15	2.8	0.5	0.2	0.2			1	2
Elliston	SA	121	I	1.6	1.1	–	–	–	fS	1		3
Port Fairy	Vic	141	H	3.9	2.0	0.7	0.3	–	fS		3	4
Recherche Bay	Tas	174	CI	2.4	1.0	0.7	1.0	0.6	S			3
Rivoli Bay	SA	127	HC	11	2.8	–	–	–	fS, M, S	3		2
Sceale Bay	SA	342	I	10	1.2	0.5	0.2	0.7	S			3
Seymour	Tas	766	H	13	3.8	1.2	0.5	0.1			2	3
Streaky Bay	SA	121	CI	27.7	1.0	–	–	–	S	1	2	4
Yeppoon	Qld	820	HC	12	3.2	–	–	–	S			3

headland. Recherche Bay (3 events) is an indented bay with complex planform and interior headlands. Seymour has a prominent headland (Long Point). The western side of Bridgewater Bay (3 events) in Victoria has log-spiral headland-bay structure, and a prominent eastern headland also provides log-spiral character to its eastern side.

Hamilton and Lindsay (2014; Fig. 2) found that all 13 sites with 3 or more beaked whale strandings were bays, with 9 (63%) having strong headland-bay character. Four of these were bays not in the above lists: Bunbury (Western Australia), Elliston and Sceale Bays (South Australia), and Yeppoon (Queensland). Elliston is a small indented bay and the other three have log-spiral character (Table 3).

Relation of Australian mass stranding sites to the surrounding coastline

As noted above, 95% (n = 63) of the strandings of 10+ individuals for Australia occurred in bays. By comparison, non-sandy coasts comprise 39% of South Australia's, 34% of Victoria's and 60% of Tasmania's coasts (Short, 2006a). Neglecting other factors, one would expect at least 15 (33%) of the 46 mass strandings in these three states, or alternatively, at least 8 of their 24 stranding sites, to occur on non-sandy coastlines.

In fact, from the available information, large stranding events may have occurred once each at three rocky locations in Tasmania (Pt Hibbs, I; Sandy Cape, H; Cape Grim, CI); although in bays, the actual stranding site within the bay may

not have been sandy. Short (2006b) provides some description of all 1,596 beaches and coastlines for Tasmania and its major islands. From Short (2006b), it is observed that the 21 stranding bays in Tasmania generally have completely different characteristics from their neighbouring coastlines (e.g. rock or reef flats, or steep, with cobbles or boulders, when the bay beaches and bay floor are clear of these descriptions). Apart from the three cases above, nine of the bays have no mention of sediments other than sands, nor of rock, or reefs whilst for the remaining nine bays there was no mention of rock or reef.

Short (2006b) described the three rocky sites as having rocks or reef areas on the bay floor. The Pt Hibbs stranding (110 long-finned pilot whales) was discovered 7–10 days after death, so the actual stranding site may not be certain. The Sandy Cape live stranding (155 long-finned pilot whales) occurred on a rocky shore in the south of the bay; 32 other animals were trapped in an offshore channel among reefs, and were guided to safety. The Cape Grim stranding (58 sperm whales) occurred on a rocky platform in a 'reef locked shallow bay', and 'putrefaction was well under way' when the whales were examined (Guiler, 1978). The presence of reefs and reef channels give the latter two bays complex bathymetric character, potentially explaining their possible strandings on non-sandy areas. These bays can be considered a type of topographic trap.

There is a correlation between absence of stranding records (for single strandings upwards) for the five species and the presence of sea cliffs on the coasts of Western Australia and South Australia (the Zuytdorp, Baxter and Bunda cliffs; Fig. 1). The entire coastline of southern Australia from 123°58'E to 132°23'E is smooth. There are only four recorded strandings (two single beaked whale events, and two single false killer whale events) in this longitude range. There are few beaches in these high-cliffed areas and the Bunda cliffs run unbroken for hundreds of kilometres; one hypothesis is that wave noise may alert animals to the presence of the cliffs (see below). However, conditions there mean that even if whales do strand along these areas, it is unlikely they would be noticed.

Comparison with New Zealand mass stranding sites

New Zealand has coastlines with many sediment types, geomorphologies, geographical aspects and oceanography as well as a long, well-maintained stranding record which makes it appropriate for comparison with Australia. Brabyn and McLean (1992) examined New Zealand mass ('herd') stranding sites (2+ animals, excluding mother-calf pairs) of 11 odontocete species, each with four or more such stranding events across all sites (Brabyn 1991, p.3). They reported 95 events at 41 sites, although several sites were in the same locality or the same bay. Details were not specified in that paper but table 7 of Brabyn (1990) reported 82 events in 12 locations (excluding Chatham Island, which has two major stranding bays). The majority of sites were where pilot whales had stranded.

Sites with two or more events were typically associated by Brabyn and McLean (1992) with 'long, gently sloping[1] beaches' with an adjacent protruding section of coastline, either a headland or a sand spit ('sandy bay beaches protected by a hook'). The only exception was Kaipara on the northwest of North Island, where five strandings were associated with 'low seabed slopes', but not coastline protrusions according to the authors. However, we note that headland-equivalents are present in the form of sandbanks <3m depth which extend 3.7km seawards from Kaipara Harbour; slopes of 0.3–0.1° from shore to the 30m contour were estimated here, which is 11km out to sea.

Half (21) of the 41 herd stranding sites examined for the 11 species were on beaches with low tide slopes generally <1°, with 83% on low tide beach slopes <3°. Slopes for herd stranding sites were significantly less than those of random sites where strandings were not recorded. Brabyn and McLean (1992) randomly selected 26 sites within 100 km of the 41 herd stranding sites to make these determinations. Only one of 95 herd strandings (of 12 killer whales) was recorded on a beach steeper than 4.4°. Bays with 16 of 34 pilot whale events had width to indentation ratios >2. Only 1 of 31 pilot whale stranding sites was on a beach with a sediment coarser than sand. No herd strandings of any species were recorded on shingle or boulder beaches, which are steeper than sand and gravel beaches. Excluding dolphins, no herd strandings of any species were recorded on rocky coasts. Brabyn and McLean (1992) concluded that whales do not strand at random locations.

[1]Beach slopes were measured by them from low tide to 20 paces up the beach.

DISCUSSION

The analysis presented here has shown that over the last 99 years, reported Australian large (10+ animals) live mass strandings for the five odontocete species considered here, occurred largely within bays (95% of the 66 well documented examples compiled for this examination) and particularly in sandy headland-bays. Many of the stranding bays are sheltered areas with simple planform and simple bathymetric configuration and would appear to have no inherent perils for odontocetes. The presence of a headland does not change this.

By contrast, the most commonly stranding baleen whale, the humpback whale was found to strand (usually singly) almost anywhere, not exclusively in bays (Hamilton and Lindsay, 2014).

The following discussion first lists properties of live mass strandings locations around Australia, then explores possible roles of headland-bays in mass strandings.

Stranding site properties

The broad qualitative terms generally used to describe stranding sites in the literature (e.g. 'wide', 'large', 'long', 'gently curving', 'sandy', 'gently sloping', 'shallow') hinder comparisons of site properties; consistent quantitative terms are needed.

Bay types and bay size

'Wide bays' with respect to strandings were up to 50–65km in width with indentation of 15–25km. The smallest bay width was 600m. Three prototype bay forms were noted, indented bays, headland-bays, and headland-bays with indented character. These are differentiated by planform, by indentation ratio and the presence or absence of an upswell headland.

Indentation ratio and coastline curvature

The authors observed that an indentation ratio of 2 separated indented bays from archetypal log spiral bays. A physical basis for this observation was found in Silvester and Ho (1972) and Kim and Lee (2009; see fig. 2); 2 is the lower bound to the ratio approached by log spiral bays in equilibrium at higher values of wave incident angle. The ratio is >2 for lower wave angles and during initial bay development when coastline indentation is slight. Indentation ratio can therefore act as a quantitative proxy for coastline curvature in terms of log-spiral geometry. Archetypal log-spiral headland-bays have indentation ratios >2 and, away from the headland, are 'gently curving'. Indented bays have ratios <2, although they may still have a headland-bay character. Of the 32 Australian bays with 10+ in a stranding, the three (9%) highest indentation ratios are between 3.5–3.8 (see Table 2).

Depths and gradients

The terms 'shallow bay' and 'deep bay' have no particular meaning unless specified through a bathymetric chart, or as a depth and distance offshore when they represent a broad slope measure. It should be noted that what is 'shallow' to a sperm whale may not be shallow to smaller species. From Brabyn and McLean (1992) for New Zealand herd strandings of 2+ animals, a gently sloping beach has low tide slope less than 1 to 3°. However, the beach is the last feature a cetacean encounters in a stranding and offshore properties and slopes may be more important than beach slope. Seabed slope determinations for Australian sites were made from bathymetric cross-sections constructed perpendicular to shore. Slopes for 0–10m chart depths are usually < 1° whilst offshore slopes (deeper than the limits of the wave base in bays) were <0.5°.

Complexity

Complexity applies to coastline and bathymetric configuration, including factors such as the presence of islands and obstacles, reefs, channels, passages and sand bars. Coastline curvature for simpler situations can be quantified usefully by the bay indentation ratio (see above), but an assessment of overall complexity of the stranding location is also required, particularly for indented bays and re-entrant coastlines. We recommend diagrams of planform and bathymetry as the simplest way to provide information on these assessments.

Beaches and sediments

Short (2006a; 2006b; 2006c) has established a widely used system for characterisation of sandy beaches. In terms of wave energy and steepness, beach types range from flatter, fine sandy beaches ultra-dissipative of wave energy, to steeper, energetic, coarse sand forms. Other salient features are bars and rips. Jennings and Schulmeister (2002) classify mixed sand and gravel beaches in a simple tripartite scheme.

The analysis uses sediment types taken from RAN bathymetry charts. As noted under methods, these chart descriptions are reliable, especially for sandy sediments, but an analysis of sediment samples for grain size distribution is recommended; beach sediment samples could be easily undertaken by scientists attending strandings.

Relation of bays to strandings

Except for Barrow Island at around 20°S, all the larger mass stranding sites for the five odontocete species occur south of 25°S (Fig. 4). However, only the long finned pilot whale is not known to occur north of 25°S[2], so that species range does not appear to explain this.

An important consideration in this is that the long period and energetic swell of the Southern Ocean is favourable to formation of headland-bays around Australia south of 25°S. Low wave energy generally occurs north of 25°S except for occasional tropical cyclones and storms. The northwest of Australia is protected from Southern Ocean swells by coastline orientation and a wide shelf. The northeast of Australia is protected by a wide shelf and the Great Barrier Reef (Fig. 1). From the southern reaches of Western Australia to west of Tasmania, perennial energetic Southern Ocean swell arrives from the southwest, resulting in formation of bays located to the north of headlands on west facing coasts, and on the eastern side of headlands on zonal coastlines. On the east and west coasts of Tasmania, bays are typically formed north of headlands (see Marion Bay and Ocean Bay). The shallow Bass Strait (80–200m) between Tasmania and Australia receives swell from both west and east.

There are many rock or reef-lined coasts across northern Australia, for example the entire Kimberly coast of northwest Australia is shown as rocky in Sharples *et al.* (2009) and no strandings of any size there appear in the database. Short (2006a) describes laterite rocks and reef flats as common along the Northern Territory coast and coral reef structures are located immediately seaward of at least 1,430 beaches from the Kimberleys to Cape York, Queensland. Most have large areas of barrier reef backed by a lagoon and lower energy beaches. Only 16% of the bedrock-dominated Kimberley coast is sandy (Short, 2006a). Elsewhere in Australia sandy beaches occupy between 38–66% of each state coastline.

It is easy to postulate how whales become trapped in deeply indented bays such as Cloudy Bay and Great Oyster Bay (Fig. 3). Deeply indented bays and bays complex in planform or bathymetry can be interpreted as topographic traps, in which odontocetes may possibly become confused or lost and be unable to find their way out. This is the general stranding mechanism postulated for 'hooked bays' in New Zealand by Brabyn (1990). Strandings in long tapering fjords and larger inlets in Europe represent a similar situation. However, this does not explain mass strandings at sites such as Booming Bay or Newmans Beach (Table 2, Fig. 3), where the indentation does not appear geometrically difficult. Neither indentation nor coastline complexity can explain mass strandings in large, gently curving bays with simple log-spiral shapes and simple bathymetry such as Geographe Bay and Wreck Bay (Fig. 3). These two bays lie perpendicular to overall coastline orientation, but the majority of bays do not, seemingly eliminating bay orientation as a major factor. Sites such as Crowdy Head, Dukes Head, Ocean Beach (Fig. 3) occur in log-spiral bays which are more hook shaped than Geographe Bay at the headland end and geometrically present greater difficulty. However, stranding sites are often towards the centre of the

[2]Department of the Environment, Australian Government (website at http://www.environment.gov.au/cgi-bin/sprat/).

bay shoreline, not at the headland end. The question remains why live mass strandings should occur in so many of the seemingly innocuous log-spiral bay shapes and simple bathymetric configurations of Fig. 3. Potential explanations related to the manner in which odontocetes are believed to navigate, simple geometry and the possible inability of odontocetes to interpret gradually shallowing depths are considered below.

Odontocete navigation

Odontocete echolocation skills are well known (e.g. Au, 2009) and they can potentially use echolocation for a number of purposes including navigation and exploration of their environment (e.g. to locate the seabed, obstacles, objects and shorelines); mysticetes are not known to use this method. Beaked whales, sperm whales and other odontocetes are known to use echolocation when hunting their prey (e.g. Johnson *et al.*, 2004; Miller *et al.*, 2004). Their echolocation capabilities in feeding suggest that they could also use echolocation to locate the seabed. Miller *et al.* (2004) note that echoes from both surface and seafloor are regularly detected on acoustic recorders attached to sperm whales producing regular clicks. This indicates sperm whale clicks display suitable intensity for using echolocation to detect seabeds. The same is noted for reception of seafloor echoes for tagged Blainville's beaked whales within 750m of the seabed (Arranz *et al.*, 2011).

Based on the premise that odontocetes use echolocation for at least local navigation and avoidance of obstacles, two different mechanisms have been proposed for active cetacean sonar to become ineffective near coastlines, leading to strandings. One is a sonar propagation condition called sonar termination (Dudok van Heel, 1966), and the other relates to coastline shape (Sundaram *et al.*, 2006).

Ray tracing

Sundaram *et al.* (2006) applied simple ray tracing to actual bay shapes associated with mass strandings, with the coastline treated as a lossless reflector and with a depth of zero (a planar calculation). Their results indicated that odontocetes may experience acoustic dead spots within the bays; this would imply that strandings might be expected at or near these sites. However, we note that the modelling amounts to saying that portions of coastline which present a convex shape to sound rays arriving from the cone of 20° Sundaram *et al.* (2006) use for odontocete acoustic emissions will not be detected as well as coastline portions that present a concave shape. Locally convex features could be expected to be harder portions of coastline more resistant to erosion (e.g. Wreck Bay, Australia has such areas, see Fig. 3), which is why they have curvature opposite to the concave curvature generally shown by beaches within bays. However, the present investigation finds that odontocetes generally strand on concave rather than convex sections of the coastline. The ray tracing inferences of Sundaram *et al.* (2006) do not appear applicable to explaining odontocete strandings on experimental or theoretical grounds.

Sonar termination

Woodings (1995) and Chambers and James (2005) postulated mass strandings of false killer whales in Western Australia to be caused by sonar termination, where acoustic transmissions directed into a gently sloping, sandy shore are returned at low signal strength, masking the presence of shallow depths (Fig. 6). This had been suggested earlier (e.g. see Dudok van Heel, 1966) and was referenced by Brabyn and McLean (1992) as a possible cause of New Zealand strandings. Through the attenuating effects of coastal micro-bubbles and multiple sea surface and seabed reflections in shallow sandy seabeds of low slope, returns may be distorted or reverberating signals of insufficient strength or fidelity relative to the output signal to be reliably detected, or may not be returned at all. Under these circumstances a whale may not know that unsafe shallow waters are up ahead. Gravel and rock typically provide stronger returns than sands.

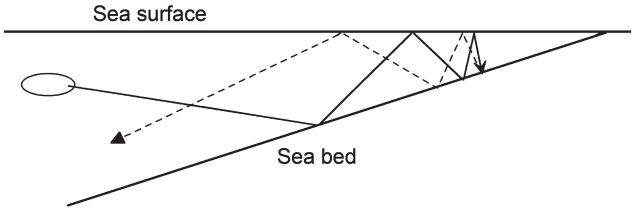

Fig. 6. Schematic of sonar termination in a wedge. An acoustic signal propagating shorewards can turn seawards before it reaches shallow depths, and experiences enhanced attenuation through multiple reflections from the sea surface and the seabed.

The emission and hearing frequency range of false killer whales is 2–120kHz, with highest sensitivity for 30–80kHz (Chambers and James, 2005). Using the frequency response for 20–120kHz, and with bay waters modelled as a wedge, their model predicted sonar termination to occur at slopes less than 1°. Slopes >5° were highly likely to be detected at a safe distance. This is consistent with the Australian examples examined here as well as the measured low tide beach slopes of 1–3° of Brabyn and McLean (1992) for New Zealand strandings. Although Chambers and James (2005) describe their modelling as a simplified indication of possible sonar termination, it appears realistic, as they couple the hearing response of a particular odontocete species with real mass stranding situations.

Gradually changing depths

With or without navigation by sonar, and quite apart from sonar termination, odontocetes may simply not recognise that a headland-bay or other location is gradually shallowing to unsafe depths as a purely geometrical effect. An offshore slope of 0.5° equates to a gradual decrease in depth of 1m every 100m, and this may simply not be noticed. When normally offshore odontocetes find themselves in shallow water, confusion may occur.

Sediment type, seabed slope and wave noise

The sonar termination hypothesis would not be consistent with large numbers of mass strandings associated with sediments coarser than sands or with slopes higher than those estimated for sonar termination. This is not the case for either Australia or New Zealand, despite the fact that mixed sand and gravel beaches, although generally relatively rare, are a common feature of the New Zealand coastline (Dawe, 2001; Jennings and Shulmeister, 2002).

The New Zealand data of Brabyn and McLean (1992) for herd strandings of 2+ animals occurred predominantly (83% of 41 events) on sandy beaches with low tide beach slopes less than 3°. Excluding dolphins, only one herd stranding (of 12 killer whales) was noted for a low tide slope greater than 4.4° (Brabyn and McLean, 1992). Only one herd stranding of ≥2 animals occurred on a gravel beach, with none on shingle and boulder beaches (Brabyn and McLean, 1992). No herd strandings have been reported anywhere on the steeper west coastline of South Island, New Zealand (Brabyn, 1990, p.38).

Log-spiral headland-bays and crenulate beaches are not limited to sandy sediments. Sediment size distribution in zetaform bays is a function of factors such as wave climate, the angle between the headland and dominant swell direction, erodability and physical properties of the coastline material, and sediment supply. Crenulate cobble and boulder beaches occur around Australia (Short, 2006a). Gravel and boulder beaches are much shorter on average than sand beaches in Australia (Short, 2006a), which could be a factor in the lack of reported mass strandings in those environments. There are no recorded larger mass strandings on gravel beaches in our database, even though they comprise more than one sixth of beaches in Tasmania. Tasmania experienced three mass strandings found on rocky platforms within bays with reefs and reef channels (Cape Grim, Point Hibbs, Sandy Cape).

In examining possible explanations for mass strandings, Chambers and James (2005) proposed that calm conditions may prevent coastline wave noise from alerting whales to the presence of shallow water. In addition, the particular log-spiral shapes of headland-bays apparently reduce wave action along the shore compared to other shapes (Silvester and Ho, 1972). A reduction in wave action on log-spiral Australian beaches was noted by Short (2006a; 2006c). This hypothesis assumes that odontocetes are sensitive to surf noise acoustic frequencies, which are typically less than 4kHz in the far field of the surf zone, and broad-band in the surf zone. Surf noise is a function of beach and seabed slope, sediment size, and incident wave energy. Seabed slope determines the breaker type, with plunging breakers producing more noise than surging and spilling breakers. Coarser beach sediments produce higher slopes and plunging breakers. Rock cliffs also produce plunging breakers. There is a link between beach sediment, beach slope and wave noise, which in principle could influence strandings. Although there is insufficient evidence to determine a causal effect, it is noteworthy that headland-bays associated with strandings produce planforms, sediments, and slopes which all combine to reduce wave noise.

Direct relation of headlands to mass strandings

If sonar termination does affect odontocete navigation, then it has been postulated that headlands can mechanically influence stranding behaviour. Odontocetes may change course to landwards or seawards to avoid headlands when they are unexpectedly encountered after having been masked by sonar termination. This would then give them no better than a 50/50 chance of surviving the sonar termination effect on their echolocation navigation facilities (e.g. Hans Wapstra of the University of Tasmania; quoted in Montgomery, 1998).

Sperm whale strandings, Tasmanian strandings, and species size

Long-finned pilot whale strandings are recorded at 19 of the 21 Tasmanian sites (Fig. 2b). Cape Grim and Greens Point in Tasmania have sperm whale strandings only. Sperm whales also stranded in Tasmania at Ocean Beach and Perkins Bay. Sperm whales had the widest range in type of mass stranding sites. Of the eight larger sperm whale stranding sites for Tasmania and mainland Australia, Gunnamatta is not embayed, Greens Point has four areas of rock and inner reefs, the indented Cape Grim has rock and reef areas within the bay, and Dundowran is the northmost site on the eastern coast. No other notable relations of stranding site with species or species size were observed.

Key geomorphological factors relevant to mass strandings

The following factors may explain why so many larger Australian mass strandings occur in headland-bays with log-spiral character and sandy sediments.

(1) The presence of a resistive headland causes a bay with log-spiral character to be formed downswell of the headland in less resistive coastline – if the resistive headland material was not present, the bay would not be present, nor would the log-spiral shape.

(2) Persistent wave and swell action acts to produce (fine) sandy sediments in headland-bays from the continued attrition and breakdown of less resistive coastline material. Finer sediments (silts and clays) are winnowed out by wave and current action. Grain sizes in headland-bays are not restricted to sandy sediments, however, these are the sediments associated with larger Australian mass strandings.

(3) Fine sandy sediments generally produce offshore headland-bay slopes less than 0.5° around southern Australia.

(4a) The combination of (fine) sands and seabed slopes less than 1° is highly favourable to the sonar termination effect (Chambers and James, 2005); or

(4b) alternatively, in the presence of seabed slopes less than 0.5°, odontocetes may simply not comprehend they are gradually heading into shallow water;

(5) If a headland is encountered in a headland-bay, whales may (perhaps randomly) turn seawards or shorewards to avoid it. Turning shorewards may expose them to the sonar termination effect and/or to gradually shallowing depths, making them susceptible to stranding; and

(6) In calmer conditions, the reduced wave action in log-spiral headland bays compared to other bay shapes may prevent coastline wave noise from alerting whales to the presence of shallow water (increased acoustic attenuation in shallow water propagation paths experiencing multiple sea surface and seabed reflections could enhance this effect).

When odontocetes find themselves in shallow water, they may become disorientated and not know the direction of deeper water. Milling behaviour, indicating confusion, is

often observed with individuals occasionally darting off and returning in apparent exploratory behaviour, then a mass stranding sometimes caused by 'follow the leader' behaviour (for example, strandings at Duke Head in Western Australia and Sandy Cape and Greens Beach in Tasmania). Confused whales in shallow water may interpret any wave noise at the beach as coming from the familiar sea, rather than from a shore, and may head shorewards.

Headlands may therefore be implicated in strandings at different time scales, and for different reasons. If there were no resistive headland, there would be no bay formed with sands and resultant low seabed slopes. The bay and the headland are intimately related, a factor seemingly previously unknown to stranding studies. Without a headland there might be no mass movement towards shore to subject odontocetes to sonar termination or confusion with a simple geometry (gradually shallowing depths) they are unable to comprehend. If wave noise were not reduced in log-spiral headland bays, odontocetes might be alerted to the presence of the shore. The formation of headland-bays leads to coastline configurations, seabed sediments, and seabed slopes which may combine to defeat or impair the echolocation and comprehension abilities of odontocetes, both passive and active.

Other factors in strandings

Coastal configuration and bathymetric trends, with or without sonar termination, are not the only factors in live strandings. For example, Brabyn (1990; 1991) lists many theories on mass stranding, believing some more plausible than others. Some of the more likely factors contributing to strandings of whales are attempted escape from predators (other whales and sharks), predation on animals that flee close to the coast, disease, age, epimeletic behaviour, bad weather, cyclones (hurricanes), storm surge, starvation, and tidal change in water levels. In themselves, these theories cannot explain the observed prevalence of headland-bays in larger Australian mass strandings and we do not further discuss them.

Species such as killer whales which often live close inshore seldom strand. That strandings occur of cetaceans which are usually found offshore may indicate that many offshore cetacean species have not evolved mechanisms to cope with inshore conditions (for example Brabyn, 1990; Klinowska, 1985). Pod sizes and social cohesion are used to explain the large numbers in strandings of odontocetes (e.g. Whitehead, 2003).

We believe it implausible that mass strandings can be normally explained in terms of the drifting of large numbers of incapacitated cetaceans into shore. For the live large stranding events considered here, this would require groups of 10 to 250 live animals to all become incapacitated at the same time and place, near a headland bay, into which they then all drift. Strong swimming accompanied by milling behaviour has been observed prior to several Australian mass strandings (for example Evans *et al.*, 2002) and milling nearshore is recognised as a sign of an imminent stranding. Cetaceans engaged in milling behaviour may be confused, but their swimming is not observed to be incapacitated, and rescues have subsequently been performed. Incapacitation may explain single strandings of sick individuals, but to extend this to larger numbers is implausible; although it is plausible that one or a few animals may be incapacitated in some way and that social cohesiveness/epimeletic behaviour may cause others to follow and get into difficulty. At least 20 of the 66 Australian strandings of ≥10 animals in the Commonwealth of Australia (2010) database were noted as being active events, as opposed to simply being live events, although we are unable to verify this information.

It remains unclear whether there is a single or predominant mechanism that can consistently cause simultaneous incapacity in large numbers of cetaceans near shore and near a headland-bay (although sonar termination is a candidate). Hurricanes or stronger storms might in a few cases, and perhaps contaminated food intake in a few others, but this leaves most cases unaccounted for. Underwater earthquakes and seismic events ('subterranean upheavals') have long been mooted as damaging or stunning cetaceans and causing strandings (for example, *Rockhampton Morning Bulletin*, 22 August 1946). However, if cetaceans were affected by this mechanism they would likely strand anywhere, not preferentially in headland-bays, and a case could be made that baleens should also be affected. However, baleens rarely strand other than singly, even when undertaking seasonal mass migrations for long distances along the Australian and New Zealand land masses (Hamilton and Lindsay, 2014; Brabyn, 1991).

SUMMARY AND CONCLUSIONS

(1) The bay usually appears the significant coastal unit in Australian mass strandings. Bays form the platforms for the majority of stranding sites around Australia. Brabyn and McLean (1992) noted that New Zealand strandings consistently occurred at particular locations within some bays, indicating the actual stranding site properties are important. However, the stranding site exists only because the bay exists, and its properties are largely a function of the processes of bay formation.

(2) Sandy log-spiral headland-bays form the dominant bay type for large Australian mass strandings. The formation of these bays from Southern Ocean swell endows many of them with properties which appear conducive to stranding (a headland, concave coastline curvature, sandy sediments, low seabed slopes, lower wave noise).

(3) Quantitative measures and thresholds are required to examine site properties relevant to strandings (planform and coastline curvature – through indentation ratio or more rigorously the geometry of the log-spiral, sediment sizes, seabed slopes); a suggested schema has been developed in this paper. This provides a simple framework for comparison of sites differing in size by orders of magnitude. An assessment of site complexity is also required, for example, the ratio of coastline length within the bay to the bay width, provided the length is measured in a consistent matter for different chart scales. Complexity is also introduced by the presence of sand banks, reefs, or islands within bays, and deep indentation.

(4) The observed correlation between larger mass strandings and quantitatively specified site properties for Australia

has predictive power, and should be further tested against observations from Australia and elsewhere. It appears likely that sandy headland-bays with low seabed slope will dominate the mass stranding record for larger events compared to other sections of a coastline.

Headland-bays have a distinctive and easily recognised log-spiral planform. Thus sites where odontocetes are more likely to strand can be predicted from coastline configuration (sediments and slopes are also important). This may allow measures to be developed to enable offshore activities to minimise possible disturbance of cetaceans that might lead to strandings.

The analysis presented here, whilst not conclusive, is consistent with the sonar termination hypothesis (e.g. Dudok van Heel, 1966; Woodings, 1995; Chambers and James, 2005). Ineffectiveness of active and passive cetacean biosonar arising through geometrical and physical properties associated with zetaform headland-bays appears a natural mechanism to explain why larger Australian mass strandings occur in them, and not the adjoining coastline, and why particular zetaform headland-bays experience repeated strandings and larger strandings.

If sonar termination and/or inability to comprehend simple wedge geometry with low seabed slopes are responsible for mass strandings of odontocetes, then the presence of a headland is not required for strandings to occur. The principal requirements for sonar termination are low seabed slopes (less than 5° from Chambers and James, 2005; and experimentally <1° in particular), fine to medium sands or finer sediments, and a shoreline or bay width of sufficient distance for the sonar termination effect to act for long enough during the passage of cetaceans to lead to a stranding. In this scenario, log-spiral headland-bays are simply coastal locations where these conditions are more likely to occur, with the additional complexity of a headland. Coastline complexity undoubtedly plays a part in mass strandings around Australia. Particular examples are Perkins Bay, Cloudy Bay, and Marion Bay in Tasmania, which have recorded repeated larger mass strandings. However, mass strandings of odontocetes could also be expected on any coastline with fine sediments and low seabed slopes. This could explain why non-embayed locations with these properties such as Petrel Point (Victoria) and Kaipara (North Island, New Zealand) are mass stranding sites.

Regardless of sonar termination, the Australian findings indicate that the physical circumstances of headlands and swell which shape portions of coastlines into the form of zetaform headland-bays can be expected to lead to conditions unfavourable to odontocetes if the bays have matured to produce sands or finer sediments. The New Zealand data of Brabyn and McLean (1992) and Brabyn (1990; 1991) support this inference although they concentrated on stranding sites as beaches, rather than bays. The only explicit mention we have found on bays other than remarks associated with indented bays and coastline complexity are by Kemper and Ling (1991). They noted that strandings in South Australia (for all dolphin and whale species, for single strandings upwards, for dead, live, or unknown status) were not evenly distributed along the coast, but were frequent in regions with ‘large bays’.

The relationship of headland-bays to larger strandings is likely to be universal, not uniquely Australasian and it is recommended that the geomorphology of mass stranding sites for other regions be examined. For example, we note that the well-known mass stranding sites of Kyparissiakos Gulf (Greece) and St. Helena Bay (South Africa) have log-spiral headland bay character.

To facilitate such a comparison and other potential analyses, stranding sites require more quantitative characterisation than is usually made, and more note of the larger scale environment in which they are situated. The emphasis has been on beach properties to the extent that offshore properties and coastline geomorphology have been largely neglected. This might explain why headland-bays are not formally recognised in the stranding literature in the context of mass strandings.

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