Volume 19 2018

ISSN 1561-0713

The Journal of CETACEAN RESEARCH AND MANAGEMENT

The Journal of Cetacean Research and Management

ISSN 1561-0713

The Journal is published by the International Whaling Commission (IWC), with at least one supplement that will contain the full report of the Scientific Committee of the IWC

The Journal has been established to publish papers on those matters of most importance to the conservation and management of whales, dolphins and porpoises, and in particular papers that are relevant to the tasks of the IWC Scientific Committee

These will include papers on:

- population assessment and trends
- population dynamics
- population biology
- taxonomy
- risk averse management strategies
- direct and indirect exploitation
- environmental changes and threats in the context of cetaceans
- scientific aspects of whale watching and sanctuaries

EDITORIAL BOARD

AVAILABILITY DETAILS

For availability, see *www.iwc.int* or contact: *IWCJournal@iwc.int*

GUIDE FOR AUTHORS

A Guide for Authors is available at: *www.iwc.int/publications/authorsguide.htm.* This must be consulted prior to submission of manuscripts to the Journal.

Editorial correspondence should be sent to:

The Editor,
Journal of Cetacean Research and Management,
The International Whaling Commission,
The Red House, 135 Station Road,
Impington, Cambridge CB24 9NP, UK.

Telephone: +44-1223-233971; Fax: +44-1223-232876

E-mail: IWCJournal@iwcoffice.org

Contents

Editorial

Welcome to this the nineteenth volume of the *Journal of Cetacean Research and Management*. This volume contains nine papers covering a wide range of conservation and management issues. This is the second of two volumes (18 and 19) published in 2018.

To submit a manuscript to the Journal, please contact in the first instance Jessica Peers (e-mail: *jessica.peers@iwc.int*). Other information for authors is available online at *http://www.iwc.int/jcrm*.

Open access online copies of the Journal are available for download at: *http://www.iwc.int/jcrm*.

G.P. DONOVAN
Editor

Author index to Volume 19

Note: Page numbers refer to first page in article

Keyword index to Volume 19

Note: Page numbers refer to first page in article.

Spatial distribution of cetacean strandings in the Falkland Islands to define monitoring opportunities

Amélie A. Augé[1,2], Helen Otley[2], Nick Rendell[3] and Veronica F. Frans[1]

Contact email: amelie.auge@gmail.com

ABSTRACT

The waters around the Falkland Islands are used by many species of cetaceans, including endangered and data deficient species, but little is known about their populations. The Falkland Islands cetacean stranding database was transformed in a geo-spatial database using the available descriptions of the locations as no GPS locations were recorded until 2015. It was then used to analyse the spatial distribution of strandings over a period spanning the 1880s to 2015. A total of 169 stranding events could be given a location and mapped. Twelve stranding hotspots were identified. This paper also reports on the first recorded stranding of false killer-whales (*Pseudorca crassidens*) and Antarctic minke whale (*Balaenoptera bonaerensis*) in the Falkland Islands, increasing the total species recorded to 26. Spatially-explicit cetacean stranding databases can provide important data to monitor cetaceans in the light of environmental changes from climate change or industrial development. In the case of the Falkland Islands (remote and sparsely inhabited), identification of hotspots could be used to design an aerial monitoring programme to increase chances of detecting stranding events, organise a rescue or necropsy team to gain samples. The results in this paper should enhance local capacity to conduct research (sample collection for pollutant analyses, genetic studies, etc.) and monitor impacts of human activities on cetacean populations, including from the historical baseline of average numbers and distribution of strandings provided.

KEYWORDS: FALKLAND ISLANDS; CONSERVATION; SOUTH ATLANTIC; DISTRIBUTION; WHALES; DOLPHINS

INTRODUCTION

The Falkland Islands are a remote archipelago in the SouthWest Atlantic Ocean, approximately 500km off the coast of Argentina (Fig. 1). The Falkland Islands' waters harbour a large number of cetacean species, with 24 species recorded in previous stranding records (Otley, 2012), 17 of which were also recorded during at-sea surveys (Thomsen, 2014; White *et al*., 2002), but very little is known about the cetacean populations that live in or frequent these waters. The Falkland Islands may represent a sanctuary for several populations of cetacean species that are globally endangered or data deficient and at risk from many pressures in other parts of the world (Parsons *et al*., 2015). With current exploration for oil and gas around the Falkland Islands, along with increases in the tourism industry, and potential development of aquaculture, threats to cetaceans in this area may also increase. The lack of data and knowledge on the cetaceans of the Falkland Islands prevent assessments of how these developments may impact the species and render management and planning less efficient. In particular, Otley *et al*. (2012) have identified the Falkland Islands as a hotspot for beaked whales (Family Ziphiidae) which are very difficult to study at-sea due to their offshore distribution, deep-diving and cryptic surface behaviour. Endangered sei whales (*Balaenoptera borealis*) were, in particular, caught in large numbers during the commercial era (1905–1979) around the Falkland Islands (Iñíguez *et al*., 2010; Frans and Augé, 2016) and the number of sightings of this species has increased significantly in the last three decades (Frans and Augé, 2016). Commerson's (*Cephalorhynchus commersonii*) and Peale's dolphins (*Lagenorhynchus australis*) are also known to be found in coastal areas (Falklands Conservation, unpublished data). Therefore, sampling of carcasses from strandings would be a way to gain more data on these species in this remote area.

The Falkland Islands are sparsely populated with less than 3,000 inhabitants, two thirds living in the only town on the islands and an average population density of less than 0.3 person/km^2. Therefore, cetacean strandings are often missed or reported only once the carcass is already decomposed. Monitoring that would allow a higher rate of recovery of relatively fresh carcasses would be helpful because it would provide invaluable opportunities to collect data on cetaceans. Cetacean strandings have long been a means for gathering much needed data on cetaceans (Jepson *et al*., 2005; Leeney *et al*., 2008; Meager and Sumpton, 2016; McLellan *et al*., 2002; Norman *et al*., 2004; Parsons and Jefferson, 2000; Parsons *et al*., 2015; Santos *et al*., 2006). Collecting samples of skin, blubber and muscle tissues for further analysis as part of genetic, fatty acids and contaminant concentration studies, as well as measurements for demographics produce important data. Undertaking gross necropsies and histopathologic analyses to investigate the cause of the stranding would also provide, along with other data, a useful monitoring tool to detect impacts on cetacean populations, in the context of increasing marine development and maritime traffic around the islands.

Otley (2012) has provided an analysis of the composition of the cetacean community of the Falkland Islands by creating a stranding database for the Falkland Islands. This database was however not spatial and the locations of the records were only described, with often local or personal names or descriptions for sites. Therefore, the spatial distribution of the records has not been analysed, except

---

[1] *South Atlantic Environmental Research Institute, Falkland Islands.*
[2] *Department of Conservation, New Zealand.*
[3] *Environmental Planning Department, Falkland Islands Government, Falkland Islands.*

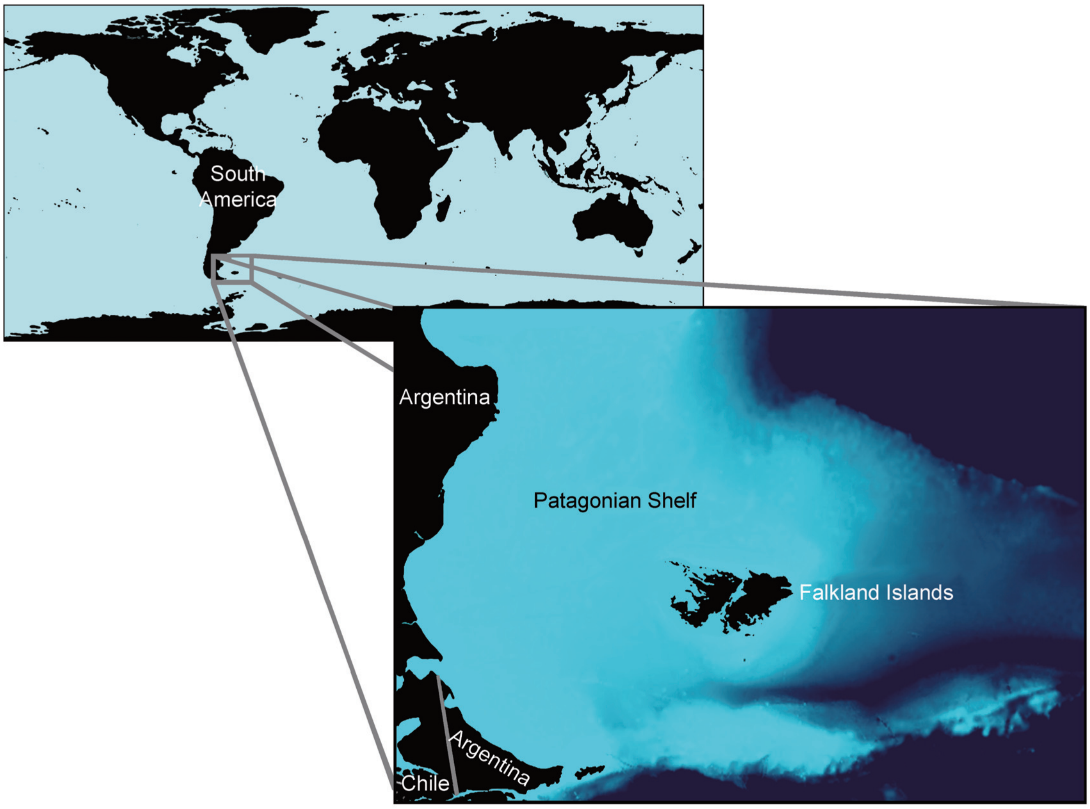


Fig. 1. Location of the Falkland Islands in the South Atlantic.

for beaked whale records (Otley *et al.*, 2012). The site descriptions could, however, be interpreted to assign locations to as many of the stranding records as possible. Spatial analyses could then be conducted on the locations of the records of the Falkland Islands cetacean stranding database to understand patterns over time and identify hotspots of strandings. Implementing a cetacean stranding plan is a top priority in the Falkland Islands Government (FIG) Cetacean Action Plan 2008–2018 (Otley, 2008). The spatial distribution of cetacean stranding events can be used as a baseline to determine patterns of strandings and identify changes in light of future climate change and potential large-scale development in Falkland Islands waters.

METHODS

The FIG Environmental Planning Department has compiled a database of cetacean strandings. It has been collating known strandings of cetaceans since the 1980s. However, prior to 2007, the reporting of strandings was *ad hoc* and consequently not all observed strandings were recorded and details were often sparse. From 2007, all observed strandings have been recorded in the database. Particular effort was also made recently to gather older stranding events to add to the database and as many details as possible from local inhabitants (as far back as the 1870s). This database was made available for analyses. A stranding event is described here as a stranding of one or more animals of one cetacean species within the same space (< 500m apart) and the same period (1–2 days). The details of stranding events included the species, the number of animals and the date. Some of these details were missing or incomplete (e.g. a range for number of animals or a year only for the date), but were used when available for the analyses.

The database was cleaned and each record inspected for location information (only two records had a GPS location). In QGIS (QGIS Development Team, 2015), a shapefile of stranding locations was created. The locations were manually digitised as points on the coastline and an approximate accuracy given to each point as an attribute. Topographic maps of the Falkland Islands were used to identify the locations based on the descriptions. For some records, localised place names were used to indicate a site. In this case, local inhabitants were asked to indicate the locations of that name on a map as accurately as possible. In the case where the location was approximate along a large section of coast, the point was created in the centre of the section (e.g. if only a beach name was given, the point was placed in the middle of the beach and given an accuracy equivalent to the half-beach length). Any stranding record that could not be located with a 20km accuracy was discarded for analyses. The database comprised of the following attributes for each stranding location: species, year, month (when available), number of animals stranded, accuracy (values in km: 0, 0.5, 1, 2, 3, 5, 10 or 20), and source (who reported the stranding). When a range was given for number of animals, the mean number was used.

A heatmap (visualisation of a point density interpolation using Kernel Density Estimation with a 5km radius; Wilkinson and Friendly, 2009) was created using all stranding locations that had an accuracy of 5km or less with a radius of 3km and weighted by the inverse of the estimated accuracy of the locations (5, 2, 1, 0.5km or exact) with 300m pixel resolution. This identified the area of highest density of strandings (hotspots).

Stranding records for all cetaceans were mapped temporally to identify discernible long-term distribution

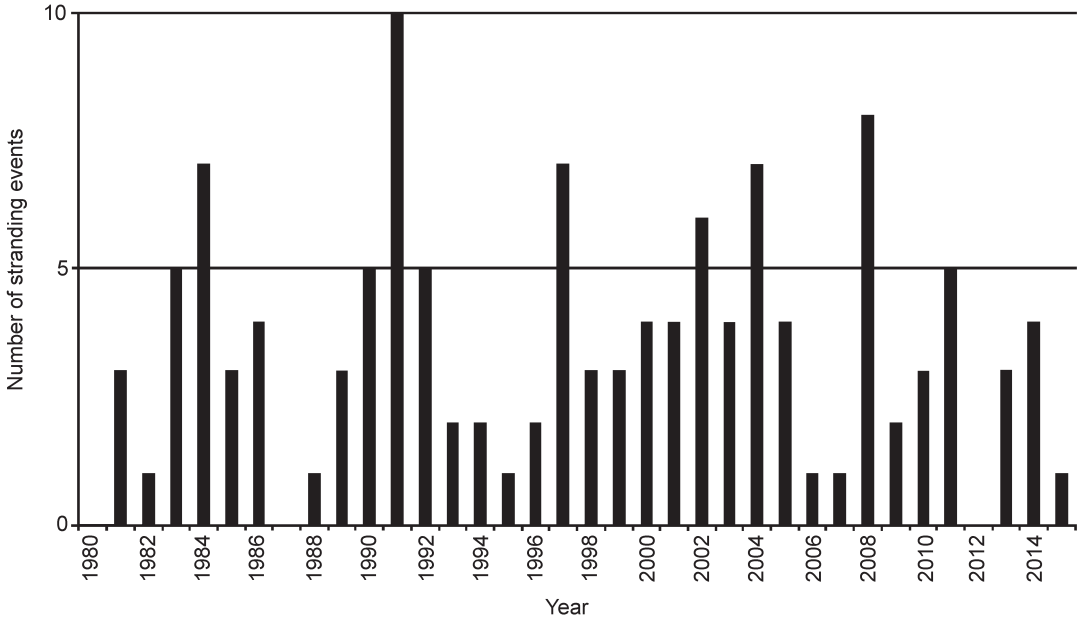


Fig. 2. Number of cetacean stranding events recorded from 1980 to 2015 in the Falkland Islands.

patterns. The monthly counts of cetacean strandings were also analysed per species to determine seasonal patterns of stranding events.

RESULTS

The database of cetacean strandings in the Falkland Islands spans from 1875 to 2015 and contained a total of 195 records, corresponding to 7,986 animals. Out of those records, it was possible to attribute a location within 20km to 169 records, with only 3 records assigned an accuracy of approximately 20km. All other records were assigned an accuracy of 500m or less (13%; only one location was a GPS location assigned a 0km accuracy), between 500m and 1km (24%), between 1 and 2km (25%), between 3 and 5km (26%) and of approximately 10km (9%). Table 1 summarises the complete database of records. Only 47% of records were associated with a specific month. On average, since 1980, 3.4 stranding events were recorded in the database each year, with a maximum of 10 in 1991 and minimum of none in several years (Fig. 2).

Stranding locations were available for 26 species (Table 1), including 6 species of beaked whales (for more details on these species see Otley *et al.*, 2012). The first stranding of false killer whales (*Pseudorca crassidens*) in the Falkland

Table 1

Summary of the records of the Falkland Islands cetacean stranding database, with location accuracies[#].

Species common name	Species Latin name	Number of stranding events	Range of animals per event	Total number of animals	Range of years	All months of stranding events*	Range of accuracies (km)
Beaked whale	Several species[1]	34	1	34	1875–2014	1–10,12	0.5–10
Common minke whale*	*Balaenoptera acutorostrata*	4	1	4	1992–2003	7	0.5–10
Antarctic minke whale	*Balaenoptera bonaerensis*	1	1	1	2016	5	0
Sei whale	*Balaenoptera borealis*	8	1	7	2002–16	1,3,4,5	0–5
Blue whale*	*Balaenoptera musculus*	3	1	3	1940–62	–	2–5
Fin whale*	*Balaenoptera physalus*	4	1	4	1955–2002	4	1–2
Unid. large whale*	*Balaenoptera* spp.	8	1	8	1959–2008	2	0.5–10
Pygmy right whale	*Caperea marginata*	1	1	1	1950	–	20
Commerson's dolphin	*Cephalorhynchus commersonii*	3	1	3	1999–2010	3,5	0.5–5
Southern right whale	*Eubalaena australis*	1	1	1	1990	–	1
Long-finned pilot whale	*Globicephalus melas*	66	1–504	7,836	1896–2014	2–12	0.5–20
Peale's dolphin	*Lagenorhynchus australis*	5	1	5	1923–98	2,3	1–5
Hourglass dolphin	*Lagenorhynchus cruciger*	2	1	2	1981–2004	1,12	1–5
Dusky dolphin	*Lagenorhynchus obscurus*	1	1	1	2008	5	1
Southern right whale dolphin	*Lissodelphis peronii*	2	1–2	3	1945–2004	2,9	1–5
Humpback whale	*Megaptera novaeangliae*	2	1	2	1984–2015	6,11	0–0.5
Killer whale	*Orcinus orca*	4	1	4	1986–96	6,12	0.5–5
Spectacled porpoise	*Phocoena dioptrica*	1	1	1	2011	–	20
Sperm whale	*Physeter macrocephalus*	16	1–18	39	1957–2011	1–3,5,7,9	0.5–10
False killer whale	*Pseudorca crassidens*	1	22	22	2013	2	0.5
Bottlenose dolphin	*Tursiops truncatus*	4	1–2	6	1984–96	5,10,12	1–5

Months are numbered as January = 1 to December = 12. Number for a month indicates a stranding even occurred during that month.

*These species compose the *Balaenoptera* group; large unidentified whales are more likely sei or fin whales as the distinction by non-specialists is difficult.

[#] It is likely that some animals recorded as common minke whale may have been mis-identified Antarctic minke whale.

[1] See Otley *et al.* (2012) for details on species of beaked whales (Family Ziphiidae).

Islands is also presented here and was recorded in 2013. Twenty-two false killer whales stranded and died, and at least another 30 turned back to deeper water. Therefore, the pod was composed of at least 52 individuals. Long-finned pilot whales (*Globicephalus melas*) represented 39% of the stranding events, and accounted for 98% of the total number of animals that were recorded. Most other strandings consisted of single individuals while this long-finned pilot whales often exhibited mass stranding of entire pods (up to 500 animals).

The heatmap of stranding records was produced using the 151 locations that had an accuracy of 5km or less. They showed a total of 12 hotspots, with only 4 on East Falkland (Fig. 3). All other hotspots were on West Falkland or the western outer islands. Three main hotspots were identified at Concordia Bay and Elephant Beach on East Falkland, and Grave Cove on West Falkland, where 6, 11 and 6 events (corresponding to 131, 956 and 122 animals) were recorded, respectively. Although the majority of these animals were pilot whales, 7 out of the 11 strandings were endangered sei and fin whales, and 9 out of 23 strandings of beaked whales also occurred at these hotspots.

A distribution pattern of stranding events appeared with the majority of stranding events found on the west coast of West Falkland and the northernmost and southernmost west coasts of East Falkland (Fig. 3). This pattern has remained constant across a century of records as decadal pattern indicates in Fig. 4, with the exception of a larger proportion of strandings recorded on the east coast of East Falkland in the 2000s than in other decades. This distribution pattern is most noticeable for pilot whales (Fig. 5), while it does not appear for beaked whales and small coastal dolphins. Ninety-six percent of all strandings of pilot whales have occurred on the exposed western side of the islands. The three main hotspots are all sandy beaches, of which two are long western facing while the third is small at the end of a narrow western facing bay.

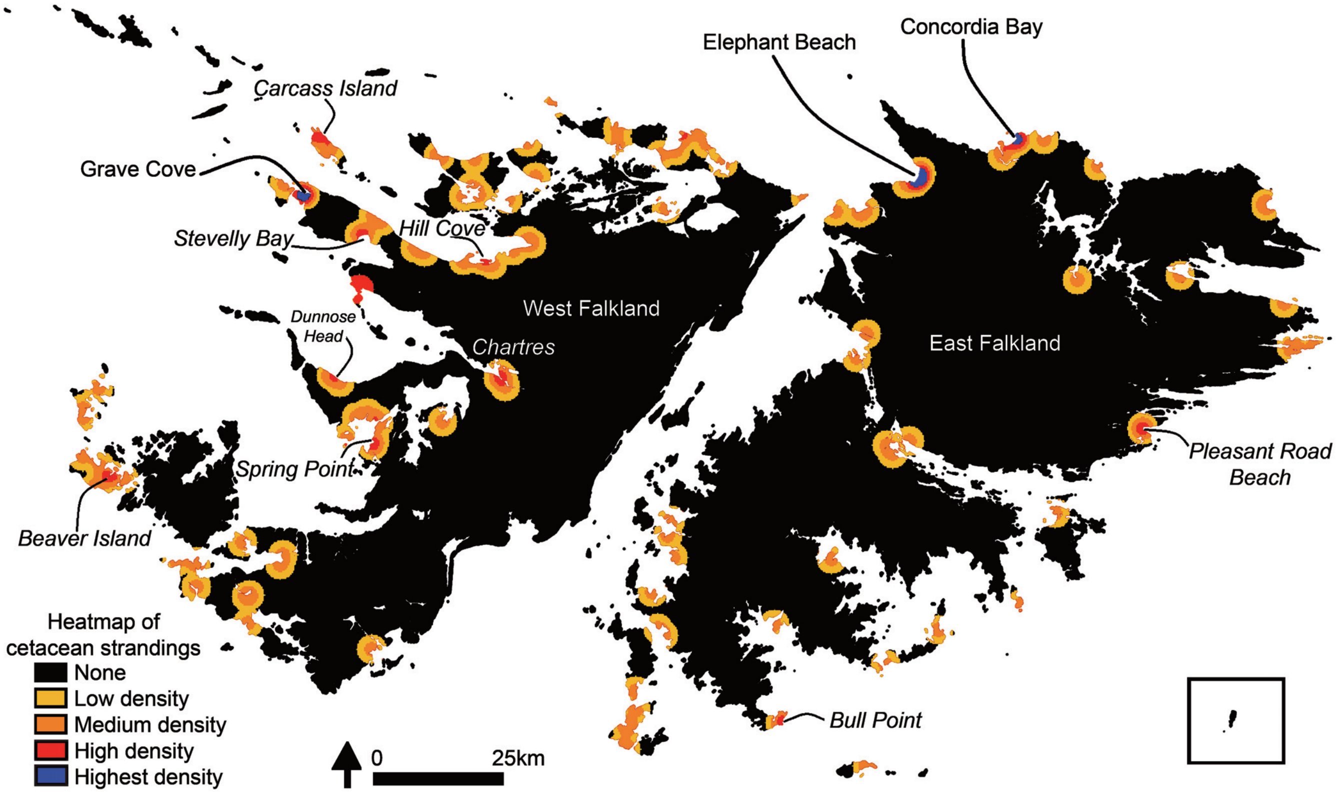


Fig. 3. Heatmap of occurrences of cetacean strandings in the Falkland Islands between the late 19th century to 2015, with the names of the sites with high (red) and the highest (blue) density. Only strandings with location accurate at 5km or less were used in the analysis.

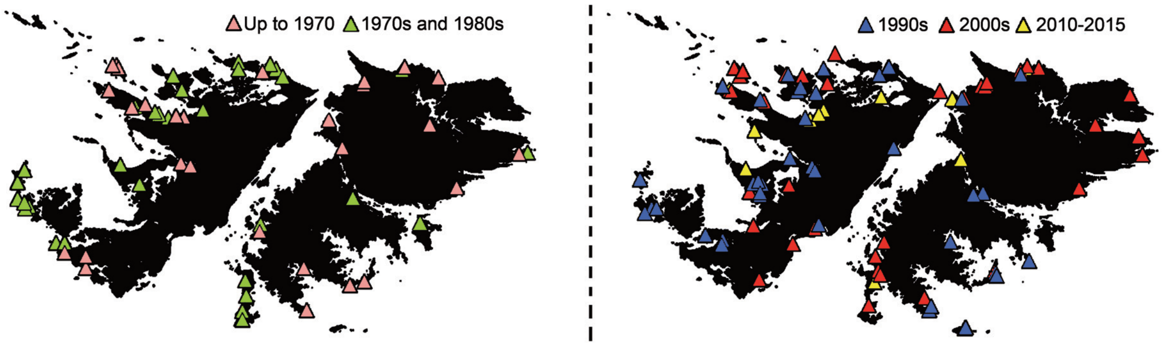


Fig. 4. Distribution of cetacean strandings in the Falkland Islands over the periods late 19th century to 1980s (historical) and 1990s to 2015 (contemporary).

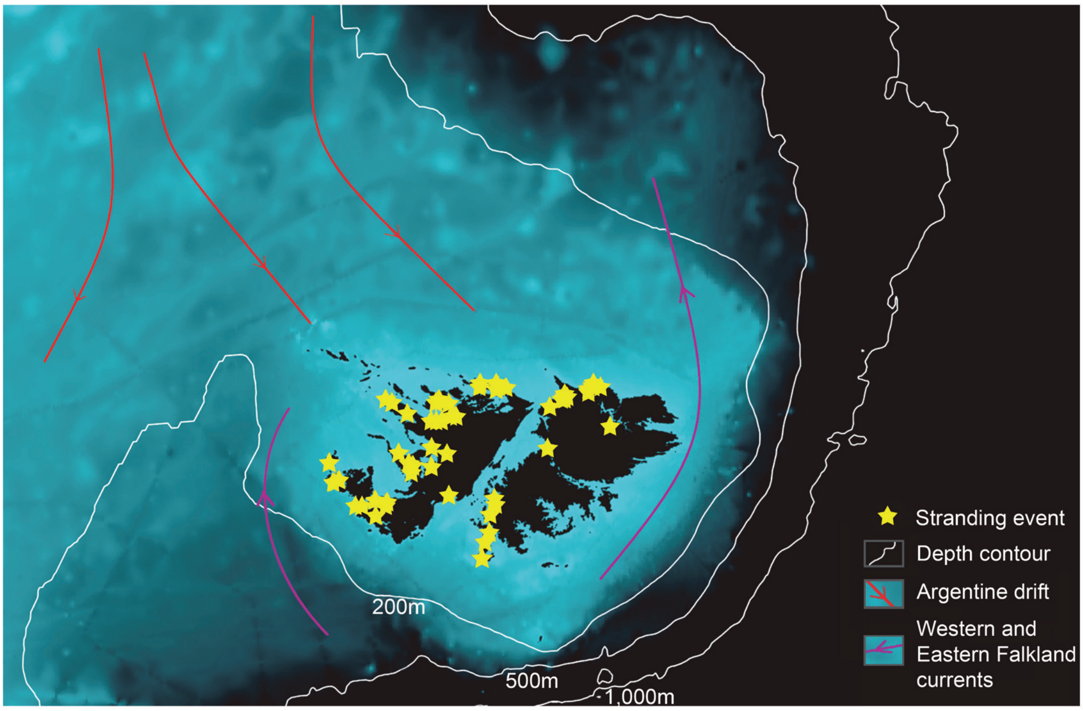


Fig. 5. Spatial distribution of long-finned pilot whale stranding events with environmental factors (bathymetry and currents).

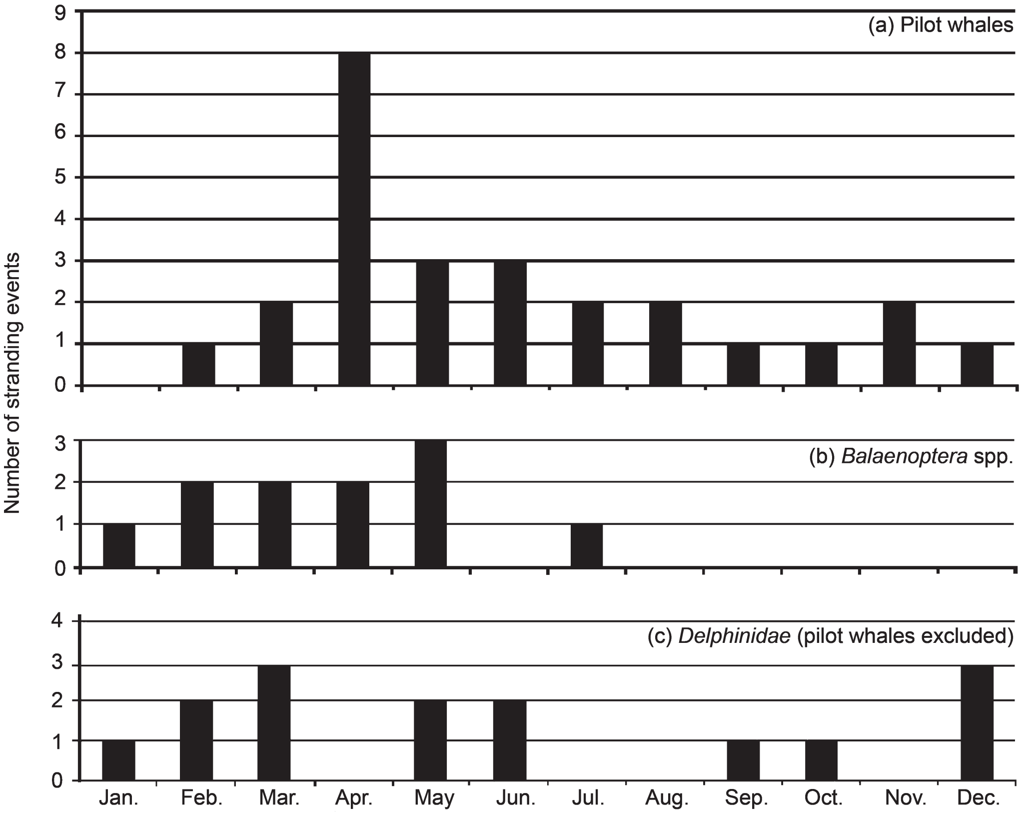


Fig. 6. Number of stranding events during each month for pilot whales, *Globicephalus melas* (top), *Balaneoptera* spp. (middle) and Delphinidae species (pilot whales excluded; bottom).

A temporal pattern in stranding occurrences exists for long-finned pilot whales, but not for other Delphinidae (Fig. 6). Pilot whale strandings occurred throughout the year but with a peak during the months of April, May and June. A temporal pattern also exists for *Balaenoptera* spp., with events only recorded from January to July.

DISCUSSION

Cetacean stranding databases can provide useful information about cetacean diversity, ecology and patterns of occurrence. When detailed geographic locations are also obtained and applied in a GIS, they can provide important information on the spatio-temporal distribution of strandings and thus improve chances of detecting strandings. This then provides more opportunities to attempt rescue if the whale is alive and sample the animals for genetic material or to conduct a full necropsy otherwise. In the remote Falkland Islands archipelago with a very small human population, hotspots of cetacean strandings at specific fine-scale locations represent the best opportunity for structured monitoring and increased chances of detecting strandings within reasonable delays. It is, therefore, recommended that ideally the 12 hotspots identified in this study, but at least the 3 main hotspots, be checked regularly as part of a cetacean stranding monitoring program.

Temporal patterns of occurrences also exist for some species. Therefore, monitoring of sites for strandings should also be temporally driven to ensure best efficiency. The period March to May appears to provide the highest opportunity window of recent strandings of both pilot whales and *Balaenoptera* spp., for example. Due to the remoteness of the sites and difficult and slow land transportation options to reach them, surveys could be conducted by the small airplanes of the islands' air transport service. Based on the results shown in this paper, the best monitoring opportunity for cetacean strandings would be weekly or bi-weekly aerial surveys of the hotspots from March to May. Once a stranding is detected, a team could then reach the site by land transport with the equipment needed for rescue or necropsy. Regular surveys outside of these months may also provide greater opportunities to detect strandings within suitable timeframes for accessing strandings of other species.

Sei whales and fin whales are listed as endangered species on the IUCN Red List with limited current scientific knowledge available (IUCN, 2016). Most species of beaked whales are classified as data deficient by the IUCN. Approximately three quarters of strandings of these species were recorded within the identified hotspots reported here in the Falkland Islands. Ensuring that strandings are detected would provide much needed data to fill in gaps about these species. With the potential development of offshore oil fields and increased shipping around the islands, systematic monitoring for strandings would also ensure that any increased mortality could be uncovered for these species of conservation priority. The spatial database of cetacean strandings now available as a GIS shapefile and its attributes will provide a tool for the Falkland Islands Government to quickly notice any changes in stranding patterns by visualising the locations of new strandings compared to historical distribution.

Reports of stranding events as described here may, however, be biased and dependent on the locations of human activities and the accessibility of the coast. Therefore, there are potentially other or more important sites where strandings occur that were not captured in this study. Nevertheless, most of the land in the Falkland Islands is used as grazing pasture for sheep. Farmers survey their entire land at least twice a year and check beaches in particular for stray stock. Only a few of the most remote or inaccessible coasts would not be checked. Some parts of the coasts are visited more often by locals (beaches close to settlements), tourists (particular cruise ships and a few sites reached by land) or researchers, but these do not match the main 12 hotspots apart for one at a main tourist destination (Carcass Island). It is therefore likely that the spatial distribution of strandings presented here is not highly affected by a reporting bias.

The western side of the Falkland Islands, and in particular exposed west facing beaches of all islands, appear to have the highest rate of cetacean strandings. This western pattern of spatial distribution is especially marked for pilot whales. Therefore, there may be a relationship between this pattern and oceanographic conditions. Fig. 5 shows known directions of the major drifts and currents around the Falkland Islands (Arkhipkin *et al*., 2013) and may indicate that the pilot whales follow these currents to the Falkland Islands under certain environmental conditions. The distribution of beached litter around the Falkland Islands has also revealed a higher rate of recovery on beaches facing west towards the open ocean (Crofts, 2014). The complex coastlines of the islands with many narrow channels and small sounds with shallow bathymetry may also disorientate animals, in particular species not typically found in shallow coastal waters such as sei, fin or beaked whales (Greg and Trites, 2001; Forney *et al*., 2012). Further studies on cetacean distribution around the Falkland Islands will help understanding of the interactions between the oceanographic environment and the distribution of cetaceans around the Falkland Islands, including the spatial pattern of strandings. Such further studies along with the spatial distribution of strandings will be an important input for marine spatial planning efforts currently being developed in the Falkland Islands.

The predominance of whale strandings, in particular, on the western part of the islands may also be caused by biological characteristics or human activities. A recent study indicated greater and larger sighting hotspots of baleen whales in coastal waters (particularly in large open bays) in the western part of the islands (Frans and Augé, 2016). Otley (2012) indicated that for most species, the general distribution of strandings may reflect habitat preferences (e.g. deep versus shallow waters) and where animals would therefore more likely to be found. There are also a range of human activities around the Falkland Islands, with a shipping route running close to the island on the western side and, over summer and early autumn, cruise ships travelling in coastal waters, mostly visiting the western parts of the islands. Most of the strandings were not investigated for signs of trauma, or only superficially. Whale numbers in Falkland Islands' inshore waters have likely been increasing considerably in the last two decades based on sighting rates (Frans and Augé, 2016). Monitoring cetacean strandings will be crucial in detecting potential impacts in light of future increases in both whale numbers and human activities around the Falkland Islands.

In this paper, the first recorded stranding of false killer whales in the Falkland Islands was reported. The species has not previously been sighted or recorded as stranded in this archipelago despite being within the southern part of what is generally considered as the distribution range of this species. False killer whales are primarily found in tropical and sub-tropical warm waters and are seldom sighted in cold waters (Baird, 2002). Climate change may lead to more occurrences of this species in the Falkland Islands and monitoring strandings will help identifying changes. The first confirmed record of an Antarctic minke whale (*Balaenoptera* *bonaerensis*) was also reported in 2016. Due to the difficulty of distinguishing this species from the common minke whale (*Balaenoptera acutorostrata*), at sea in particular but also at strandings, it is possible that previous records may have been mis-reported. Antarctic minke whales are listed as data deficient by the IUCN, with limited knowledge on this species worldwide (IUCN, 2016).

In conclusion, cetacean strandings provide invaluable knowledge on cetacean species. In particular, spatially-explicit stranding databases deliver two main benefits: (1) identification of hotspots of strandings to facilitate monitoring of key sites when resources are limited, and increasing chances of detecting and attending strandings; and (2) detection of future changes in distribution patterns as well as numbers of strandings, potentially due to environmental shifts from climate change or in the context of industrial development at sea or in coastal areas. This is particularly useful in remote, sparsely populated areas, like the Falkland Islands.

ACKNOWLEDGMENTS

We would like to thank the numerous people and organisations who have reported cetacean strandings over the years to the Falkland Islands Government or Falklands Conservation, and provided data on these events. We acknowledge Darwin Plus (UK Department for Environment, Food and Rural Affairs) under the project DPLUS027 (Marine Spatial Planning for the Falkland Islands) and the Falkland Islands Environmental Studies Budget for funding to AAA and VFF. The Falkland Islands Environmental Planning Department is thanked for making available the original Falkland Islands cetacean stranding database and was provided with the QGIS project and database shapefile to start recording strandings with detailed locations.

REFERENCES

Arkhipkin, A., Brickle, P. and Laptikhovsky, V. 2013. Links between marine fauna and oceanic fronts on the Patagonian shelf and slope. *Arquipel. Life Mar. Sci.* 30:19–37.

Baird, R.W. 2002. False killer whale. pp. 411–12. *In:* W.F. Perrin, B. Würsig and J.G.M. Thewissen (Eds) *Encyclopedia of Marine Mammals*. Academic Press, San Diego, CA, USA.

Crofts, S., 2014. An interim report on baseline levels of beached marine debris at the Falkland Islands. Falklands Conservation, Stanley, Falkland Islands.

Forney, K.A., Ferguson, M.C., Becker, E.A., Fiedler, P.C., Redfern, J.V., Barlow, J., Vilchis, I.L. and Balance, L.T. 2012. Habitat-based spatial models of cetacean density on the eastern Pacific Ocean. *Endang. Species Res*. 16:113–33.

Frans V.F and Augé, A.A. 2016. Use of local ecological knowledge to investigate endangered baleen whale recovery in the Falkland Islands. *Biol. Conserv*. 202: 127–37.

Greg, E.J. and Trites, A.W. 2001. Predictions of critical habitat for five whale species in the waters of coastal British Colombia. *Can. J. Fish. Aquat. Sci*. 58:1265–85.

Iñíguez, M., Masello, J.F., Gibraudo, C., Arcucci, D., Krohling, F. and Belgrano, J. 2010. On the occurrence of sei whales, *Balaenoptera borealis*, in the south-western Atlantic. *Mar. Biod. Rec.* 3:e68.

IUCN, 2016. The International Union for Conservation of Nature Red List of Threatened Species. Version 2016-1. [Available at: *http://www.iucnredlist.org*. Downloaded on 1 May 2016].

Jepson, P.D., Bennett, P.M., Deaville, R., Allchin, C.R., Baker, J.R. and Law, R.J. 2005. Relationships between polychlorinated biphenyls and health status in harbor porpoises (*Phocoena phocoena*) stranded in the United Kingdom. *Environ. Toxicol. Chem*. 24:238–48.

Leeney, R.H., Amies, R., Broderick, A.C., Witt, M.J., Loveridge, J., Doyle, J. and Godley, B.J. 2008. Spatio-temporal analysis of cetacean strandings and bycatch in a UK fisheries hotspot. *Biol. Conserv.* 17:2323–38.

McLellan, W.A., Friedlaender, A.S., Mead, J.G., Potter, C.W. and Pabst D.A. 2002. Analysing 25 Years of bottlenose dolphin (*Tursiops truncatus*) strandings along the Atlantic Coast of the USA: Do historic records support the coastal migratory stock hypothesis? *J. Cetacean Res. Manage.* 4: 297–304.

Meager, J.J. and Sumpton, W.D. 2016. Bycatch and strandings programs as ecological indicators for data-limited cetaceans. *Ecol. Indic*. 60:987–95.

Norman, S.A., Bowlby, C.E., Brancato, M.S., Calambokidis, J., Duffield, D., Gearin, P.J., Gornall, T.A., Gosho, M.E., Hanson, B., Hodder, J., Jeffries, S.J., Lagerquist, B., Lambourn, D.M., Mate, B., Norberg, B., Osborne, R.W., Rash, J.A., Riemer, S. and Scordino, J. 2004. Cetacean strandings in Oregon and Washington between 1930 and 2002. *J. Cetacean Res. Manage*. 6:87–100.

Otley, H. 2008. *Falkland Islands Species Action Plan for Cetaceans 2008–2018*. The Environmental Planning Department, Stanley, Falkland Islands.

Otley, H. 2012. The composition of the cetacean community in the Falkland (Malvinas) Islands, southwest South Atlantic Ocean. *Rev. Biol. Mar. Oceano*. 47:537–51.

Otley, H., Smith, J. and Dalebout, M.L. 2012. Beaked whale strandings on the Falkland Islands and South Georgia, South Atlantic Ocean, between 1866 and 2008. *J. Mar. Biol. Assoc. U.K.* 92:1851–64.

Parsons, E.C.M., Baulch, S., Bechshoft, T., Bellazzi, G., Bouchet, P., Cosentino, A.M., Godard-Codding, C.A.J., Gulland, F., Hoffmann-Kuhnt, M., Hoyt, E., Livermore, S., MacLeod, C.D., Matrai, E., Munger, L., Ochiai, M., Peyman, A., Recalde-Salas, A., Regnery, R., Rojas-Bracho, L., Salgado-Kent, C.P., Slooten, E., Wang, J.Y., Wilson, S.C., Wright, A.J., Young, S., Zwamborn, E. and Wutherland, W.J. 2015. Key research questions of global importance for cetacean conservation. *Endang. Species Res.* 27:113–18.

Parsons, E.C.M. and Jefferson, T.A. 2000. Post-mortem investigations on stranded dolphins and porpoises from Hong Kong waters. *J. Wildl. Dis*. 36:342–56.

QGIS Development Team, 2015. *QGIS Geographic Information System*. Open Source Geospatial Foundation. Available at: *http://qgis.osgeo.org*.

Santos, M.B., Pierce, G.J., Lopez, A., Reid, R.J., Ridoux, V., and Mente, E. 2006. Pygmy sperm whales *Kogia breviceps* in the Northeast Atlantic: New information on stomach contents and strandings. *Mar. Mammal Sci*. 22:600–16.

Thomsen, I. 2014. Results from the pilot line transect survey for inshore cetaceans in the Falkland Islands and designing a full Falkland Island line transect survey for inshore cetaceans. Falklands Conservation, Stanley, Falkland Islands.

White, R.W., Gillon, K.W., Black, A.D., and Reid, J.B. 2002. *The Distribution of Seabirds and Marine Mammals in Falkland Islands Waters*. Joint Nature Conservation Council, Peterborough, UK. 107pp.

Wilkinson, L. and Friendly, M. 2009. The history of the cluster heat map. *Am. Stat*. 63:179–84.

Review of potential line-transect methodologies for estimating abundance of dolphin stocks in the eastern tropical Pacific

CLERIDY E. LENNERT-CODY[1], STEPHEN T. BUCKLAND[2], TIM GERRODETTE[3], ANDREW WEBB[4], JAY BARLOW[3], PETER T. FRETWELL[5], MARK N. MAUNDER[1], TOSHIHIDE KITAKADO[6], JEFFREY E. MOORE[3], MICHAEL D. SCOTT[1] AND HANS J. SKAUG[7]

Contact email: clennert@iattc.org

ABSTRACT

A twelve-year hiatus in fishery-independent marine mammal surveys in the eastern tropical Pacific Ocean (ETP), combined with a mandate to monitor dolphin stock status under international agreements and the need for reliable stock status information to set dolphin bycatch limits in the tuna purse-seine fishery, has renewed debate about how best to assess and monitor ETP dolphin stock status. The high cost of replicating previous ship-based surveys has intensified this debate. In this review, transect methods for estimating animal abundance from dedicated research surveys are considered, with a focus on both contemporary and potential methods suitable for surveying large areas for dolphin species that can form large, multi-species aggregations. Covered in this review are potential improvements to the previous ship-based survey methodology, other ship-based methods, alternative approaches based on high-resolution imagery and passive acoustics, and combinations of ship-based and alternative approaches. It is concluded that for immediate management needs, ship-based surveys, with some suggested modifications to improve precision, are the only reliable option despite their high cost. However, it is recommended that a top research priority should be development of composite methods. Pilot studies on the use of high-resolution imagery and passive acoustics for development of indices of relative abundance to be used in composite methods should be part of any future ship-based survey efforts.

KEYWORDS: ABUNDANCE ESTIMATE; INDEX OF ABUNDANCE; TRENDS; SURVEY-VESSEL; SURVEY-AERIAL; SURVEY-ACOUSTIC; SURVEY-COMBINED

INTRODUCTION

For almost 50 years, the tuna-dolphin issue in the eastern tropical Pacific Ocean (ETP) has been studied and debated. Purse-seine vessels fishing for tuna in the ETP have exploited the co-occurrence of yellowfin tuna (*Thunnus albacares*) and conspicuous dolphin species to locate the fish since at least the 1940s (Silva, 1941; NRC, 1992). Purse-seine vessels began encircling dolphins in the late 1950s to catch the tunas (McNeely, 1961; NRC, 1992) and this fishing method resulted in substantial bycatch of dolphins (Perrin, 1968; Lo and Smith, 1986; NRC, 1992; Wade, 1995). Through fishermen's ingenuity and implementation of national and international management measures mortality has been reduced to a very small fraction of previous levels (NRC, 1992; Joseph, 1994; Hall, 1998; IATTC, 2016). Population dynamics modeling of dolphins has been the preferred approach used for evaluating stock status (Hoyle and Maunder, 2004; Gerrodette and Forcada, 2005; Reilly *et al.*, 2005; IATTC, 2006; Wade *et al.*, 2007, Gerrodette *et al.*, 2008) with respect to historical bycatch levels, and those models have relied on estimates of abundance from fishery-independent cetacean and ecosystem assessment surveys conducted by the National Marine Fisheries Service (NMFS) periodically between 1979 and 2006.

As a result of a hiatus in the NMFS surveys since 2006, there are currently no reliable indicators with which to monitor the abundance of the ETP dolphin populations. In addition to the fishery-independent surveys previously conducted by the NMFS, indices of relative abundance from purse-seine observer data have been proposed (Hammond and Laake, 1983; Buckland and Anganuzzi, 1988; Anganuzzi and Buckland, 1989) because of the large amount of observer data that are available, especially relative to data from fishery-independent surveys. At the time these methods were proposed, the primary method of dolphin school detection was by the vessel crew using high-powered binoculars (Buckland and Anganuzzi, 1988; Lennert-Cody *et al.*, 2001). However, since that time searching for dolphins associated with tunas has evolved and sightings associated with helicopter or radar constitute the majority of sightings. There are serious challenges to developing a reliable index from fisheries observer data, including potential differences in availability of sighting information by search method, changes in the use of different search methods depending on the vessel's perception of the local abundance of dolphins with tunas, and non-random distribution of tuna vessel search effort (Lennert-Cody *et al.*, 2001; 2016).

This lack of information on current dolphin stock status is problematic because, despite the current low levels of reported mortality (IATTC, 2016), high levels of historical mortality (Wade, 1995) and low estimated population rates of increase (Gerrodette *et al.*, 2008) have meant that population modelling results are sensitive to assumptions (Gerrodette and Forcada, 2005; Gerrodette *et al.*, 2008;

---

[1] *Inter-American Tropical Tuna Commission, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA.*
[2] *Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews, Fife, KY16 9LZ, Scotland, United Kingdom.*
[3] *Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, CA, USA 92037.*
[4] *HiDef Aerial Surveying Limited, Phoenix Court, Earl Street, Cleator Moor, Cumbria, CA25 5AU, United Kingdom.*
[5] *British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, United Kingdom.*
[6] *Tokyo University of Marine Science and Technology, 5-7 Konan 4, Minato, Tokyo, 108-8477, Japan.*
[7] *University of Bergen, Postboks 7803, Bergen, Norway.*

IATTC, 2015a). The lack of information poses obvious problems for management. For example, the Antigua Convention[8] of the Inter-American Tropical Tuna Commission (IATTC) requires that the status of all species potentially impacted by the tuna fisheries in the eastern Pacific Ocean be monitored. In addition, abundance estimates are needed to ensure that dolphin mortalities are both sustainable and insignificant because the stock mortality limits for the purse-seine fishery are based on estimates of abundance (IATTC, 2006; NMFS, 2016). Recent efforts to obtain MSC certification by a segment of the purse-seine fleet operating in the ETP[9] also require determination of dolphin stock status. These needs provide impetus for updating the assessment of these stocks and resuming regular monitoring. However, fishery-independent surveys are expensive; the latest estimate of a one-year survey, were it to be conducted by the NMFS, is approximately US$10M (in 2017 dollars)[10]. Therefore, development of cost-effective means for monitoring dolphin stock status is desirable. To address this problem, a review of current abundance estimation methods and possible alternatives was undertaken.

In this review, line-transect methods for estimating animal abundance are considered, with a focus on both contemporary and potential methods suitable for surveys of dolphin species that have been involved in the ETP tuna purse-seine fishery. Of particular interest are methods for use on stocks of the offshore pantropical spotted dolphin (*Stenella attenuata*) and the spinner dolphin (*S. longirostris*), stocks that typically occur in large schools over extensive areas of ocean (Dizon *et al*., 1994; Scott and Cattanach, 1998, Scott and Chivers, 2009). This paper focuses on methods for dedicated research surveys; use of fishery-dependent data has been reviewed most recently by Lennert-Cody *et al*. (2016).

SHIPBOARD SURVEYS

Current methods

Line transect surveys conducted by the NMFS in the ETP began in 1974 using a combination of aircraft and ships (Smith, 1981; Holt and Powers, 1982). Shipboard procedures were refined each year and, by 1979, were close to current procedures. Since 1986, the surveys have used a stratified random design. In general, about three times more effort per unit area has been allocated in the central core area than in the outer or peripheral area (Fig. 1). The core area includes the main dolphin stocks of interest, namely northeastern offshore spotted and eastern spinner dolphins, and is the main area where purse-seiners set on tunas associated with dolphins (IATTC, 1999; 2015b). Because the ETP area is large and the research vessels have a limited range of 20–30 days, it is not possible to lay transect segments strictly at random. Instead, prior to departure, waypoints are chosen to achieve the desired allocation of effort among strata, approximately even spatial coverage within each stratum, and a length of trackline that returns the ship to port at the end of each leg. Since 1986, each survey has utilised 2 ships (3 in 1998) for 120 sea days each, with 4–5 legs per ship from late July to early December. During the survey, the ships proceed from waypoint to waypoint at 10 knots. Waypoints are typically hundreds of miles apart. Search effort takes place when there is sufficient light for effective detection of animals (normally about 30 minutes after sunrise to about 30 minutes before sunset). Search effort is suspended if it is too windy (normally Beaufort sea state > 5), if visibility is severely limited by rain or fog, or if the horizon is not visible due to haze. At night and during such periods of suspended effort, the ships continue along the planned tracklines to stay on schedule.

The surveys have used teams of three observers. Early experiments with helicopters established that dolphin schools ahead of the vessel were seen by observers on the vessel (i.e. that availability bias was low), and that most dolphin schools

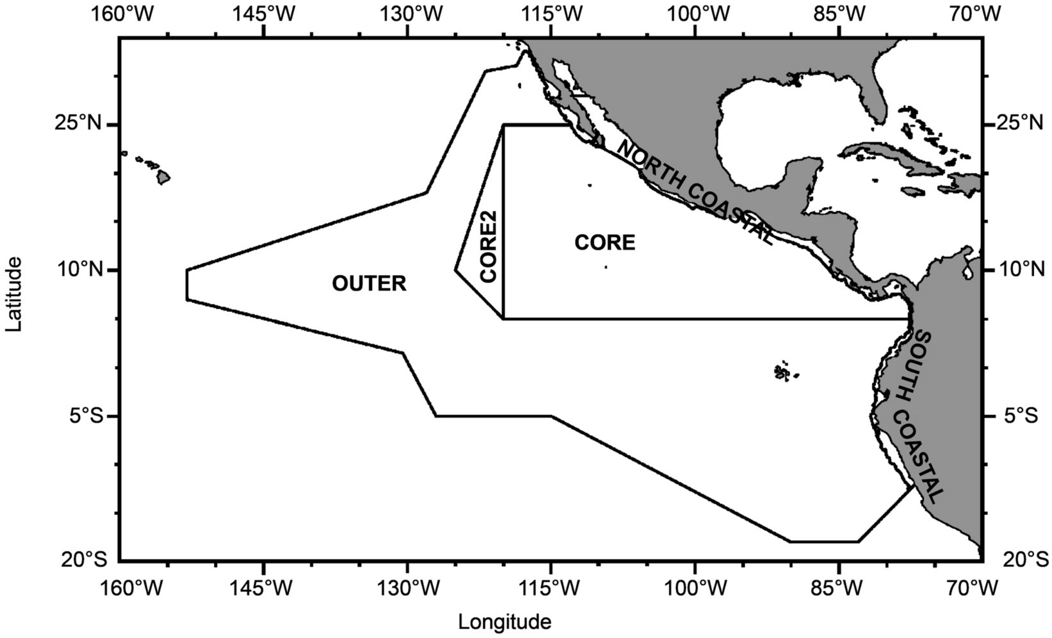


Fig. 1. Strata for the STAR06 cruise (used with permission; Gerrodette *et al*., 2008). The ‘core’ area was expanded to include the ‘core2’ area during the 2003 and 2006 surveys.

---

[8] *https://www.iattc.org/iattcdocumentationeng.htm.*

[9] *https://fisheries.msc.org/en/fisheries/northeastern-tropical-pacific-purse-seine-yellowfin-and-skipjack-tuna-fishery/.*

[10] Lisa Ballance, NMFS, pers. comm., 15 July 2016.

were detected by observers before there was a significant reaction of the dolphins to the vessel (Au and Perryman, 1982; Hewitt, 1985). Therefore, observer search was based on the assumption that the probability of detection on the trackline, $g(0)$, is 1.0. While 'on effort,' two observers search through 25× pedestal-mounted binoculars, one on each side of the flying bridge, from 90° abeam to the centerline. (In the early years, observers searched out to 10° on the other side as well, to ensure some overlap of effort near the line.) The third observer searches by naked eye or with hand-held 7× binoculars over the whole 180° in front of the ship. Data recorded include the observers on duty, and sighting conditions, such as sea state, swell height and sun angle. When a group of cetaceans is sighted, the angle and reticle to the sighting are recorded (radial distance to the sighting is computed per Kinzey and Gerrodette, 2001), and the observer team typically goes 'off effort' and directs the ship to leave the transect line and approach the dolphins. The purpose of 'closing' on the sighting is to identify the proportion of each species present in the group (because spotted and spinner dolphins often occur in mixed-species schools in the ETP) and to obtain the best possible estimates of school size. Experiments have shown that both kinds of data are compromised if the ship remains on the trackline and does not close on the sighting (Schwarz *et al*., 2010).

Estimating the size of dolphin schools is a crucial but difficult component of absolute abundance estimation. The accuracy of group size estimates made by research vessel observers varies considerably from observer to observer, and from group to group for a single observer. Research vessel observers' estimates have been compared extensively to counts from aerial photographs (Gerrodette *et al*., 2002; Gerrodette *et al*., 2018). On average, over all schools and all observers, group size is estimated accurately for schools of up to about ten dolphins. Above that number, group size tends to be underestimated, and the tendency to underestimate increases with group size. A group of 50 dolphins is underestimated by about 10% on average, but a group of 500 dolphins is underestimated by about 50% on average. Moreover, group size estimates are highly variable, with CVs > 0.5. To reduce this variance and to improve accuracy, the NMFS has used three main strategies. First, during pre-cruise training, observers learn group size estimation techniques. They practice estimating group sizes using photographs, videos and computer simulations. Second, after the ship approaches a sighting, the three on-duty observers make independent estimates of group size. The mean of the three independent estimates is used as it is less variable than single estimates. Third, the tendency of each observer to under- or over-estimate group size has been assessed with aerial photographs of the schools, as described above. Each observer's estimates are adjusted according to his/her individual tendency, and this improves the overall accuracy of group size estimation. These procedures also allow group size estimation error to be included in the variance of the estimate of abundance.

Abundance has been estimated from these survey data using a multivariate extension of conventional line transect methods (Gerrodette and Forcada, 2005; Gerrodette *et al*., 2008). This methodology is used to account for covariate effects on the estimated probability of detection (Buckland *et al*., 2004). Covariate effects considered in the analyses include: school size, sea state, swell height, time of day, survey ship, sighting cue, method of sighting, presence/absence of glare on the trackline, and presence/absence of seabirds.

Advantages and disadvantages of the current methods

The above methods have the considerable advantage that they are tried and tested. The target species are appropriate for ship-board surveys because they form large, easily detected schools, and a wide strip can be surveyed using the pedestal-mounted 25× binoculars. In good conditions schools are likely to be detected before any significant response to the vessel occurs. Movement of animals (independent of the vessel) will generate some upward bias in estimates (Glennie *et al*., 2015), and although this bias may not be negligible, incorporation of an explicit animal movement model into the distance sampling methodology allows for bias correction (Glennie *et al*., 2017). In addition, although it can be difficult to estimate group size and species proportions in mixed-species groups, as noted above, aerial photographs of a sample of schools are used to quantify and correct for bias.

There are three main shortcomings of the current methodology. First, Barlow (2015) has conducted analyses that indicate that $g(0)$ might be appreciably below one in all but the best sighting conditions, which may be linked to a reduced window in which a school is available for detection in poorer sighting conditions together with responsive movement. Second, it is costly to conduct effective shipboard surveys over such a large study area, even absent concerns about estimation of $g(0)$. Therefore, conducting surveys in blocks of several years at a time, as has been done previously (e.g. 1986–1990 and 1998–2000), or for multiple years in general, as has been recommended to obtain reliable trend estimates (Punt, 2013), may be prohibitively expensive. Finally, despite the extensive resources dedicated to the surveys, the level of precision of the abundance estimates remains problematic (Gerrodette *et al*., 2008). The precision of the estimates has improved over time, and the most recent five surveys achieved a median CV of 0.17 for the northeastern spotted dolphin and 0.24 for the eastern spinner dolphin. Despite this, it is not possible with the data of these five surveys to distinguish between an expected growth rate of 0.04 (Reilly and Barlow, 1986) and no population increase (i.e. 95% confidence intervals contain both 0 and 0.04), and 95% confidence intervals for growth rates based on the full 10 years of surveys contain the value 0 for both species (see table 13 of Gerrodette *et al*., 2008).

Suggestions for improvement within the current framework

Changes in field methods might be made to evaluate and estimate $g(0)$, and improve precision of the abundance estimates (see Oedekoven *et al*., 2018, for some detailed survey design considerations). If $g(0)$ is less than one, using a double-platform approach may allow its estimation (Borchers *et al*., 1998), particularly if the apparent effect on $g(0)$ of sea state may arise due to responsive movement of schools prior to detection. Attempts to study responsive movement in 1998 used an observer searching with 25×

binoculars from a higher 'tracker' platform but failed to detect groups appreciably before the primary search team. However, a drone or helicopter might provide a more effective tracker platform, operating ahead of the survey vessel, and setting up trials for the main observation platform. This allows estimates to be corrected for both responsive movement and $g(0)$ (Buckland and Turnock, 1992). Improved designs based on adaptive sampling may be able to contribute to higher precision, although gains would be expected to be rather modest (Pollard *et al*., 2002). However, it is noted that any changes risk compromising comparability between new and existing time series of abundance estimates.

Model-based analysis methods, applied to data generated under the current survey design, may help to resolve issues associated with the estimation of g(0), and perhaps also provide estimates of abundance with greater precision. As regards $g(0)$ estimation, Barlow (2015) used a generalised additive model approach to estimate the effects of factors such as sea state on the probability of a sighting. Coefficients from the fitted model provided $g(0)$ correction factors for poor sighting conditions, relative to the best sighting conditions. These correction factors were applied to an estimate of absolute $g(0)$ for the best sighting conditions to obtain estimates of $g(0)$ in poor sighting conditions. As regards improving precision, model-based methods are useful both for modeling encounter rate and for modeling the detection function (Buckland *et al*., 2004). In the latter case, using multiple covariate distance sampling methods, it is possible to jointly model data from different species, with species as a factor in the detection function model, to improve precision (e.g. Barlow *et al*., 2011). In addition, given that a larger source of variance is encounter rate (Gerrodette *et al*., 2008), encounter rate modeling also merits more attention, especially in light of recent developments in spatial distance sampling methods (e.g. Yuan *et al*., 2017).

Model-based methods may also be useful if the precision of group size estimates varies with specific covariates because this is not taken into consideration with the current methods and could cause bias. Whether the use of 'uncorrected' group size could lead to a large amount of bias in the estimates of abundance depends on the magnitude of the error in group size and the extent to which the effective strip width depends on the true group size. This source of bias can be minimised by taking into consideration the distribution of uncertainty about observed group size, as a function of covariates, when computing a Horvitz-Thompson-like estimator of abundance (Borchers *et al.,* 1998). Another option for adjusting the estimate of effective strip width for uncertainty in group size would be to estimate the detection function using an errors-in-variables type of model.

Finally, there could be several benefits to further decomposing the precision of the abundance estimates generated under the current survey design according to all the sources of uncertainty. In addition to the variance components attributable to encounter rate, effective strip width (including $g(0)$ uncertainty), and group size, there is uncertainty due to measurement error in perpendicular distances, calibration factors for correcting distance and survey modes, and process error arising from inter-annual/seasonal variation of spatial distribution of dolphins. Estimating these other sources of error and incorporating these estimates into the estimated abundance error would lead to more realistic estimates of overall uncertainty, which could have implications for conservation and management. It could also improve understanding of the main causes of uncertainty and provide information relevant to the design of future surveys, potentially improving precision of the abundance estimates.

In summary, the main suggestions for improving the current framework are:

- Adapt field methods to use a double-platform approach using a tracker platform that can operate with sufficient autonomy and in a range of survey conditions, so that $g(0)$ can be evaluated, and if necessary, estimated.
- Account for covariate effects on encounter rate using model-based methods.
- Improve the estimation of the detection function by pooling data across species (with species as a factor-type covariate) and taking account of uncertainty associated with group size estimates via model-based methods.
- Obtain more realistic estimates of overall uncertainty by estimating all sources of error (e.g. measurement error, calibration factors).

Ship-based alternatives – use of purse-seine vessels

With a designed, randomised survey to ensure that units of survey effort are placed randomly with respect to the distribution of groups of animals (Buckland *et al*., 2001; 2004), data might be collected aboard tuna purse-seine vessels to either supplement data collected by research vessels, or as the primary data source for abundance estimation. The best option for a purse-seine vessel survey to produce abundance estimates of similar quality and precision as those of the previous NMFS surveys would be for the commercial vessel survey to replicate all aspects of the NMFS survey methods and design (with the obvious exception of use of the same vessels), including: the number of vessels, the amount of search effort, the set-up of the observation platforms, the use of specially trained observers, and the calibration of observers' estimates of group size by aerial photogrammetry. Ideally, a survey using purse-seiners would be designed to yield unbiased estimates of absolute abundance, and therefore biases due to the use of different vessels, and possibly different observers, would be minimised. Whether such a survey would be advantageous depends in part on vessel cost, which is the most costly aspect of ship-based surveys, and which for purse-seine vessels will vary with the size and age of the vessel, and country-specific costs of fuel and insurance, among other factors.

If purse-seine vessel time for surveys were to be provided (e.g. donated) by vessel owners, it might be that more than two vessels would be involved in the survey, each for a shorter period of time than the sea-days of the NMFS vessels. The optimal number of vessels that should participate in the survey would need to be evaluated based on target CVs and logistical constraints. Several aspects of a many-vessel survey, however, are worthy of further discussion. First, if each commercial vessel were to survey during a portion of a fishing trip, it would be important to determine the optimal allocation of survey segments from a randomised design to each vessel so as to minimise transit time from the fishing location to the survey location, taking into consideration spatial gradients in dolphin abundance (Reilly, 1990; Redfern *et al*., 2008; Forney *et al*., 2012) and the constraint that vessels should all operate at the same time of year to avoid any potential biases due to dolphin population movement. A simulation using historical commercial vessel fishing trip trajectories, in combination with historical NMFS survey tracklines, or new survey tracklines, and information on dolphin spatial distributions, could be conducted to determine how best to allocate blocks of survey segments from an ETP-wide design to individual tuna vessels in time and space. In addition, minimising heterogeneity in the data as much as is practical through survey design would be important, given concerns about perfect detection on the trackline (Barlow, 2015). Without the assumption that $g(0) = 1$, the property of 'pooling robustness' (Buckland *et al*., 2004) would no longer hold and it could not be assumed that unmodeled heterogeneity in the data would have little effect on the estimation.

Finally, because of an evasive response of dolphins to tuna vessels (e.g. Pryor and Norris, 1978; Lennert-Cody and Scott, 2005 and references therein), which varies spatially across the ETP, it would be important to have a commercial vessel survey design that allows for testing of the assumption that $g(0, \mathbf{z}) = 1$ for covariates $\mathbf{z}$, and if necessary, estimation of $g(0,\mathbf{z})$. This would require a different survey design compared to previous NMFS surveys, as well as additional equipment. Double-count survey designs, from which $g(0,\mathbf{z})$ can be estimated by mark-recapture distance methods (e.g. Borchers *et al*., 1998; Buckland *et al*., 2004), typically involve two teams of observers; for the more robust approaches, one of these teams searches at greater distance, possibly from a helicopter or using video from a drone flying ahead of the ship, while the other carries out normal search. Although commercial vessels that are suitable for a survey tend to carry a helicopter, it would first need to be ascertained whether the helicopters elicit an evasive response in dolphins, given that helicopters are used during fishing operations. In addition, observer safety may be a concern with respect to helicopter use; if helicopter use is restricted to good conditions, the data would be of limited value for quantifying $g(0,\mathbf{z})$, which is expected to be lowest in poor conditions. Drones might provide a less disruptive vehicle for detecting and tracking schools in a double-count survey design, but might also be restricted to good sighting conditions.

AERIAL SURVEYS

Aerial line transect surveys were conducted in the ETP in the 1970s (Smith, 1981; Holt and Powers, 1982) but because of safety concerns and because the range of shore-based aircraft could not cover the entire offshore area, they were discontinued. For these reasons, surveys using observers on board manned aircraft are not considered in this review.

Digital aerial surveys

Manned aircraft

Commercial manned digital aerial survey methods were developed in the United Kingdom to provide survey data on potential impacts of developing offshore wind farms. Early tests demonstrated their effectiveness for census of seaduck at one coastal site, with abundance estimates that exceeded those of traditional visual aerial survey methods (Buckland *et al*., 2012). Digital survey methods have since replaced visual aerial methods for seabirds in offshore waters of the United Kingdom, Germany, Denmark, and increasingly in the eastern United States with thousands of sorties now flown (Thaxter *et al*., 2016; Weiß *et al*., 2016; Williams *et al*., 2015). Digital video aerial survey methods have been found to give comparable results to dedicated visual aerial survey methods for harbour porpoise *Phocoena phocoena* in the United Kingdom (Williamson *et al*., 2016), and for other marine megafauna (Williams *et al*., 2015; Gordon *et al*., 2013).

Two technologies have emerged for commercial census by digital aerial survey: high resolution video and high resolution digital still imagery. In general, the video methods use bespoke camera rigs to scan a strip transect using four cameras in a comb pattern over the sea. Stills methods usually use medium-format photogrammetry cameras to sample plots (or quadrats) or transects at sea. For seabird surveys, cameras ideally collect images at a ground sample distance (GSD) of 2–3cm, and this allows species identification rates of at least 80% of all seabird species in the United Kingdom, and considerably higher rates for cetaceans. Lower resolutions of 3–5cm also achieve high identification rates for cetaceans. The higher camera resolutions are achieved while flying at 550m above sea level (a.s.l.) for digital video methods and 270–400m a.s.l. for digital stills, depending on the GSD used.

Both methods in the United Kingdom use a two-phase method for analysing digital data generated. The first phase requires a review of all material, with 10% or 20% of all material subjected to a random blind audit, and robust procedures for handling failed audits. The second phase requires all objects to be assigned to the lowest order taxon possible. Again 10–20% of all objects are subjected to a randomised blind audit, with procedures for handling failed audits. Digital stills and digital video methods have attempted to use automated methods for detection and identification of objects using machine learning methods, with varying success. While detection methods are reasonably successful in calm sea conditions, they have much poorer accuracy at higher sea states, particularly for marine mammals. Automated methods for identification of objects require considerable human intervention and oversight, negating the potential efficiency benefits of such methods. Although success so far has been low in these methods, it is likely that more sophisticated artificial intelligence algorithms will ultimately be able to replicate the undoubted accuracy of experienced human operators.

Digital aerial methods offer a number of advantages over conventional aerial survey methods:

- Because the aircraft operate at greater altitudes and have fewer crew, digital methods are considerably safer than visual aerial surveys.
- Detection rates are uniform across the whole image for digital methods, meaning that it is not necessary to account for missed detections using distance methods, and double-review methods are simpler.

- All individual animals can be counted and group sizes do not influence detection rates in digital methods, removing the need to account for group size detection bias when estimating abundance.
- A permanent record of the survey can be kept for subsequent analysis should the need arise with digital aerial methods.
- Bespoke rigs are used to angle digital cameras away from sun glare and avoid detection problems of fixed camera systems and visual aerial survey methods.
- Digital video methods are still effective at higher sea states, when compared to digital stills and visual methods, although there is some unpublished evidence for lower detection rates in video methods, mainly for sub-surface marine mammals at higher sea states.
- Identification rates are higher for digital methods.

Some issues remain for digital aerial methods when compared to other methods and the survey requirements of the ETP surveys:

- In general, digital aerial methods are more expensive than visual aerial methods but typically cheaper than dedicated ship-based methods in like-for-like surveys (Thaxter *et al.,* 2016).
- While automated data review methods are available, they are still not sufficiently efficient compared to manual review. Considerable investment is required to develop methods that will provide significant time and cost savings.
- Availability bias for diving seabirds and cetaceans in digital survey methods is acute but difficult to account for. There exists a theoretical method for measuring this bias *in situ* using digital video methods which so far is untested. This is most likely to be effective for cetacean species with relatively short dive cycles (typically 2–3 minutes or less). No method exists for measuring this bias *in situ* for digital stills methods. Generic methods can be used, based upon known dive rates where these exist, for estimating availability bias for digital survey methods (Webb *et al*., 2015).
- Although it would be possible to survey the majority of the ETP survey area, as with visual aerial survey methods, the endurance of the aircraft used for these surveys is limited and insufficient for reaching the furthest limits safely from suitable airports. While deploying helicopters from boats offshore is possible, helicopters have been found not to provide a sufficiently stable platform for digital transect-based surveys. Some aircraft are able to re-fuel mid-air, and one of the aircraft used for digital video aerial surveys has a pilot-less version which increases the endurance and safety significantly, but see below.
- While good species identification is possible using this method, it is untried for the ETP species, thus in order to estimate absolute abundance, methods might be needed to estimate the species proportions within mixed-species dolphin schools, which are commonly seen in the ETP.

Commercial aircraft could potentially be fitted with cameras to gather high-resolution images. This has the advantage of low cost relative to dedicated aerial surveys, although potentially costly certification of aircraft for installing cameras might negate this advantage. The main disadvantages are: commercial aircraft fly at a much greater altitude than dedicated survey aircraft, resulting in low-quality images; commercial aircraft usually fly much faster which would compromise the number of images or frames that can be captured; and commercial aircraft routes do not sample the ETP evenly, so that spatial modelling methods will be required to extrapolate across the whole region.

Unmanned aircraft

The use of Unmanned Aerial Systems (UAS), also known as drones, has proliferated in the ecological survey sector in the last decade (e.g. Anderson and Gaston, 2013; Christie *et al*., 2016; Hodgson *et al*., 2016; Marine Mammal Commission, 2016; Colefax *et al*., 2018) and, much like in manned digital aerial surveys, can be used for transect or plot sampling of marine mammal distribution and abundance. UAS are available in many forms, from small multi-copter systems that carry small video cameras that have high definition or ultra-high definition (4×) resolution and save images to flash memory cards, up to military-grade fixed wing UAS that are capable of carrying much larger payloads with higher resolution cameras and server-based image storage systems. At the smallest end of the size spectrum, the camera systems are unlikely to deliver images of sufficient quality. Most attention in the use of UAS for marine census has been given to small- to medium-sized systems, such as the AH22, that are able to carry sensors of sufficient payload to capture higher quality images or video material.

Some small- to medium-sized UAS are designed to be recovered at sea, and most would need to be deployed and recovered from the deck of a ship if they were to be used to census the entire ETP. This would elevate the cost benefit considerably by the addition of the price of a mother ship that is able to reach the more distant parts of the previous study area (Fig. 1). Part of this restriction is imposed by limited access to airspace; in Europe and the United States, aviation regulations require that UAS are flown within line of sight of an operator. A further limitation on the use of such systems is their endurance, both in the number of hours that can be surveyed in a single mission and in the storage capacity for the images. The endurance of even medium-sized systems is limited to about five hours at about 100km per hour, which would mean that a survey of the ETP would be slow, unless carried out by multiple UAS. Storage capacity also limits the duration of sorties to a few hours and also means that raw image formats cannot be stored, thus reducing image quality slightly.

Military-grade systems are able to take much larger payloads and would be able to carry the payload of a commercial digital aerial survey system on board, including multiple cameras and server-based data storage systems. This gives them considerably greater endurance. Such systems would need to take off and land at commercial or military airstrips and cannot be recovered at sea at present. The *Diamond Aviation* DA42, used by HiDef for its digital video aerial surveys, has a pilotless version used for military purposes. It would have an endurance of about 15 hours and would be licensed to carry cameras and increased data storage capacity for a wider-area survey such as the ETP. To use such as system would require negotiated access to airspace of the ETP study area. At present, cost estimates for an ETP survey with military-grade UAS systems are not available. A preliminary estimate of the cost of an ETP survey with a *FlexRotor* drone, which is a commercial/civil-use drone, is less than $2M US (Johnson *et al*., 2018). However, these drones currently have an ~2,000km range and thus would require at-sea refueling on platforms of opportunity (e.g. tuna purse-seine vessels) to cover the full ETP survey area at no additional cost. Nonetheless, these figures are encouraging with regards to the potential savings that may be possible in the future with drone surveys compared to ship-based surveys.

There are several issues that remain to be worked out for surveys with unmanned aircraft. First, as with imagery from manned aircraft, there is a lack of automated detection methods that will work in a range of weather conditions. Automated detection is possible in near calm conditions, but becomes problematic in the likely sea states typical of the ETP. Second, there may be reliability issues with UASs being lost and not re-located at sea. There is also the need for development of better international airspace management to avoid collisions or interference with commercial aircraft and purse-seiner-based helicopters.

SATELLITE SURVEYS

Very High Resolution (VHR) satellites now have the ability to capture large areas of ocean (> 1000km^2 per image) at a spatial resolution of 30cm per pixel (Platonov *et al*., 2013; Stapleton *et al*., 2014). Recent work on cetaceans using lower resolution imagery (50cm) has shown the utility for counting baleen whales in optimal conditions and initial tests using 30cm imagery on humpback whales have shown a clear improvement in detection, both on the surface and beneath it (Fretwell *et al*., 2014). With 30cm satellite imagery it should be possible to identify the pattern of breaching small cetaceans in relatively calm seas, although species identification is unlikely. In calm conditions the signature of the splashes will be very bright relative to the surrounding waters, and due to the radiometric resolution of the satellites, it may also be possible to automate or semi-automate the process of finding these patches for large pods of dolphins. If agreements could be made with the satellite provider, this could be a very cost-effective way to survey large expanses of ocean to give first order abundance or presence estimates, or estimated indices of relative abundance. Other advantages are the ease of use of satellites, the ability to capture extremely large amounts of imagery in any area of ocean, the non-invasive nature and the lack of logistical set-up or flight planning effort for satellites.

However, this use of satellite technology is still developing and much testing would be needed before a workable system using satellite data could be incorporated into other survey methods. There are some comparisons to be drawn between satellites and the use of high-resolution aerial survey using digital stills; each has similar drawbacks – the need for favourable sea conditions, the problem of single instantaneous image acquisition and potential problems, and the need for automation over large areas. An additional drawback of satellite imagery is that image quality is affected by cloud cover. The main differences between the two systems are the higher resolution of the aerial imagery and the greater potential coverage from satellites.

The potential cost of the highest resolution imagery could be high for large area studies unless an agreement can be gained from the satellite provider; this is more likely either over areas with less demand for imagery (open ocean) or areas where high-profile research could be conducted. As the use of this technology is unproven for small cetacean surveys, the algorithms needed for automated or semi-automated identification still need to be constructed and proven. Manual checking over 1000's of square kilometres is difficult, although crowd-sourcing the imagery might solve this in the longer term. Species identification will be impossible with satellites as the resolution is too coarse and estimating school size could be difficult without ground truthing.

PASSIVE ACOUSTICS

Distance sampling, adapted for acoustic data, is the most commonly used approach to estimate abundance from passive acoustic data (Heinemann *et al*., 2016). Acoustic methods may be most valuable for estimating trends in relative abundance rather than absolute abundance for ETP dolphin stocks because of the difficulty of estimating group size from acoustic data. Assuming a species can be unequivocally identified by its vocalisation repertoire, to estimate trends in relative abundance from acoustic data, there are two key requirements for acoustic distance sampling methods, as follows.

The first is that detection probability can be estimated as a function of horizontal distance from the 'cue' (e.g. vocalisation count) to the acoustic instrument. To obtain detection as a function of horizontal distance, the depth of the cue (i.e. animal or group of animals) is often assumed, and this may bias the estimated detection function. In addition, the detection probability has to be corrected for the false detection rate (i.e. vocalisations that were incorrectly assigned to the target species during data processing). Although sound-propagation modelling has been used to estimate detection range in order to estimate distance to the cue, accurate estimation of range from these models is currently challenging. This is especially true for highly directional signals like echo-location clicks. A drifting vertical hydrophone array can be used to estimate range empirically which holds more promise than model-based range estimation.

The second is that density estimation methods can be based on individual-count methods, group-count methods, or cue-count methods. Individual-count methods are typically not practical because individuals within a group cannot be discriminated acoustically. Group-count methods require an estimate of group size, and methods to estimate group size from only acoustic data currently do not exist. (Group size is often obtained from concurrently-collected visual survey data.) Methods to convert cue counts to individual density require estimates of the cue production rate (vocalisations per unit time) under environmental and social conditions that are likely to be encountered during the survey.

At present, statistical methodological challenges exist for estimating abundance from acoustic data collected with slow-moving autonomous platforms. The accuracy of estimated trends in abundance will depend on the number and location of acoustic platforms used in the survey, and whether parameters such as detection probability, vocalisation rates, and area effectively surveyed can be estimated or assumed to be constant. The number of surface drifters can be increased at relatively little cost to obtain the number of detections to achieve a desired power to detect changes in abundance. For repeated long-duration surveys, such as might be conducted for ETP dolphin species, a passive acoustic system that was integrated into a glider or float would be preferable from a data-collection perspective. Buoyancy-driven floats and gliders can collect data continuously for weeks to a few months. Floats drift with the current at a specified depth; gliders can control both vertical and horizontal position (average speed is ~0.5 knots). Techniques for categorising whistles of ETP dolphin species are being developed (Oswald *et al*., 2004; 2007) but more research is needed to reliably distinguish species. Assuming that detection distances can be measured for each acoustic detection, the remaining key uncertainties are the degree to which acoustic behaviour and group size vary over time.

Similar data processing challenges are encountered when processing passive acoustics data, as with processing of high-resolution imagery data. As with all passive acoustic systems, the large volumes of data generated require processing to remove unwanted noise, identify vocalisations of the target species and locate those vocalisations in space. This data processing must be done by skilled analysts and specialised computer software.

COMPOSITE METHODS

There are many ways in which ship-based surveys might be combined with ‘auxiliary’ sources, either simultaneously or at different points in time, to obtain a ‘composite’ method. The use of composite methods would be an effective use of other line-transect data sources that may not require costly ship time but, as discussed above, are unlikely by themselves to provide estimates of absolute abundance in the near future due to limitations on the ability to identify species and/or estimate group size. Auxiliary source availability biases may be reduced or mitigated with technological advances; however, the biological sources of biases would remain. The large CVs on mean group size from the NMFS surveys (Gerrodette *et al*., 2008) provide further motivation to explore an index based on encounter rate. Auxiliary sources include passive acoustics, high-resolution imagery from helicopters, drones and satellites, and data collected by observers aboard tuna vessels. The possible reasons to develop auxiliary sources for composite methods include:

(1) Correct any bias in ship-based estimates. As noted above, a drone could operate ahead of a ship, providing a second platform, and data from which corrections for responsive movement and for $g(0)$ may be estimated. Drones or helicopters also could be used to check school sizes and species identifications and proportions in mixed schools, and hence estimate bias in observer group-size estimates by species.

(2) Improve precision of the ship-based estimates.

(3) Develop annual indices of relative abundance from which trends can be estimated at lower cost than for ship-based surveys.

Points (2)–(3) are discussed in more detail below.

Improving precision

The variance on encounter rate is one of the largest components of the variance of the estimated trend for ETP dolphin species (Gerrodette *et al*., 2008). Given this, there are two ways in which precision might be improved.

First, precision might be improved by increasing the number of dolphin group sightings, n, (e.g. see variance decomposition eq. 3.3 of Buckland *et al*., 2004). Increasing n can be done in several ways:

(a) Use high-resolution imagery from a short-range drone, operated from the survey vessel, to increase the effective area surveyed. Detections made by the drone would be added to those made by the vessel, and their location recorded as distance from the ship transect.

(b) Add subsidiary transects in the vicinity of shipboard transects using a short-range drone to increase the total transect length.

(c) Use satellite data to estimate the proportion of dolphin schools detected, P_a. If the ship-based survey estimator is viewed as a Horvitz-Thompson estimator (e.g. eq. 2.17 of Buckland *et al*., 2004), then dolphin group size might be estimated from the ship-based data but P_a from the satellite data. Using the satellite data to estimate P_a would increase n because the imagery represent strip transects. Also, this would avoid the potential problem of $g(0)\neq1$ (Barlow, 2015); having to estimate $g(0)$, which has been assumed to be 1.0 (Gerrodette *et al*., 2008), would increase the variance of the estimated trend by increasing the variance of density (eq. 3.3 of Buckland *et al*., 2004).

In terms of allocation of survey effort with respect to (a)–(b), the most effective allocation to increase n would be to adopt a stratified survey design and allocate proportionally more survey effort to high-density areas. For all three scenarios, experiments on estimation of availability bias for adjusting encounter rate estimates, such as those outlined in Johnson *et al*. (2018), would need to be conducted.

Second, auxiliary sources might be used to spatially ‘extend’ the sparse shipboard survey data such that the time series of shipboard estimates could be combined with a time series of annual auxiliary indices (see below) to improve the precision of the trend estimate. For example, surface drifters or gliders might be used to gather acoustic data, and jointly modelled with ship-based survey data or high-resolution imagery data, using a model-based approach. A similar strategy may allow utilisation of tuna vessel observer data together with research vessel or unmanned aerial survey data. Exploratory analyses using existing tuna vessel observer data and research vessel data may be useful in this regard. It is noted that the tuna vessel observer data have good spatial coverage (e.g. Lennert-Cody *et al*., 2016), and acoustic/high-resolution imagery data might have the same advantage, and thus, spatially-varying calibration against relatively sparse ship-based sightings data would in principle allow conversion to absolute density.

Relative abundance indices based on auxiliary sources

Because of anticipated lower costs of collecting auxiliary data in the future (Johnson *et al*., 2016), auxiliary sources could be used to develop a relative abundance index on a more frequent temporal basis (e.g. annually). This relative index could be combined with estimates from infrequent ship-based surveys, which might allow for more informed management. ETP dolphin species have low population growth rates (e.g. Reilly and Barlow, 1986), therefore the relative index would need to be precise enough to allow detection of small changes over time. Bias in the index would be tolerable as long as the bias was temporally invariant. To evaluate the assumption of temporally-invariant bias, the relative index would need to be compared periodically to a time series of ship-based survey estimates, even if the shipboard survey estimates were only conducted infrequently (e.g. every 5 years). This would only be informative, however, if the precision of the ship-based estimates were high.

Similarities in the existing abundance and the encounter rate trends for four dolphin stocks, two highly involved in the purse-seine fishery on tunas associated with dolphins (northeastern spotted and eastern spinner dolphins), one stock less involved in the fishery (short-beaked common dolphin) and one rarely involved in the fishery (striped dolphin), suggest that an encounter rate-based index may be worth further consideration (Fig. 2). Mean-scaled estimates of abundance and encounter rate show nearly identical overall trends for the northeastern spotted dolphin and the striped dolphin, and similar trends for the eastern spinner dolphin. It would be useful to conduct analyses with the existing survey data to further evaluate options for relative indices, including encounter rate of all dolphins. Relative abundance indices that might be considered are shown in Table 1. However, indices based on encounter rate require the strong assumption that group size is constant (Table 1). If encounter rate indices were to be used, to be precautionary, it might be possible to develop an index of school size that could be compared statistically among surveys to evaluate the assumption that mean group size was constant or had not changed to a meaningful extent.

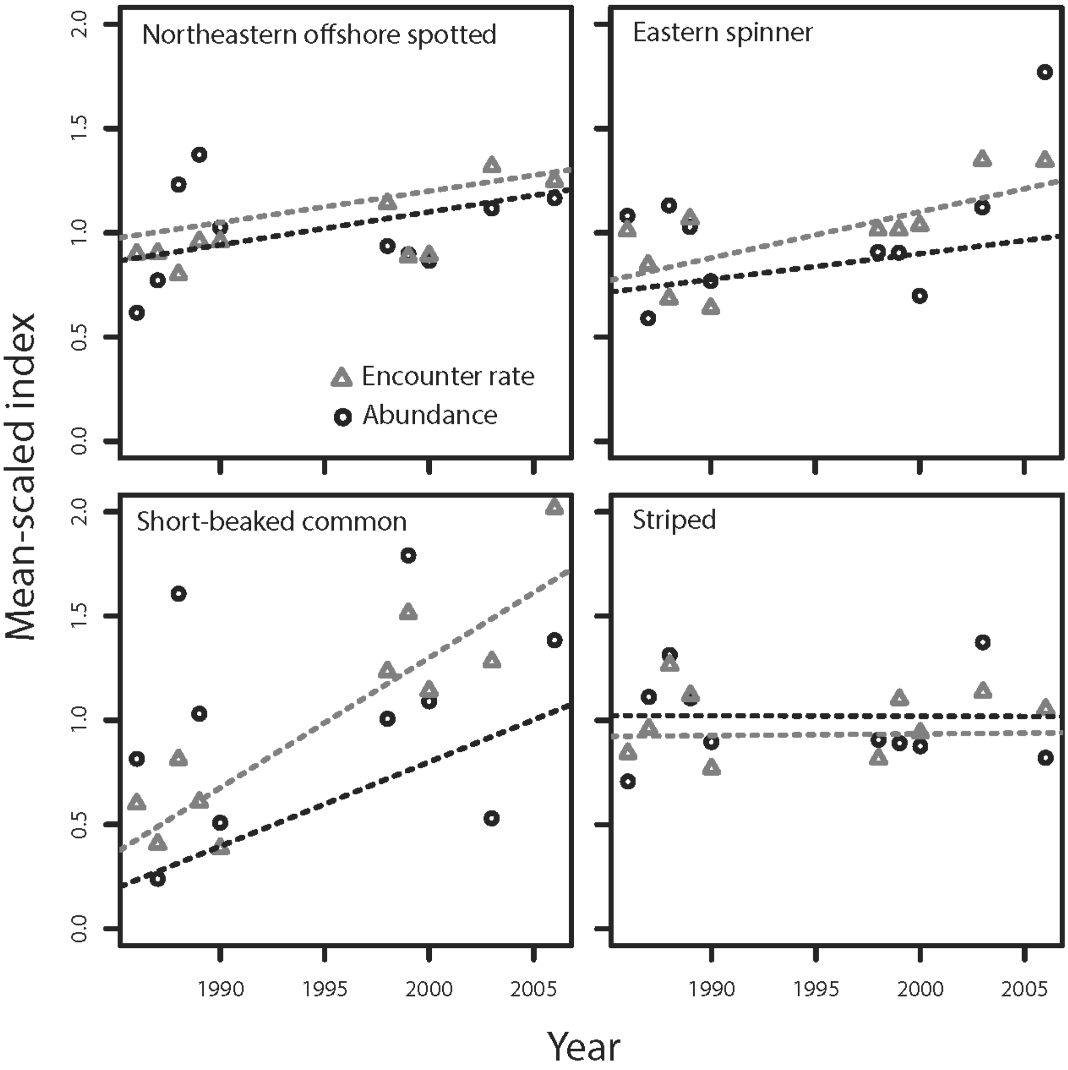


Fig. 2. Mean-scaled indices *versus* year for four dolphin stocks in the ETP. Shown on the y-axis is y/average(y), where y is either encounter rate (grey triangles) or abundance (black circles) (both from tables in Gerrodette *et al*., 2008). The dashed lines are the fitted lines obtained from weighted least squares, with weights = $1/(SE)^2$ (SE = standard error (y), also from tables in Gerrodette *et al*., 2008). The large difference in fitted lines for the short-beaked common dolphin, relative to the point patterns, is due to different weighting of the various data points; i.e. in some instances SE for encounter rate was low but the SE for abundance was high or *vice versa*.

Table 1

Types of relative abundance indices that might be considered for ETP dolphin stocks. 'Encounter rate' refers to encounter rate of dolphin schools, not individual animals. Assumptions regarding constant biases differ with the index type, as well as with the auxiliary data source (see discussion of availability biases in Johnson *et al*., 2018).

Index type	Assumptions	Auxiliary source data
Encounter rate, all dolphins	Species composition of groups and group size are constant. Availability biases constant.	Passive acoustics High-resolution imagery (long-range drone, satellite)
Encounter rate, species	Group size is constant. Availability biases constant.	High-resolution imagery (long-range drone)
Abundance, all dolphins	Species composition of groups is constant. Availability biases constant.	High-resolution imagery (long-range drone)

The similarity of existing abundance and encounter rate trends (Fig. 2) also suggest priorities for research and development for high-resolution imagery. If relative abundance indices based on encounter rate are possible, then developing methods for estimating dolphin group size might be given lower priority than developing methods to identify species. Encounter rate is based on presence/absence of dolphin schools and thus the task of identifying a dolphin school and the species within the school comes down to identifying at least one individual of each species in the school. This should simplify to some extent the problems associated with availability bias.

DISCUSSION

To obtain future abundance estimates for ETP dolphins, the safest and most effective option would be to replicate past research vessel surveys to the extent possible. However, it is not clear that this is the best option. These ship-based surveys are costly, and precision of the abundance estimates is not high. Of course, other approaches would incur development costs, and unforeseen problems may arise. And, unless both research vessel surveys and any new methods provide unbiased estimates of abundance, estimates from a new approach are unlikely to be directly comparable with past estimates. Implementing a new approach together with a research vessel survey would allow the two approaches to be calibrated, but the cost of the exercise would be high, and unless it was repeated over several years, the calibration factor would be imprecisely estimated. A possible alternative would be to implement a less-costly approach (e.g. using drones or satellite images) with the aim of obtaining an annual index of relative abundance, together with an occasional full survey (perhaps using methods closely comparable with past research vessel surveys) to attempt to estimate absolute abundance.

Of the potential new approaches discussed in this review, perhaps the most promising in terms of cost, practicality and precision is the use of high-resolution video taken from long-range drones. Suitable drones have until recently been the preserve of the armed forces, but are now becoming commercially available. A pilot survey followed by annual surveys for perhaps four or five years would allow a new time series of abundance estimates to be generated quickly. If the drones can be flown from land rather than from a ship (which is feasible for military drones, given their range), after initial development costs, this option could have an appreciably lower cost than research vessel surveys, even after accounting for the narrower strip width of high-resolution imagery (Johnson *et al*., 2018). Satellite surveys may be a viable alternative, too, especially if resolution improves to the point that species identification becomes reliable. They would be dependent on obtaining images when sighting conditions are good over a large region, and effective software would be needed for reliable automated search of dolphin schools in vast images.

This review has focused on transect methods for fishery-independent data, however, there are other options for abundance estimation, including mark-recapture methods. Advantages and disadvantages of the use of mark-recapture methods, such as close-kin, for estimating abundance have been discussed for ETP dolphin stocks, and an outline of a pilot study using tuna vessels to assist with recaptures has been presented (Johnson *et al*., 2018). Although mark-recapture methods may be less costly than ship-based line-transect surveys (once research and development phases are completed), problems that may arise when applying these methods to ETP dolphin stocks may be expected from several sources: large population size; heterogeneous and non-independent probabilities of capture and recapture; possible errors in matching marked animals; tag loss; and, difficulty in defining the population that is being estimated, given the potential for movement in and out of the ETP. Buckland and Duff (1989) summarised the problems of estimating numbers of Antarctic minke whales by mark-recapture methods; their population size is similar to that of the main ETP dolphin stocks. The recently proposed close-kin mark-recapture methods (Bravington *et al*., 2016) may increase the number of recaptures, but a large number of tagged individuals would still be required.

The estimates of abundance are used for two main purposes in the management of dolphin stocks in the ETP, and these will determine what attributes of the abundance estimates are most important. The first is to evaluate if the stock has rebuilt from the depleted levels caused by the high levels of historic mortalities (e.g. Lo and Smith, 1986; Wade, 1995). The second is to calculate dolphin mortality limits that are used to ensure that current mortality levels are sustainable (IATTC, 2006). To evaluate the current stock status and whether the population has rebuilt, a population dynamics model is fit to the abundance estimates conditioned on the historical mortalities to reconstruct the population trajectory (Hoyle and Maunder, 2004; Wade *et al*., 2007). The population dynamics model is also used to define a reference point or rebuilding target. The current abundance estimate from the population dynamics model is compared to the reference point to determine the status of the population. The abundance estimates can be treated as indices of relative abundance and the proportionality constant (catchability) can be estimated as a parameter of the model to account for consistent biases in the estimates of abundance, but this will reduce the precision on the estimates from the population dynamics models. Therefore, the abundance estimates can be absolute or relative, but it is preferable that the abundance estimates are absolute and unbiased. However, abundance estimates are only one component of the population dynamics modelling, and the population dynamics models are based on many assumptions that are uncertain (e.g. Hoyle and Maunder, 2004), so the stock status may still be uncertain even if accurate estimates of absolute abundance are available.

The dolphin mortality limits[11] take uncertainty into consideration and lower limits are obtained when the precision of the abundance estimates is poor. Therefore, the precision of the estimates of abundance are an important consideration when choosing a method to estimate abundance. Because historic estimates of abundance have been imprecise, methods have been used to combine multiple survey estimates together to try to improve precision. This is most appropriately done using a population dynamics model since the surveys have been conducted in different years and the population dynamics model automatically takes the changes in abundance over time into account. The population dynamics model also can predict the abundance in years after the last survey estimate of abundance. However, the longer the time since an abundance estimate is available, the less reliable the management benefit of the dolphin mortality limits.

In conclusion, the following recommendations are put forward for methods for estimating abundance of ETP dolphin stock status from dedicated research surveys.

- For immediate management needs, a ship-based survey is the only reliable option. Survey methodology should:
    - ◦ Evaluate, and if necessary, adjust for imperfect detection on the trackline;
    - ◦ Consider an errors-in-variables approach to take the uncertainty of group size estimates into consideration when estimating the detection function;
    - ◦ Incorporate approaches to reduce variance, including: encounter-rate modeling using spatial distance methods, and joint modelling of the detection function with data from multiple species.
- The following pilot studies for development of relative abundance methods that might be considered in composite approaches should be conducted in tandem with any future ship-based survey:
    - ◦ Encounter rate estimation using high-resolution imagery from drones and from satellites;
    - ◦ Encounter rate estimation with passive acoustic drifters.
- For the longer term, it should be a top research priority to develop methods of estimating relative abundance that are less expensive than frequent ship-based surveys so that composite approaches to abundance estimation can be used.

ACKNOWLEDGEMENTS

Special thanks to the participants of the IATTC Workshop on Methods for Monitoring the Status of Eastern Tropical Pacific Ocean Dolphin Populations, 18–20 October 2016, La Jolla, California, for insightful and productive discussion, and specifically to Megan Ferguson for her contribution to survey cost estimates produced by the break-out group on UAS surveys. Funding for the workshop was provided by the European Union and the Pacific Alliance for Sustainable Tuna. We thank Wayne L. Perryman for helpful comments on a previous draft of this manuscript, Lisa Ballance and Toby Garfield for reviewing this manuscript, and two anonymous reviewers for comments that improved this manuscript.

REFERENCES

Anderson, K. and Gaston, K.J. 2013. Lightweight unmanned aerial vehicles will revolutionize spatial ecology. *Front Ecol. Environ.* 11: 138–146. [Available at: *https://doi.org/10.1890/120150*].

Anganuzzi, A. A. and Buckland, S.T. 1989. Reducing bias in estimated trends from dolphin abundance indices derived from tuna vessel data. *Rep. int. Whal. Commn.* 39:323–34.

Au, D. and Perryman, W. 1982. Movement and speed of dolphin schools responding to an approaching ship. *Fish. Bull.* 80:371–9.

Barlow, J. 2015. Inferring trackline detection probabilities, *g*(0), for cetaceans from apparent densities in different survey conditions. *Mar. Mamm. Sci.* 31, 923–43.

Barlow, J. Swartz, S.L., Eagle, T.C., and Wade, P.R. 1995. US marine mammal stock assessments: Guidelines for preparation, background, and a summary of the 1995 assessments. NOAA Tech. Memo. NMFS-OPR-6. 73pp.

Barlow, J., Ballance, L.T. and Forney, K.A. 2011. Effective strip widths for ship-based line-transect surveys of cetaceans. NOAA Tech. Memo. NMFS-SWFSC-484.

Borchers, D.L., Buckland, S.T., Goedhart, P.W., Clarke, E.D. and Hedley, S.L. 1998. Horvitz-Thompson estimators for double-platform line transect surveys. *Biometrics* 54: 1,221–37.

Bravington, M.V., Skaug, H.J. and Anderson, E.C. 2016. Close-kin mark-recapture. *Stat. Sci.* 31: 259–74.

Buckland, S.T. and Anganuzzi, A.A. 1988. Estimated trends in abundance of dolphins associated with tuna in the eastern tropical Pacific. *Rep. int. Whal. Commn.* 38: 411–37.

Buckland, S.T. and Duff, E.I. 1989. Analysis of the Southern Hemisphere minke whale mark-recovery data. pp.121–43. *In*: G.P. Donovan (ed.) *The Comprehensive Assessment of Whale Stocks: the Early Years*. International Whaling Commission, Cambridge.

Buckland, S.T. and Turnock, B.J. 1992. A robust line transect method. *Biometrics* 48: 901–09.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling*. Oxford University Press, Oxford.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2004. *Advanced Distance Sampling*. Oxford University Press, Oxford.

Buckland, S.T., Burt, M.L., Rexstad, E.A., Mellor, M., Williams, A.E. and Woodward, R. 2012. Aerial surveys of seabirds: the advent of digital methods. *J. App. Ecol.* 49: 960–7.

Christie, K.S., Gilbert, S.L., Brown, C.L., Hatfield, M. and Hanson, L. 2016. Unmanned aerial systems in wildlife research: current and future applications of a transformative technology. *Front Ecol Environ.* [Available at: *https://doi.org/10.1002/fee.1281*].

Colefax, A.P., Butcher, P.A. and Kelaher, B.P. 2017. The potential for unmanned aerial vehicles (UAVs) to conduct marine fauna surveys in place of manned aircraft. *ICES J. Mar. Sci.* 75(1): 1–8.

Dizon, A.E., Perrin, W.F. and Akin, P.A. 1994. Stocks of dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific: A phylogeographic classification. NOAA Technical Report NMFS 119. 20pp.

---

[11] The dolphin mortality limits are calculated as 0.1% of the estimate of the minimum abundance estimate (N_{min}) (IATTC, 2006), where N_{min} is defined as the 20th percentile of a log-normal distribution based on an estimate of the number of animals in the stock (Barlow *et al*., 1995).

Forney, K.A., Ferguson, M.C., Becker, E.A., Fiedler, P.C., Redfern, J.V., Barlow, J. Vilchis, I.L. and Balance, L.T. 2012. Habitat-based spatial models of cetacean density in the eastern Pacific Ocean. *Endanger. Species Res.* 16: 113–33.

Fretwell, P.T., Staniland, I.J. and Forcada. J. 2014. Whales from space: counting southern right whales by satellite. *PLOS ONE* 9, e88655.

Gerrodette, T., Perryman, W. and Barlow, J. 2002. Calibrating group size estimates of dolphins in the eastern tropical Pacific Ocean. Southwest Fisheries Science Center Administrative Report LJ-02-08. [Available at: *https://swfsc.noaa.gov/uploadedfiles/divisions/prd/programs/etp_cetacean_assessment/lj_02_08.pdf*].

Gerrodette, T. and Forcada, J. 2005. Non-recovery of two spotted and spinner dolphin populations in the eastern tropical Pacific Ocean. *Mar. Ecol. Prog. Ser.* 291:1–21.

Gerrodette, T., Watters, G., Perryman, W. and Ballance, L. 2008. Estimates of 2006 dolphin abundance in the eastern tropical Pacific, with revised estimates from 1986–2003. NOAA Technical Memorandum NMFS-SWSFC 421: 1–45.

Gerrodette, T., Perryman, W.L. and Oedekoven, C.S. 2018. Accuracy and precision of dolphin school size estimates. Mar. Mamm. Sci., Early view. [DOI: 10.1111/mms.12506].

Glennie, R., Buckland, S.T. and Thomas, L. 2015. The effect of animal movement on line transect estimates of abundance. *PLoS ONE*. 10: e0121333.

Glennie, R., Buckland, S.T., Langrock, R., Gerrodette, T., Ballance, L., Chivers, S., Scott, M. and Perrin, W.F. 2017 Incorporating animal movement into distance sampling. [Available at: *http://research_repository.st-andrews.ac.uk*]

Gordon, C., Kujawa, M., Luttrell, J., MacArthur, D., Robinson-Willmott, J. and Thaxter, C. 2013. High-resolution aerial imaging surveys of marine birds, mammals, and turtles on the US Atlantic Outer Continental Shelf — Utility assessment, methodology recommendations, and implementation tools. Final Report by Normandeau Associates to Bureau of Ocean Energy Management. OCS Study BOEM 2013-01130.

Hall, M. 1998. Ecosystem research and tuna fisheries management: Some key questions. *ICCAT Scientific Papers* 50(2):671–72.

Hammond, P. S. and Laake, J.L. 1983. Trends in estimates of abundance of dolphins (*Stenella* spp. and *Delphinus delphis*) involved in the purse-seine fishery for tunas in the eastern Pacific Ocean, 1977–1981. *Rep. int. Whal. Commn* 33:565–88.

Heinemann, D., Gedamke, J., Oleson, E., Barlow, J., Crance, J., Holt, M., Soldevilla, M. and Van Parijs, S. 2016. Report of the Joint Marine Mammal Commission-National Marine Fisheries Service Passive Acoustic Surveying Workshop, 16–17 April 2015, La Jolla, California. NOAA Tech. Memo. NMFS-F/SPO-164. 107pp.

Hodgson, J.C., Baylis, S.M., Mott, R., Herrod, A., Clarke, R.H. 2016. Precision wildlife monitoring using unmanned aerial vehicles. *Sci Rep.* 6: 22574. [Available at: *https://doi.org/10.1038/srep22574* – PMID: 26986721].

Hewitt, R.P. 1985. Reaction of dolphins to a survey vessel: effects on census data. *Fishery Bulletin* 83:187–93.

Holt, R.S. and Powers, J.E. 1982. Abundance estimation of dolphin stocks involved in the eastern tropical Pacific yellowfin tuna fishery determined from aerial, and ship surveys to 1979. NOAA Technical Memorandum, National Marine Fisheries Service, Southwest Fisheries Science Center 23. 95pp.

Hoyle, S.D. and Maunder, M.N. 2004. A Bayesian integrated population dynamics model to analyze data for protected species. *Anim. Biodivers. Conserv.* 27: 247–66.

IATTC, 1999. Inter-American Tropical Tuna Commission Special Report 11. [Available at: *http://www.iattc.org/PDFFiles2/SpecialReports/SpecialReport11.pdf*].

IATTC, 2006. Report of the Inter-American Tropical Tuna Commission Technical Workshop on Calculating Nmin for the Dolphin Stocks of the Eastern Pacific Ocean. Special Report 14. [Available at: *http://www.iattc.org/PDFFiles2/SpecialReports/IATTC-Special-Report-14ENG.pdf*].

IATTC, 2015a. Updated scientific report on the status of dolphin stocks in the eastern Pacific Ocean. [Available at: *http://www.iattc.org/PDFFiles2/Update-of-Sec-of-Commerce-letter-Apr2015.pdf*].

IATTC, 2015b. Inter-American Tropical Tuna Commission Fishery Status Report 13. [Available at: *http://www.iattc.org/FisheryStatusReportsENG.htm*].

IATTC, 2016. Report on the International Dolphin Conservation Program, Inter-American Tropical Tuna Commission, MOP, October 2016. Document MOP-34-05. [Available at: *http://www.iattc.org/Meetings/Meetings2016/Oct/Pdfs/MOP-34-05-Report-on-IDCP.pdf*].

Johnson, K.F., Punt, A.E. and Lennert-Cody, C.E. (Eds.) 2018. Report of the Inter-American Tropical Tuna Commission Workshop on Methods for Monitoring the Status of Eastern Tropical Pacific Ocean Dolphin Populations, 18–20 October 2016, SWFSC, La Jolla, California. Inter-American Tropical Tuna Commission Special Report 22. [Available at: *http://www.iattc.org/PDFFiles/SpecialReports/_English/No-22-2018-JOHNSON%20KELLI%20FAYE,%20Andre%20E.%20Punt%20and%20Cleridy%20E.%20Lennert%20Cody_Report%20of%20the%20workshop%20on%20methods%20for%20monitoring%20the%20status%20of%20EPT%20dolphin%20populations.pdf*].

Joseph, J. 1994. The tuna-dolphin controversy in the eastern Pacific Ocean: Biological, economic, and political impacts. *Ocean Development and International Law* 25:1–30.

Kinzey, D. and Gerrodette, T. 2001. Conversion factors for binocular reticles. *Mar. Mamm. Sci.* 17: 353–61.

Lennert-Cody, C. E., Buckland, S.T. and Marques, F.C. 2001. Trends in dolphin abundance estimated from fisheries data: A cautionary note. *J. Cetacean Res. Manage.* 3(3):305–19.

Lennert-Cody, C.E. and Scott, M.D. 2005. Spotted dolphin evasive response in relation to fishing effort. *Mar. Mamm. Sci.* 21: 13–28.

Lennert-Cody, C.E., Maunder, M.N., Fiedler, P.C., Minami, M., Gerrodette, T., Rusin, J., Minte-Vera, C.V., Scott, M. and Buckland, S.T. 2016. Purse-seine vessels as platforms for monitoring the population status of dolphin species in the eastern tropical Pacific Ocean: the use of fishing vessels as scientific platforms. *Fish. Res.* 178, 101–13.

Lo, N.C.H. and Smith, T.D. 1986. Incidental mortality of dolphins in the eastern tropical Pacific, 1959–1972. *Fish. Bull.* 84:27–34.

Marine Mammal Commission, 2016. Development of use of UASs by the National Marine Fisheries Service for surveying marine mammals. Marine Mammal Commission, Bethesda, MD, USA. 40pp. [Available from *http://www.mmc.gov*]

McNeely, R.L. The purse seine revolution in tuna fishing. *Pacific Fisherman* 59(7):27–58.

NMFS. 2016. Guidelines for preparing stock assessment reports pursuant to Section 117 of the Marine Mammal Protection Act. [Available at: *http://www.nmfs.noaa.gov/pr/sars/pdf/gamms2016.pdf*].

National Research Council (NRC). 1992. *Dolphins and the Tuna Industry*. National Academy Press, Washington, D.C. 176pp.

Oedekoven, C.S., Buckland, S.T., Marshall, L. and Lennert-Cody, C.E. 2018. Design of a survey for eastern tropical Pacific dolphin stocks. Inter-American Tropical Tuna Commission Document MOP-37-02. [Available at: *http://www.iattc.org/Meetings/Meetings2018/AIDCP-37/PDFs/Docs/_English/MOP-37-02_Design%20of%20a%20survey%20for%20eastern%20tropical%20Pacific%20dolphin%20socks.pdf*]

Oswald, J.N., Rankin, S. and Barlow, J. 2004. The effect of recording and analysis bandwidth on acoustic identification of delphinid species. J. Acoustic Soc. Am. 116: 3178–85.

Oswald, J.N., Rankin, S. and Barlow, J. 2007. A tool for real-time acoustic species identification of delphinid whistles. *J. Acoust. Soc. Am.* 122: 587–95.

Perrin, W.F. 1968. The porpoise and the tuna. *Sea Frontiers* 14:166–74.

Platonov, N.G., Mordvintsev, I.N. and Rozhnov, V.V. 2013. The possibility of using high resolution satellite imagery for detection of marine mammals. *Biol. Bull.* 40: 197–205.

Pollard, J.H., Palka, D. and Buckland, S.T. 2002. Adaptive line transect sampling. *Biometrics* 58: 862–70.

Pryor, K. and Norris, K.S. 1978. The tuna-porpoise problem: behavioral aspects. *Oceanus* 21: 31–7.

Punt, A.E. 2013. Independent review of the eastern Pacific Ocean dolphin population assessment. Inter-American Tropical Tuna Commission Special Report 21. [Available at: *http://www.iattc.org/PDFFiles2/SpecialReports/IATTC-Special-Report-21.pdf*].

Redfern, J.V., Barlow, J., Balance. L.T., Gerrodette, T. and Becker, E.A. 2008. Absence of scale dependence in dolphin-habitat models for the eastern tropical Pacific Ocean. *Mar. Ecol. Prog. Ser.* 363: 1–14.

Reilly, S.B. 1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Mar. Ecol. Prog. Ser.* 66: 1–11.

Reilly, S. B., and Barlow, J. 1986. Rates of increase in dolphin population size. *Fish. Bull.* 84: 527–33.

Reilly, S.B., Donahue, M., Gerrodette, T., Forney, K., Wade, P., Balance, L., Forcada, J., Fiedler, P., Dizon, A., Perryman, W., Archer, F. and Edwards, E. 2005. Report of the scientific research program under the International Dolphin Conservation Program Act. NOAA Tech. Memo. NMFS-SWFSC-372. 100pp.

Schwarz, L. K., Gerrodette, T. and Archer, F.I. 2010. Comparison of closing and passing mode from a line-transect survey of delphinids in the eastern Tropical Pacific Ocean. *J. Cetacean Res. Manage*. 11(3):253–65.

Scott, M.D. and Cattanach, K.L. 1998. Diel patterns in aggregations of pelagic dolphins and tunas in the eastern Pacific. *Mar. Mamm. Sci.* 14, 401–28.

Scott, M.D. and Chivers, S.J. 2009. Movements and diving behavior of pelagic spotted dolphins. *Mar. Mamm. Sci.* 25, 137–60.

Silva, G. 1941. Porpoise fishing. *Pacific Fisherman* 39(3):36.

Smith, T.D. 1981. Line-transect techniques for estimating density of porpoise schools. *J. Wild. Manage.* 45:650–7.

Stapleton, S., LaRue, M., Lecomte, N., Atkinson, S., Garshelis, D., Porter, C. and Atwood, T. 2014. Polar bears from space: assessing satellite imagery as a tool to track Arctic wildlife. *PLoS ONE* 9, e101513.

Thaxter, C.B., Ross-Smith, V.H. and Cook, A.S.C.P. 2016. How high do birds fly? A review of current datasets and an appraisal of current methodologies for collecting flight height data: Literature review. Report No. 666 by the British Trust for Ornithology, Thetford, Norfolk IP24 2PU, UK. [Available from *www.bto.org*].

Wade, P.R. 1995. Revised estimates of incidental of dolphins (Delphinidae) by the purse-seine tuna fishery in the eastern tropical Pacific, 1959–1972. *Fish. Bull.* 93:345–54.

Wade, P.R., Watters, G.M., Gerrodette, T. and Reilly, S.B. 2007. Depletion of spotted and spinner dolphins in the eastern tropical Pacific: modelling hypotheses for their lack of recovery. *Mar. Ecol. Prog. Ser.* 343: 1–14.

Webb, A., Irwin, C. and Elgie, M. 2015. Kincardine Offshore Wind Farm: Final report on aerial surveys from April 2013 to September 2014. Report by HiDef Aerial Surveying Limited to Pilot Offshore Wind Limited. [Available at: *http://pilot-renewables.com/pdf_docs/KOWL_ES_AppendixB_FinalAerialSurveysReport_Issued.pdf*].

Weiß, F., Büttger, H., Baer, J., Welcker, J. and Nehls, G. 2016. Erfassung von Seevögeln und Meeressäugetieren mit dem HiDef Kamerasystem aus der Luft. *Seevögel* 37: 14–21. [In German]

Williams, K.A., Connelly, E.E., Johnson, S.M. and Stenhouse, I.J. (Eds) 2015. *Baseline Wildlife Studies in Atlantic Waters Offshore of Maryland: Final Report to the Maryland Department of Natural Resources and the Maryland Energy Administration.* Report BRI 2015–17, Biodiversity Research Institute, Portland, Maine. 437pp.

Williamson, L.D., Brookes, K.L., Scott, B.E., Graham, I.M., Bradbury, G., Hammond, P.S. and Thompson, P.M. 2016. Echolocation detections and digital video surveys provide reliable estimates of the relative density of harbour porpoises. *Methods in Ecology and Evolution* 7: 762–9.

Yuan, Y., Bachl, F.E., Lindgren, F., Borchers, D. L., Illian, J. B., Buckland, S.T., Rue, H. and Gerrodette, T. 2017. Point process models for spatio-temporal distance sampling data from a large-scale survey of blue whales. *Annals of Applied Statistics* 11: 2270–97.

Sightings of a bowhead whale (*Balaena mysticetus*) in the Gulf of Maine and its interactions with other baleen whales

Corey M. Accardo[1], Laura C. Ganley[1,2], Moira W. Brown[3], Peter A. Duley[4], John C. George[5], Randall R. Reeves[6], Mads Peter Heide-Jørgensen[7], Cynthia T. Tynan[8] and Charles A. Mayo[1]

Contact e-mail: coreyturtle505@gmail.com

ABSTRACT

Bowhead whales generally migrate into high Arctic waters in the summer months and move to lower latitudes in the wintertime. During the 1800s and early 1900s commercial whaling greatly reduced the numbers of bowhead whales in waters adjacent to the North Atlantic Ocean. In recent decades their numbers have been increasing. Thirteen sightings of a bowhead whale were recorded in four areas of the Gulf of Maine in 2012, 2014, and 2017 between latitudes 44°43'N and 41°36'N, far south of the normal range (54°N) for this species. Photographs obtained during these sightings were compared by experienced photo analysts and, based on scarring patterns, the sightings were confirmed to be of the same individual. The bowhead whale was observed alone, in addition to interacting in a social group and engaged in coordinated feeding with other mysticetes at times. The feeding and social behaviour of the bowhead whale was typical for the species but well south of its normal Arctic waters range and in the absence of conspecifics.

KEYWORDS: BOWHEAD WHALE; ATLANTIC OCEAN; FEEDING; PHOTO-ID; GULF OF MAINE

The bowhead whale (*Balaena mysticetus*) is an ice-adapted species with a circumpolar distribution in Arctic waters (Shelden and Rugh, 1995). Bowhead whales are generally assessed as four separate geographical populations: two in the northern Atlantic (the Eastern Canada-West Greenland stock and the Svalbard-Spitsbergen/Barents Sea stock) and two in the northern Pacific (the Bering-Chukchi-Beaufort Seas stock and the Okhotsk Sea stock) (IWC, 2009; Rugh and Shelden, 2009; Ferguson *et al.*, 2010; Lydersen *et al.*, 2012; Laidre *et al.*, 2015). This paper describes multiple sightings of an individual bowhead whale far south of its present-day range and its interactions with two other mysticete species in the western North Atlantic. This bowhead whale was observed on 13 separate occasions during 2012, 2014, and 2017 in four areas of the Gulf of Maine (GOM) between latitudes 44°43'N and 41°36'N (Fig. 1).

These are the southernmost confirmed sightings of a bowhead whale in the western North Atlantic, approximately 1,800km (~1,000 nautical miles) from the southern extent of the closest population's range, but they are not the only records of bowhead whales south of the known present-day range. Four dead bowhead whales were documented in Newfoundland, Canada (one each year in 1998, 2005, 2008, and 2014) as far south as 47°14'N (Ledwell *et al.*, 2007, 2014; Ledwell and Huntington, 2009). A small live individual (~4m) judged to have been a calf of the year was observed in Trinity Bay, Newfoundland in August 2014 (47°35'N; Ledwell *et al.*, 2014). There are also several verified records in the eastern North Atlantic Ocean, as follows (all body lengths estimated by eye and reported by the observer): one whale (~8m long) observed in February 2015 off Isles of Scilly, Cornwall, England (49°57'N; James, 2015); a set of three sightings, thought to be of the same ~7m individual (de Boer *et al.*, 2017), in May 2016 near Bénodet, Brittany, France (47°51'N; Anonymous, 2016), a week later, near Long Rock, Cornwall, England (50°06'N; de Boer, 2016), and finally in late May 2016 skim feeding outside the Carlingford Lough mouth, Ireland (54°00'N; Whooley, 2016); one animal possibly entangled in fishing gear seen on two days in March 2017 off the Flemish coast near Middelkerke, Belgium (51°11'N; Andersen, 2017); and another animal seen almost two weeks later in Dutch waters off of Vlissingen, Netherlands (51°26'N'; Pieters, 2017). The majority of these eastern North Atlantic sightings were made near shore (some of them from shore). A vessel log dated April 1998 from the central North Atlantic describes the sighting of a small group of bowhead whales (43°23'N, 38°24'W; Anonymous, 1999); but in the absence of supporting photographic, genetic, or other documentation this record must remain unconfirmed. The southernmost confirmed sighting of a bowhead whale anywhere was in the North Pacific in Osaka Bay, Japan at 34°32'N in June 1969 (Nishiwaki and Kasuya, 1970).

Bowhead whales can be individually identified based on unique marks and scarring patterns (Rugh and Braham, 1992; Koski *et al.*, 1988). Although the individual documented in the GOM was not particularly well-marked, aerial and vessel photographs examined by experienced

---

[1] *Center for Coastal Studies, 5 Holway Avenue, Provincetown, Massachusetts 02657, USA.*
[2] *University of Massachusetts, Boston, 100 Morrissey Boulevard, Boston, Massachusetts 02125, USA.*
[3] *Anderson Cabot Center for Ocean Life at the New England Aquarium, Central Wharf, Boston, Massachusetts 02110, USA.*
[4] *Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA.*
[5] *Department of Wildlife Management, North Slope Borough, P.O. Box 69, Barrow, Alaska, 99723, USA.*
[6] *Okapi Wildlife Associates, 27 Chandler Lane, Hudson, QC J0P 1H0, Canada.*
[7] *Greenland Institute of Natural Resources, Greenland Representation, Strandgade 91, 2, DK-1401, Copenhagen K, Denmark.*
[8] *Associated Scientists at Woods Hole, 3 Water Street, Woods Hole, Massachusetts, 02543, USA.*

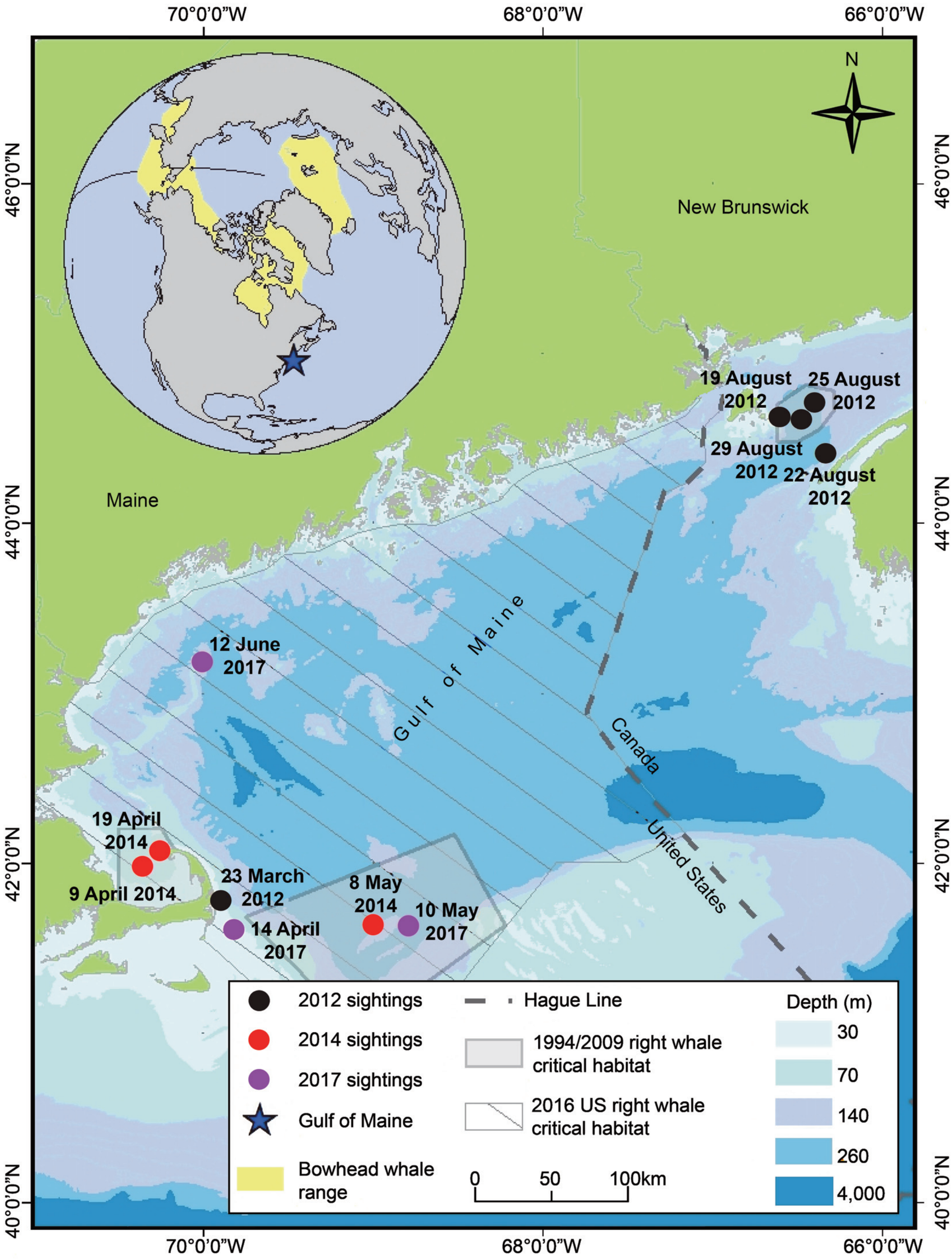


Fig. 1. Information on bowhead whale sightings in the Gulf of Maine during 2012, 2014 and 2017. The inset map displays the typical range of bowhead whale stocks (IUCN, 2012) in relation to the Gulf of Maine.

bowhead whale and North Atlantic right whale (*Eubalaena glacialis)* photo analysts and judged by scarring patterns, including scars that appear to be from a prior fishing gear entanglement (Philo *et al*., 1992; Knowlton *et al*., 2012; George *et al*., 2017), confirmed that all sufficiently photographed sightings were of the same individual bowhead whale.

The first sighting of the bowhead whale in the GOM was on 23 March 2012, 12km (7 nautical miles) northeast of Chatham, Massachusetts, USA. The bowhead whale was in a social group with four right whales (Figs 1 and 2, Table 1). This type of aggregation, known as a surface active group (SAG), is observed in both species and has been described as involving copulatory behaviour (Everitt and Krogman, 1979; Kraus and Hatch, 2001). The main conception season of bowhead whales (in Alaskan waters) is late winter and spring (Koski *et al*., 1993; Reese *et al*., 2001), but SAGs of bowhead whales may involve 'practice mating' behaviour or play a role in social bonding, as is believed to be the case with right whales (Kraus and Hatch, 2001; Parks *et al*., 2007). All of the right whales in this SAG were identified from the North Atlantic Right Whale Consortium Identification Database to be males, most of them juveniles (Right Whale Consortium, 2015). There is no data-derived estimate of the body size of the Gulf of Maine bowhead whale but its length relative to known-aged right whales was judged to be approximately 10m. Such a body length, this bowhead whale's head profile, and its lack of markings suggest that it was a large sub-adult

Fig 2. A bowhead whale and North Atlantic right whales in a surface active group during the 23 March 2012 sighting, east of Cape Cod. The rostrum, chin, and back of the bowhead whale are visible at the top of the image along with the associated four right whales below. [Center for Coastal Studies Image, NOAA Permit 14603]

Table 1

Details for the bowhead whale sightings in the Gulf of Maine during 2012, 2014 and 2017.

Date	Location	Position	Behaviour	Observer	Association with other species
23 Mar. 2012	East of Cape Cod	41°46'N; 69°53'W	Social activity	Center for Coastal Studies	Right whales
19 Aug. 2012	Bay of Fundy	44°36'N; 66°28'W	Mud on head	New England Aquarium	–
22 Aug. 2012	Bay of Fundy	44°24'N; 66°19'W	–	Pirate's Cove Whale Watch	–
25 Aug. 2012	Bay of Fundy	44°42'N; 66°23'W	–	Coastwise Consulting	–
25 Aug. 2012	Bay of Fundy	44°43'N; 66°22'W	–	Coastwise Consulting	–
29 Aug. 2012	Bay of Fundy	44°37'N; 66°35'W	–	Whales-n-Sails Adventure Ltd	–
09 Apr. 2014	Cape Cod Bay	41°58'N; 70°20'W	Skim feeding	Center for Coastal Studies	–
19 Apr. 2014	Cape Cod Bay	42°04'N; 70°14'W	Echelon skim feeding	NE Fisheries Science Center	Right whales
19 Apr. 2014	Cape Cod Bay	42°05'N; 70°12'W	Skim feeding	Center for Coastal Studies	–
08 May 2014	Great South Channel	41°37'N; 68°59'W	Coordinated skim feeding	NE Fisheries Science Center	Sei whales
14 Apr. 2017	Great South Channel	41°36'N; 69°49'W	Coordinated skim feeding	NE Fisheries Science Center	Sei whales
10 May 2017	Great South Channel	41°37'N; 68°47'W	Skim and subsurface feeding	NE Fisheries Science Center	–
12 Jun. 2017	Jeffreys Ledge	43°11'N; 70°00'W	–	Granite State Whale Watch, Blue Ocean Society	–

(Koski *et al*., 1993; Sironi *et al*., 2005). Bowhead whales attain sexual maturity when they are 12–14m in length (Koski *et al*., 1993; George *et al*., 1999). They are long-lived animals (George and Bockstoce, 2008) and are difficult to age from body length alone (Lubetkin *et al*., 2008).

Sightings of a bowhead whale were reported on four separate days from 19 to 29 August 2012 in the Bay of Fundy (located between New Brunswick and Nova Scotia, Canada). Photographic confirmation of the species identification is available for three of the sightings and for two of the sightings photographs show that it was the same individual as documented earlier in the year in the GOM. While right whales were present in the lower Bay of Fundy at the time, the bowhead whale was observed alone and not in close association with any other mysticetes (Fig. 1, Table 1).

The Gulf of Maine bowhead whale was re-sighted, almost two years after its initial sighting in the southern GOM, on two days, 9 and 19 April 2014, in the vicinity of Cape Cod Bay (CCB) and once on 8 May 2014 in the Great South Channel (GSC), 80km (43 nautical miles) east of Cape Cod (Fig. 1, Table 1). Photographs confirmed the first sighting to species and the later sightings as matches to the 2012 individual. During these sightings the bowhead whale was observed feeding at or near the surface, either alone or among right whales or sei whales (*Balaenoptera borealis*). The times when this bowhead whale was observed coincided with the peak season in which right whales typically form feeding aggregations (April in CCB: Hamilton and Mayo, 1990; Nichols *et al.,* 2008; May in GSC: Wishner *et al*., 1988; Kenney *et al*., 1995; Pershing *et al*., 2009). During the 19 April 2014 sighting, the bowhead whale was participating in 'echelon skim feeding'[9] with at least one right whale within an aggregation of surface-feeding right whales (Fig. 3) of both sexes and which included a range of age classes (Right

---

[9] Whales swimming at the surface with at least part of the rostrum exposed above the surface are considered to be skim feeding (Würsig *et al*., 1989); if they are moving in a tightly coordinated 'V' formation, they can be described as 'echelon skim feeding' (Würsig *et al*., 1985; Fish *et al*., 2013).

Fig. 3. A bowhead whale echelon skim feeding with a North Atlantic right whale during the 19 April 2014 sighting, northeast of Cape Cod. The bowhead whale is at the bottom of the image, with the left side of its head clearly visible above the surface and its back and flukes visible below the surface. [Northeast Fisheries Science Center Image, NOAA Permit 17355]

Fig. 4. A bowhead whale (top right) skim feeding in close proximity to a sei whale and a North Atlantic right whale during the 14 April 2017 sighting. The bowhead whale has its rostrum above the surface and the rest of the head and body are visible below the surface. [Northeast Fisheries Science Center Image, NOAA Permit 17355]

Whale Consortium, 2015). During the 8 May 2014 sighting the bowhead whale was feeding alone and participating in coordinated skim feeding[10] with two sei whales within an aggregation of feeding right whales and sei whales.

Almost three years after the last sighting mentioned above, the Gulf of Maine bowhead whale was re-sighted on two days, 14 April and 10 May 2017, in the GSC, and on 12 June 2017 near Jeffreys Ledge (Fig. 1, Table 1). Photographed markings on the 2017 individual confirmed all sightings as matches to the 2012/2014 Gulf of Maine bowhead whale. During the first two sightings the bowhead whale was observed high-skim and subsurface feeding in close proximity to right whales and coordinated skim feeding with sei whales (Fig. 4). During the 12 June 2017 sighting the bowhead whale was in the vicinity of several fin whales (*Balaenoptera physalus*) and one humpback whale (*Megaptera novaeangliae*); the behaviour of the bowhead whale, characterised by dives of approximately 20 minutes and random surfacings, is consistent with subsurface feeding but as this was a vessel-based sighting, such an interpretation cannot be considered definitive.

---

[10] If multiple whales, during skim feeding, are turning at the same time while directly in line or side by side they can be described as ‘coordinated skim feeding’ (Würsig *et al.*, 1985).

Zooplankton collected by surface and oblique conical net tows (standard 333-micrometer mesh) and vertical pumps as part of a regular right whale habitat monitoring program in CCB on 9 April 2014, and during the subsequent two weeks, consisted primarily of the copepod *Calanus finmarchicus*. During the 19 April 2014 sighting, a zooplankton surface dip sample collected in the feeding path of the bowhead whale indicated that it was feeding on a mixture of mainly calanoid copepods, *C. finmarchicus* (72%) and *Pseudocalanu*s spp. (25%) (Burke and Cunningham, 2014). In the Arctic, calanoid copepods are among the most important prey of bowhead whales (Lowry, 1993; Finley, 2000; Laidre *et al.*, 2007; Pomerleau *et al.*, 2011; Walkusz *et al.*, 2012; Heide-Jørgensen *et al.*, 2013) and the same is true of right and sei whales in the North Atlantic (Mayo and Marx, 1990; Wishner *et al.*, 1995; Baumgartner and Fratantoni, 2008; Baumgartner *et al.*, 2011).

Although acoustic recordings were obtained in the vicinity of the CCB bowhead whale sightings, all of the balaenid calls detected were attributed to right whales and no bowhead whale vocalizations could be distinguished (C.W. Clark, pers. comm.[11]). Bowhead whales, like many large cetaceans, produce a variety of sounds (Clark and Johnson, 1984; Würsig and Clark, 1993; Johnson *et al.*, 2015). Some of the bowhead whale sightings in 2014 were within range of an array of acoustic buoys specifically deployed to record low-frequency (< 1000Hz) baleen whale sounds. Recordings from those buoys were analysed by specialists on days when the bowhead whale was seen in the vicinity of CCB. The simple, low-frequency, frequency-modulated calls of North Atlantic right whales and humpback whales, which also regularly occupy these waters during the same season, are similar to bowhead whale calls (Clark and Clark, 1980; Clark and Johnson, 1984; Würsig and Clark, 1993; Baumgartner *et al.*, 2013); however, the structure and other features of bowhead whale vocalizations are sufficiently distinct that they can usually be distinguished from those of the other species (Stafford *et al.*, 2012).

All sightings of the bowhead whale in the GOM were made during systematic aerial and vessel surveys targeting other species, particularly right whales, or during whale watching tourism cruises (Fig. 1, Table 1). At the time of the 2012/2014 sightings most of the Gulf of Maine bowhead whale sightings were within right whale critical habitat areas (Fig. 1), two legally designated in US waters (US Federal Register, 1994) and one identified in Canadian waters (Brown *et al.*, 2009; Fisheries and Oceans Canada, 2014). Since the time of these sightings the right whale critical habitat in the northeastern US was expanded (US Federal Register, 2016), encompassing all of the locations of the bowhead whale sightings in US waters of the GOM.

Efforts to match this individual bowhead whale to all known photographic catalogues from the range of each population have yielded no positive results to date. Attempts to obtain a skin biopsy for genetic analysis were unsuccessful. During all documented sightings the animal appeared to be healthy and in good condition (Pettis *et al.*, 2004; Hunt *et al.*, 2013). Sighting and life history data from the North Atlantic Right Whale Consortium Identification and Sightings Databases (RWC, 2015) were examined but no consistent association was found between the bowhead whale and the various individually identified right whales. While regular surveys have continued in all areas where the bowhead whale was observed, there have been no further sightings of this animal to date.

Bowhead whales and right whales do not typically occur in the same areas at the same time, however some geographical overlap in their range has been noted in historical whaling records (McLeod *et al.*, 2008; Reeves *et al.*, 2008), and at least one brief observation has been reported of a North Pacific right whale (*Eubalaena japonica*) and bowhead whales occupying the same habitat at the same time in the Okhotsk Sea (Shpak and Paramonov, 2012). We are not aware of any previous reports of interactions between bowhead whales and sei whales but North Atlantic right whales and sei whales are frequently observed in the same habitat (Mitchell *et al.*, 1986; Horwood, 1987; COSEWIC, 2003; Baumgartner *et al.*, 2011).

Bowhead whales were occasionally taken by whalers or found stranded in both the North Pacific and North Atlantic in the mid-50s°N latitude (Bockstoce *et al.*, 2005; McLeod, 2008; Higdon, 2010). Their normal range in the western North Atlantic, and specifically in the Gulf of St. Lawrence, appears to have extended as far south as 48°N during the late 16th century, a period of climatic cooling often referred to as the Little Ice Age (McLeod *et al.*, 2008). In very recent years there has been a shift in the distribution and density of North Atlantic right whales away from areas where they were regularly observed from the 1980s to early 2000s (Burke and Cunningham, 2014; Khan *et al.*, 2014), and this has coincided with an increase of sightings in latitudes somewhat further north to at least 48°40’N (Khan *et al.*, 2014; New England Aquarium and Northeast Fisheries Science Center unpublished data, 2015 and 2016), still well south of what has been regarded as the southern limit of the bowhead whale’s current range (Moore and Reeves, 1993; Mellinger *et al.*, 2011).

Bowhead whale sightings in the GOM, as well as in Newfoundland and European waters in recent years, together with the changes observed in North Atlantic right whale distribution and density, are of great interest as they may represent the early stages of shifting ranges. Populations of bowhead whales and North Atlantic right whales had been decimated by commercial whaling by the early 20th century (Reeves *et al.*, 2007; Higdon, 2010). Since then the populations of both species have increased (Heide-Jørgensen *et al.*, 2007; Boertmann *et al.*, 2015; Pettis and Hamilton, 2015) although in recent years North Atlantic right whales have been experiencing a decline in overall population health and fecundity (Kraus *et al.*, 2016, Pace *et al.*, 2017). In the last decade, sightings of North Atlantic right whales (Jacobsen *et al.*, 2004; Hamilton *et al.*, 2007; Silva *et al.*, 2012) and bowhead whales (Heide-Jørgensen *et al.*, 2007; 2011) have been documented outside the limits of their assumed ranges. While the feeding and social behaviour of the Gulf of Maine bowhead whale was typical of the species, its occurrence south of the species’ supposed range and its associations with right whales and sei whales were unusual.

---

[11] Christopher W. Clark, Bioacoustics Research Program, Cornell Laboratory of Ornithology, Cornell University, Ithaca, NY 14850, USA. 15 March 2015.

ACKNOWLEDGMENTS

We sincerely appreciate and thank the following colleagues for their contributions: Mark Baumgartner, Christine Callaghan, Joe Chronic, Phil Clapham, Chris Clark, Tim Cole, Genevieve Davis, Steve Ferguson, Jennifer Gatzke, Jonathan Gwalthney, Allison Henry, Christy Hudak, Bob Kenney, Christin Khan, Scott Landry, Elizabeth Larson, Wayne Ledwell, Julie Mocklin, Laurie Murison, Sofie Van Parijs, Jessica Peers, Heather Pettis, The Right Whale Consortium, Jooke Robbins, Dave Rugh, Dianna Schulte, Chris Slay, Olga Shpak, Kate Stafford, Melanie White, the data collection Survey Teams, Barb Tudor, and Linda Vate Brattstrom. Also, we greatly appreciate the pre-submission reviews by Lois Harwood, Fisheries and Oceans Canada and Peter Corkeron, Northeast Fisheries Science Center, along with the anonymous reviewers whose comments helped to improve and finalise this manuscript.

North Atlantic right whale research in the United States was conducted under NOAA/NMFS Scientific Research Permit Numbers: 14603, 17355, and 932-1905; and in Canada under Fisheries and Oceans Canada license number 325863.

REFERENCES

Andersen, L. 2017. Bowhead whale seen offshore of Belgian coast potentially hampered by net. *The Brussels Times, Tuesday 4 April 2017*. [Available from: *https://www.brusselstimes.com/belgium/7937*].

Anonymous. 1999. Rare whales from the Arctic sighted in mid-Atlantic. *Mar. Obs.* 69:180–82.

Anonymous. 2016. Un cétacé en goguette devant la grande plage. *Le Télégramme*. [Retrieved from: *www.letelegramme.fr*. 10 May 2016; In French].

Baumgartner, M.F. and Fratantoni, D.M. 2008. Diel periodicity in both sei whale vocalization rates and the vertical migration of their copepod prey observed from ocean gliders. *Limnol. Oceanogr.* 53:2197–209.

Baumgartner, M.F., Lysiak, N.S.J., Schuman, C., Urban-Rich, J. and Wenzel, F.W. 2011. Diel vertical migration behavior of *Calanus finmarchicus* and its influence on right and sei whale occurrence. *Mar. Ecol. Prog. Ser.* 423:167–84.

Baumgartner, M.F., Fratantoni, D.M., Hurst, T.P., Brown, M.W., Cole, T.V., Van Parijs, S.M. and Johnson, M. 2013. Real-time reporting of baleen whale passive acoustic detections from ocean gliders. *J. Acoust. Soc. Am.* 134:1814–23.

Bockstoce, J.R., Botkin, D.B., Philp, A., Collins, B.W. and George, J.C. 2005. The geographic distribution of bowhead whales, *Balaena mysticetus*, in the Bering, Chukchi, and Beaufort Seas: Evidence from whaleship records, 1849–1914. *Mar. Fish. Rev.* 67(3):1–43.

Boertmann, D., Kyhn, L.A., Witting, L. and Heide-Jørgensen, M.P. 2015. A hidden getaway for bowhead whales in the Greenland Sea. *Polar Biol.* 38:1315–19.

Brown, M.W., Fenton, D., Smedbol, K., Merriman, C., Robichaud-Leblanc, K. and Conway, J.D. 2009. Recovery Strategy for the North Atlantic Right Whale (*Eubalaena glacialis*) in Atlantic Canadian Waters. Species at Risk Act Recovery Strategy Series, Fisheries and Oceans Canada. vi + 66pp. [Available from *https://www.registreclep-sararegistry.gc.ca/virtual_sara/files/plans/rs_north_atl_right_whale_0609_e.pdf*].

Burke, E. and Cunningham, S. 2014. Massachusetts Large Whale and Sea Turtle Conservation Program, Final Report: August 1, 2013–July 31, 2014. Massachusetts Division of Marine Fisheries, National Oceanic and Atmospheric Administration Report. 12pp. [Available from the author: *erin.burke@state.ma.us*].

Clark, C.W. and Clark, J.M. 1980. Sound playback experiments with southern right whales (*Eubalaena australis*). *Science* 207(4431):663–5.

Clark, C.W. and Johnson, J.H. 1984. The sounds of the bowhead whale, *Balaena mysticetus,* during the spring migrations of 1979 and 1980. *Can. J. Zool.* 62:1436–41.

COSEWIC. 2003. Assessment and Status Report on the Sei Whale *Balaenoptera borealis* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa. vii + 27pp. [Available from: *http://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/sr_sei_whale_e.pdf]*.

de Boer, M.N. 2016. An account of the bowhead whale encountered by Dr. Marijke de Boer. Marine Discovery, Penzance, Cornwall. [Retrieved from: *www.marinediscovery.co.uk/blog*. 18 May 2016].

de Boer, M.N., Jones, D. and Jones, H. 2017. Ocean Wanderers: Extralimital encounters with bowhead whales (*Balaena mysticetus*) in Temperate European shallow waters. *Aquat. Mamm*. 43(3):279–88.

Everitt, R.D. and Krogman, B.D. 1979. Sexual behavior of bowhead whales observed off of the north coast of Alaska. *Arctic* 32:277–80.

Ferguson, S.H., Dueck, L., Loseto, L.L. and Luque, S.P. 2010. Bowhead whale *Balaena mysticetus* seasonal selection of sea ice. *Mar. Ecol. Prog. Ser.* 411:285–97.

Finley, K.J. 2000. Natural history and conservation of the Greenland whale, or bowhead, in the northwest Atlantic. *Arctic* 54:55–75.

Fish, F.E., Goetz, K.T., Rugh, D.J. and Brattström, L.V. 2013. Hydrodynamic patterns associated with echelon formation swimming by feeding bowhead whales (*Balaena mysticetus*). *Mar. Mamm. Sci.* 29:498–507.

Fisheries and Oceans Canada. 2014. Recovery Strategy for the North Atlantic Right Whale (*Eubalaena glacialis*) in Atlantic Canadian Waters [Final]. Species at Risk Act Recovery Strategy Series.Fisheries and Oceans Canada. vii + 68 pp. [Available at *https:// www.sararegistry.gc.ca*

George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T. and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic acid racemization. *Can. J. Zool.* 77:571–80.

George, J.C. and Bockstoce, J.R. 2008. Two historical weapon fragments as an aid to estimating the longevity and movements of bowhead whales. *Polar Biol.* 31:751–4.

George, J.C., Sheffield, G., Reed, D.J., Tudor, B., Stimmelmayr, R., Person, B.T. and Suydam, R. 2017. Frequency of injuries from line entanglements, killer whales, and ship strikes on Bering-Chukchi-Beaufort Sea bowhead whales. *Arctic* 70(1):37–46.

Hamilton, P.K. and Mayo, C.A. 1990. Population characteristics of right whales (*Eubalaena glacialis*) observed in Cape Cod and Massachusetts Bays, 1978–1986. *Rep. int. Whal. Commn* (special issue) 12:203–8.

Hamilton, P.K., Knowlton, A.R. and Marx, M.K. 2007. Right whales tell their own stories: The photo-identification catalog. pp.75–104 *In:* S.D. Kraus and R.M. Rolland (Eds.) *The Urban Whale: North Atlantic Right Whales at the Crossroads*. Harvard University Press, Cambridge, Massachusetts, 543pp.

Heide-Jørgensen, M.P., Laidre, K.L., Borchers, D., Samarra, F. and Stern, H. 2007. Increasing abundance of bowhead whales in West Greenland. *Biol. Lett.* 3:577–80.

Heide-Jørgensen, M.P., Laidre, K.L., Quakenbush, L.T. and Citta, J.J. 2011. The Northwest Passage opens for bowhead whales. *Biol. Letters* 8:270–3.

Heide-Jørgensen, M.P., Laidre, K.L., Nielsen, N.H., Hansen, R.G. and Røstad, A. 2013. Winter and spring diving behavior of bowhead whales relative to prey. *Anim. Biotelem.* 1:1–13.

Higdon, J. 2010. Commercial and subsistence harvests of bowhead whales (*Balaena mysticetus*) in eastern Canada and West Greenland. *J. Cetacean Res. Manage.* 11:185–216.

Horwood, J. 1987. *The Sei Whale: Population Biology, Ecology and Management*. Croom Helm, London, New York, Sydney. [xi]+ 375pp.

Hunt, K.E., Moore, M.J., Rolland, R.M., Kellar, N.M., Hall, A.J., Kershaw, J., Raverty, S.A., Davis, C.E., Yeates, L.C., Fauquier, D.A., Rowles, T.K. and Kraus, S.D. 2013. Overcoming the challenges of studying conservation physiology in large whales: a review of available methods. *Conserv. Physiol.* 1:1–24.

International Union for Conservation of Nature (IUCN). 2012. *Balaena mysticetus*. *The IUCN Red List of Threatened Species*. Version 2015.2. [Available at *http://www.iucnredlist.org*, downloaded 2017]

International Whaling Commission. 2009. Report of the Scientific Committee. Annex F. Report of the sub-committee on bowhead, right and gray whales. *J. Cetacean Res. Manage.* (*Suppl.*) 11:169–92.

James, K. 2015. Rare whale – A first for Britain! *Sea Watch Foundation*. [Available from: *www.seawatchfoundation.org*. Downloaded 27 Feb 2015].

Jacobsen, K., Marx, M. and Øien, N. 2004. Two-way trans-Atlantic migration of a North Atlantic right whale (*Eubalaena glacialis). Mar. Mamm. Sci.* 20:161–6.

Johnson, H.D., Stafford, K.M., George, J.C., Ambrose, W.C. and Clark, C.W. 2015. Song sharing and diversity in the Bering-Chukchi-Beaufort population of bowhead whales (*Balaena mysticetus*), spring 2011. *Mar. Mamm. Sci.*: 31:902–22.

Kenney, R.D., Winn, H.E. and Macaulay, M.C. 1995. Cetaceans in the Great South Channel, 1979–1989: right whale (*Eubalaena glacialis*). *Cont. Shelf Res.* 15(4–5):385–414.

Khan, C., Duley, P., Henry, A., Gatzke, J. and Cole, T. 2014. North Atlantic Right Whale Sighting Survey (NARWSS) and Right Whale Sighting Advisory System (RWSAS) 2013 Results Summary. US Department of Commerce, Northeast Fisheries Science Centre Reference Doc. 14–11. 10pp. [Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026 or online at: *http://www.nefsc.noaa.gov/publications/*]

Knowlton, A.R., Hamilton, P.K., Marx, M.K., Pettis, H.M. and Kraus, S.D. 2012. Monitoring North Atlantic right whale *Eubalaena glacialis* entanglement rates: a 30 yr retrospective. *Mar. Ecol. Prog. Ser.* 466:193–302.

Koski, W.R., Miller, G.W. and Davis, R.A. 1988. The potential effects of tanker traffic on the bowhead whale in the Beaufort Sea. Environmental Studies 58. Report from LGL Limited, King City, Ontario, for the Department of Indian Affairs and Northern Development, Hull, Quebec. Springfield, Virginia: National Technical Information Service. NTIS MIC-90-04552. 150pp.

Koski, W.R., Davis, R.A., Miller, G.W. and Withrow, D.E. 1993. Reproduction. pp.239–74 *In:* J.J. Burns, J.J. Montague and C.J. Cowles (eds.) *The Bowhead Whale*. Special Publication Number 2, Society for Marine Mammalogy, Lawrence, Kansas, i–xxxvi+787pp.

Kraus, S.D. and Hatch, J.J. 2001. Mating strategies in the North Atlantic right whale (*Eubalaena glacialis*). *J. Cetacean Res. Manage. (special issue)* 2:237–44.

Kraus, S.D., Kenney R.D., Mayo C.A., McLellan W.A., Moore M.J. and Nowacek, D.P. 2016. Recent scientific publications cast doubt on North Atlantic right whale future. *Front. Mar. Sci.* 3:137.

Laidre, K.L., Heide-Jørgensen, M.P. and Nielsen, T.G. 2007. Role of the bowhead whale as a predator in West Greenland. *Mar. Ecol. Prog. Ser.* 346:285–97.

Laidre, K.L., Stern, H., Kovacs, K.M., Lowry, L., Moore, S.E., Regehr, E.V., Ferguson, S.H., Wiig, O., Boveng, P., Angliss, R.P., Born, E.W., Litovka, D., Quakenbush, L., Lydersen, C., Vongraven, D. and Ugarte, F. 2015. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conserv. Biol.* 29(3):724–37.

Ledwell, W., Benjamins, S., Lawson, J. and Huntington, J. 2007. The most southerly record of a stranded bowhead whale, *Balaena mysticetus*, from the western North Atlantic Ocean. *Arctic* 80:17–22.

Ledwell, W. and Huntington, J. 2009. Incidental entrapments in fishing gear and strandings reported to the Whale Release and Strandings Group in Newfoundland and Labrador and a summary of the Whale Release and Strandings Program during 2008. Report to the Department of Fisheries and Oceans, Canada-Newfoundland and Labrador Region. 30pp. [Available from: the author: *caplinbay@nl.rogers.com*].

Ledwell, W., Huntington, J. and Sacrey, E. 2014. Incidental entrapments and entanglements of cetaceans and leatherback sea turtles, strandings, ice entrapments reported to the Whale Release and Strandings Group in Newfoundland and Labrador, and a summary of the Whale Release and Strandings Program during 2014. Report to the Department of Fisheries and Oceans, Canada-Newfoundland and Labrador Region. 23 pp. [Available from the author, *caplinbay@nl.rogers.com*]

Lowry, L.F. 1993. Foods and feeding ecology. pp.201–238 *In:* J.J. Burns, J.J. Montague and C.J. Cowles (Eds.) *The Bowhead Whale*. Special Publication Number 2, Society for Marine Mammalogy, Lawrence, Kansas, i–xxxvi+ 787pp.

Lubetkin, S.C., Zeh, J.E., Rosa, C. and George, J.C. 2008. Age estimation for young bowhead whales (*Balaena mysticetus)* using annual baleen growth increments. *Can. J. Zool.* 86:525–38.

Lydersen C., Freitas, C., Wiig, Ø., Bachmann, L., Heide-Jørgensen, M.P., Swift, R. and Kovacs, K.M. 2012. Lost highway not forgotten: satellite tracking of a bowhead whale (*Balaena mysticetus*) from the critically endangered Spitsbergen stock. *Arctic* 65:76–86

Mayo, C.A. and Marx, M.K. 1990. Surface foraging behaviour of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. *Can. J. Zool.* 68(10):2214–20.

McLeod, B.A., Brown, M.W., Moore, M.J., Stevens, W., Barkham, S.H., Barkham, M. and White, B.N. 2008. Bowhead whales, and not right whales, were the primary target of 16th- to 17th-century Basque whalers in the western North Atlantic. *Arctic* 61:61–75.

Mellinger, D.K., Nieukirk, S.L., Klinck, K., Klinck, H., Dziak, R.P., Clapham, P.J. and Brandsdotti, B. 2011. Confirmation of right whales near a nineteenth-century whaling ground east of southern Greenland. *Biol. Letters* 7:411–13.

Mitchell, E.D., Kozicki, V.M. and Reeves, R.R. 1986. Sightings of right whales, *Eubalaena glacialis*, on the Scotian Shelf, 1966–1972. *Rep. int. Whal. Commn* (special issue) 10:83–107.

Moore, S.E. and Reeves, R.R. 1993. Distribution and movement. pp.313–386 *In:* J.J. Burns, J.J. Montague, and C.J. Cowles (Eds.) *The Bowhead Whale*. Special Publication Number 2, Society for Marine Mammalogy, Lawrence, Kansas, i–xxxvi+ 787pp.

Nichols, O.C., Kenney, R.D. and Brown, M.W. 2008. Spatial and temporal distribution of North Atlantic right whales (*Eubalaena glacialis*) in Cape Cod Bay, and implications for management. *Fish. Bull.* 106:270–80.

Nishiwaki, M. and Kasuya, T. 1970. A Greenland right whale caught at Osaka Bay. *Sci. Rep. Whales Res. Inst., Tokyo* 22:45–62.

Pace, R.M., III, Corkeron P.J. and Kraus, S.D. 2017. State-space mark-recapture estimates reveal a recent decline in abundance of North Atlantic right whales. *Ecology and Evolution* 7*:* 8730–8741.

Parks, S.E., Brown, M.W., Conger, L.A., Hamilton, P.K., Knowlton, A. R., Kraus, S.D., Slay, C.K. and Tyack, P.L. 2007. Occurrence, composition, and potential functions of North Atlantic right whale (*Eubalaena glacialis)* surface active groups. *Mar. Mamm. Sci.* 23:868–87.

Pershing, A.J., Record, N.R., Monger, B.C., Mayo, C.A., Brown, M.W., Cole, T.V.N., Kenney, R.D., Pendleton, D.E. and Woodard, L.A. 2009. Model-based estimates of right whale habitat use in the Gulf of Maine. *Mar. Ecol. Prog. Ser.* 378: 245–257. [*https://doi.org/10.3354/meps07829*]

Pettis, H.M., Rolland, R.M., Hamilton, P.K., Brault, S., Knowlton, A.R. and Kraus, S.D. 2004. Visual health assessment of North Atlantic right whales (*Euabalaena glacialis*) using photographs. *Can. J. Zool.* 82:8–19.

Pettis, H.M. and Hamilton, P.K. 2015. North Atlantic Right Whale Consortium 2015 annual report card. Report to the North Atlantic Right Whale Consortium, November 2015. [Available from: *https://www.narwc.org/uploads/1/1/6/6/116623219/2014_report_card.pdf*]

Philo, L.M., George, J.C. and Albert, T.F. 1992. Rope entanglement of bowhead whales (*Balaena mysticetus*). *Mar. Mamm. Sci.* 8:306–11.

Pieters, J. 2017. Bowhead whale spotted of Vlissingen Coast; First ever spotted in Netherlands waters. *NL Times, 11 April 2017*. [Available from: *https://nltimes.nl/2017/04/11/bowhead-whale-spotted-vlissingen-coast-first-ever-spotted-netherlands-waters*]

Pomerleau, C., Ferguson, S.H. and Walkusz, W. 2011. Stomach contents of bowhead whales (*Balaena mysticetus*) from four locations in the Canadian Arctic. *Polar Biol.* 34:615–20.

Reese, S., Calvin, J.A., George, J.C. and Tarpley, R.J. 2001. Estimation of fetal growth and gestation in bowhead whales. *J. Am. Stat. Assoc.* 96:915–28.

Reeves, R.R., Smith, T. and Josephson, E. 2007. Near-annihilation of a species: Right whaling in the North Atlantic. pp.39–72 *In:* S.D. Kraus and R.M. Rolland (Eds.) *The Urban Whale: North Atlantic Right Whales at the Crossroads*. Harvard University Press, Cambridge, Massachusetts. 543pp.

Reeves, R.R., Smith, T.D. and Josephson, E.A. 2008. Observations of western gray whales by ship-based whalers in the 19th century. *J. Cetacean Res. Manage.* 10(3):247–56.

Right Whale Consortium. 2015. North Atlantic Right Whale Consortium Identification and Sightings Database. New England Aquarium, Boston, MA, USA. [Accessed 24 April 2015]

Rugh, D.J. and Braham, H.W. 1992. Methods for photographic identification of bowhead whales, *Balaena mysticetus*. *Can. J. Zool.* 70:617–24.

Rugh, D.J. and Shelden, K.E.W. 2009. Bowhead whale. pp.131–133. *In:* W.F. Perrin, B. Würsig and J.G.M. Thewissen (Eds.) *Encyclopedia of Marine Mammals*. 2nd ed. Academic Press, Amsterdam. 1,352pp.

Shelden, K.E.W. and Rugh, D.J. 1995. The bowhead whale, *Balaena mysticetus*: Its historic and current status. *Mar. Fish. Rev.* 57(3–4):1–20.

Shpak, O.V. and Paramonov, A.Y. 2012. Observations on belugas (*Delphinapterus leucas*), killer whales (*Orcinus orca*), and right whales (Balaenidae) in Ulbansky Bay, the Okhotsk Sea. Paper presented at the 7th Conference, Marine Mammals of Holarctic, Suzdal, Russia, 24–28 September 2012. [Available from *http://beluga.sevin-expedition.ru/netcat_files/106/57/vol2_final_24122012_15.pdf*].

Silva, M.A., Steiner, L., Cascao, I., Cruz, M.J, Prieto, R., Cole, T., Hamilton, P.K. and Baumgartner, M.F. 2012. Winter sighting of a known western North Atlantic right whale in the Azores. *J. Cetacean Res. Manage.* 12(1):65–9.

Sironi, M., Kraus, S.D., Nordheim, E.V., Rowntree, V.J. and Snowdon, C.T. 2005. Age estimation of North Atlantic right whales (*Eubalaena glacialis*) by allometric measurements on photographs. Paper SC/57/BRG7 presented to the IWC Scientific Committee, June 2005, Ulsan, Korea (unpublished). 14pp. [Paper available from the Office of this Journal]

Stafford, K.M., Moore, S.E., Berchok, C.L., Wiig, O., Lydersen, C., Hansen, E., Kalmbach, D. and Kovacs, K.M. 2012. Spitsbergen's endangered bowhead whales sing through the polar night. *Endanger. Species Res.* 18:95–103.

US Federal Register. 1994. Designated Critical Habitat; Northern Right Whale. FR 50(226). 30pp. (3 June 1994). National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Department of Commerce, Washington, DC.

US Federal Register. 2016. Endangered and Threatened Species; Critical Habitat for Endangered North Atlantic Right Whale. 81 FR 4837. 38pp. (27 January 2016). National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Department of Commerce, Washington, DC.

Walkusz, W., Williams, W.J., Harwood, L.A., Moore, S.E., Stewart, B.E. and Kwasniewski, S. 2012. Composition, biomass and energetic content of biota in the vicinity of feeding bowhead whales (*Balaena mysticetus*) in the Cape Bathurst upwelling region (south eastern Beaufort Sea). *Deep-Sea Res.* 69:25–35.

Wishner, K., Durbin, E., Durbin, A., Macaulay, M., Winn, H. and Kenney, R. 1988. Copepod patches and right whales in the Great South Channel off New England. *Bull. Mar. Sci.* 43(3):825–44.

Wishner, K.F., Schoenherr, J.R., Beardsley, R. and Chen, C. 1995. Abundance, distribution and population structure of the copepod *Calanus finmarchicus* in a springtime right whale feeding area in the southwestern Gulf of Maine. *Cont. Shelf Res.* 15(4):475–507.

Whooley, P. 2016. Bowhead whale: a new species for Irish waters. Irish Whale and Dolphin Group, Merchants Quay, Kilrush, Co. Clare, Ireland. [Retrieved from: *http://www.iwdg.ie/news/?id=2631*. 1 June 2016].

Würsig, B. and Clark, C. 1993. Behavior. pp.157–199 *In:* J.J. Burns, J.J. Montague and C.J. Cowles (Eds.) *The Bowhead Whale*, Special Publication Number 2, The Society for Marine Mammalogy. Allen Press, Inc., Lawrence Kansas, i–xxxvi+ 787pp.

Würsig, B., Dorsey, E.M., Fraker, M.A., Payne, R.S. and Richardson, W.J. 1985. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: A description. *Fish. Bull.* 83:357–77.

Würsig, B., Dorsey, E.M., Richardson, W.J. and Wells, R.S. 1989. Feeding, aerial and play behaviour of the bowhead whale, *Balaena mysticetus*, summering in the Beaufort Sea. *Aquat. Mamm.* 15:27–37.

J. CETACEAN RES. MANAGE. 19: 31–42, 2018

Acoustic data from the spring 2011 bowhead whale census at Point Barrow, Alaska

C.W. Clark[1], R.A. Charif[1], D. Hawthorne[1], A. Rahaman[1], G.H. Givens[2], J.C. George[3] and C.A. Muirhead[1]

Contact e-mail: geof@geofgivens.com

ABSTRACT

Arrays of bottom-mounted passive acoustic recorders were used to continuously record the sounds of bowhead whales migrating past Point Barrow, Alaska for a period of 105 days in April–July 2011, spanning the duration of the visual census. Recorders were deployed in a roughly linear array configuration near the edge of the shorefast ice bordering the open lead. The recorded acoustic data were analysed from 156 sample periods comprising a total of 331 hours coincident with the visual census. Bowhead sounds in the sample periods were found by manual inspection of multi-channel sound spectrograms of the array recordings. Source locations for bowhead sounds that were received on three or more sensors within the array were calculated using a robust localisation algorithm. Very high levels of bowhead acoustic activity were observed in comparison to recording efforts undertaken during past censuses, including high rates of singing and call sequences. A total of 22,426 bowhead sounds yielded 15,647 reliable locations. Of these, 6,944 were within the rectangular aperture zone directly in front of the array and therefore used in the calculation of a new population estimate. This paper summarises one of three critical component of the research program leading to the 2011 estimate of abundance of Givens *et al.* (2016) and is therefore a cornerstone of the scientific basis for IWC Scientific Committee advice for this whale stock.

KEYWORDS: ARCTIC; WHALING-ABORIGINAL; SURVEY-ACOUSTIC; ACOUSTICS; MIGRATION

INTRODUCTION

During the spring, bowhead whales, *Balaena mysticetus*, from the Bering-Chukchi-Beaufort (BCB) population migrate past Point Barrow, Alaska, USA, en route from wintering areas in the Bering Sea to summer feeding grounds in the Beaufort Sea.

Since 1984, the census of the BCB population during its spring migration past Point Barrow has included an acoustic monitoring component combined with a visual survey effort (Clark *et al.,* 1986; Clark *et al.,* 1996; George *et al.,* 2004). In 2011, between 12 April and 7 June, the North Slope Borough's Department of Wildlife Management successfully completed a combined acoustic-visual census. The acoustic monitoring effort, conducted from mid-April through late July, used arrays of passive acoustic recording devices to continuously record underwater sounds. The primary objective of the acoustic study was to detect and locate vocalising bowheads throughout their migration past Point Barrow, Alaska in order to estimate the proportion of acoustically located whales that swam within 4km of the perch from which the visual census was conducted. An important benefit of this study is that it continues the acoustic component of a long-term research project in which both visual observation and acoustic monitoring were collected. As a result, some basic comparisons of acoustic results are available over a span of 27 years.

This paper describes the methods used to collect and analyse the 2011 bowhead census acoustic array data, and provides a summary of bowhead acoustic activity and locations during selected sub-sample periods. This is one of three critical components of the overall bowhead research program; the other two components are the estimation of visual detection probabilities (Givens *et al.*, 2014) and the estimation of total abundance (Givens *et al.*, 2016), which depends on the combination of acoustic detection and visual detection results. This paper is therefore a cornerstone of the abundance estimate upon which the IWC Scientific Committee bases management advice for this whale stock.

METHODS

Acoustic data collection

Recording arrays

Acoustic data were recorded using arrays of marine autonomous recording units (MARUs) developed by the Cornell Bioacoustics Research Program (Clark *et al.,* 2010). A MARU consists of a digital audio recording system in a positively buoyant glass sphere that can be deployed on the bottom of the ocean for periods of many months. Once deployed, the recorder floats several meters above the sea floor, tethered to an anchor via an acoustically activated release device. A hydrophone mounted outside the sphere transduces sound pressure into an analog electrical signal, which is then filtered, digitised, and stored as a continuous series of time-stamped binary files on an internal hard disk. At the conclusion of a deployment, the recorder's acoustic release device is activated from a recovery vessel, causing the instrument to float to the surface for retrieval.

The MARUs used in this study were programmed to record continuously at a digital audio sampling rate of 2000Hz. The effective acoustic bandwidth of the MARUs, accounting for effects of high-pass and low-pass filters, was 10–800Hz, a frequency range that adequately spans the frequency range of bowhead calls and the lower frequency range of bowhead song notes (Clark and Johnson, 1984; Würsig and Clark, 1993).

---

[1] *Bioacoustics Research Program, Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA.*
[2] *Givens Statistical Solutions LLC, 4913 Hinsdale Drive, Fort Collins, CO 80526, USA.*
[3] *North Slope Borough, Department of Wildlife Management, Barrow AK 99723, USA.*

Late on 12 April 2011, a 6m skiff was used to deploy a five-element array of MARUs in a ‘zigzag’ formation along the edge of the nearshore lead system in the vicinity of the ice-based observation perch. Attempts to deploy buoys more than ≈ 250m north of the perch became impossible because of dangerous ice conditions and –23°C air temperatures. Two additional MARUs were deployed on 1–2 May 2011 by being dropped into the open lead from the nearshore ice edge. One of the five MARUs deployed initially was never retrieved. Because the audio data from differing numbers of MARUs were processed separately, the four MARUs that were recovered from the set deployed on 12 April were considered to comprise a 4-channel array; these four plus the two that were deployed on 2 May comprise a 6-channel array.

Relative positions and details of the individual MARU deployment sites are given in Fig. 1 and Table 1. Depths at the deployment sites varied between 26 and 44m.

Since the two MARUs deployed on 1–2 May were dropped directly from the ice edge, the line connecting their deployment sites was used to define the nominal ice edge for calculating offshore distances of whale locations; the actual ice edge was not perfectly linear. A rectangular zone directly in front of the array is defined as the *aperture zone* (Fig. 1). The aperture zone is the area within which the distribution of offshore distances of acoustic locations is used by Givens *et al.* (2016). One end of the aperture zone is defined by the nominal ice edge. The sides of the aperture zone are perpendicular to the ice edge. The northern side intersects the ice edge at the northernmost MARU position; the southern side intersects the ice edge at a point midway between the two southernmost MARU positions. This midpoint is used, rather than the position of the southernmost MARU, because whale sounds with their first arrival on the southernmost MARU were excluded from the analysis. This is because the vast majority of these sounds are from distant whales approaching the array from the south, and their positions would be in the 30° ‘endfire’ zone where locations tend to be highly unreliable. Since such locations are discarded later in the analysis process (see below), considerable time was saved in the initial data browsing by skipping such calls. However, if the aperture zone is defined as extending all the way to the southernmost MARU, the exclusion of calls with first arrivals on the southernmost channel would result in the omission of some locations between the two southernmost MARU sites. Using the midpoint between the two southernmost MARUs to define the edge of the aperture zone prevents this omission.

MARUs were retrieved on 27 and 29 July, after the sea ice had retreated from the deployment area. One of the MARU units (Site-5) deployed on 12 April failed to surface in response to the release command and was never recovered.

This is the first time that acoustic monitoring data have been collected beyond the end of the visual census period, which historically has been around 1 June, with end recording dates dictated by ice conditions and whale passage rates.

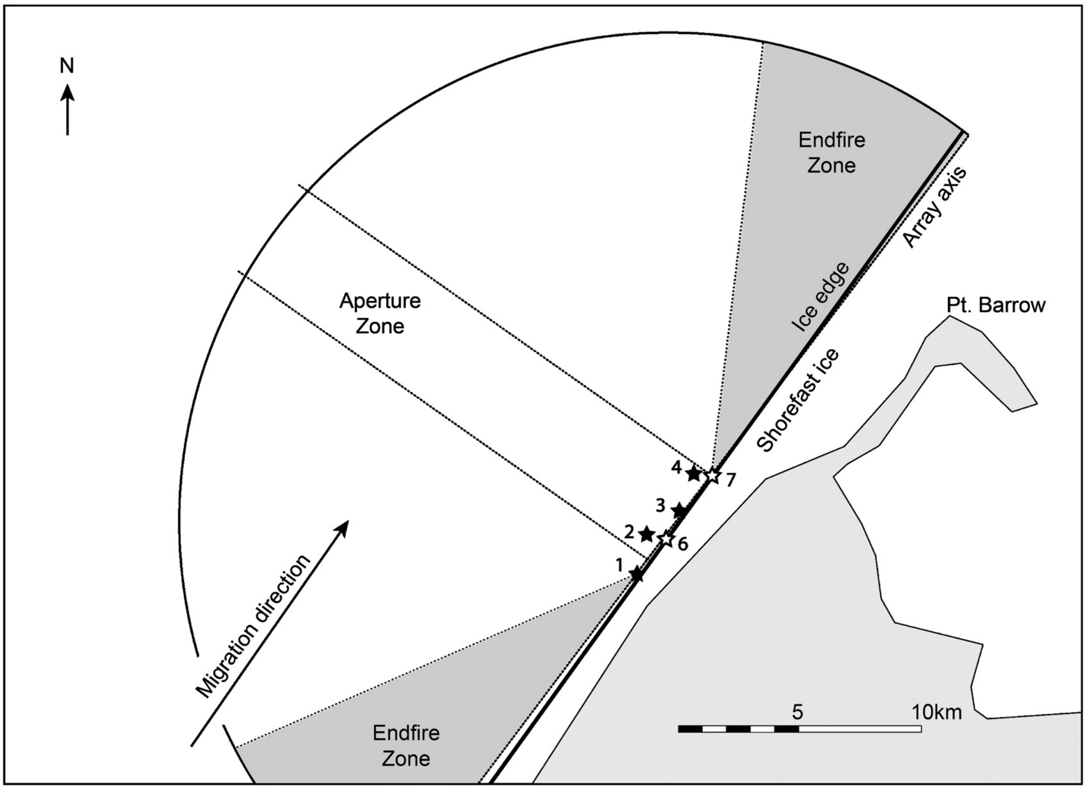


Fig. 1. Passive acoustic arrays deployed near Point Barrow, Alaska. The filled black stars represent MARU positions in the 4-channel array; open stars represent MARUs deployed on 1–2 May to make the 6-channel array. Numbers next to MARU positions are the site numbers as given in Table 1, while noting that Site-5 is not shown because that MARU was not recovered. The large semi-circle (radius = 20km) indicates the area within which acoustic locations were considered reliable. The nominal ice edge used for computing offshore distances is shown. The array axis and aperture zone (see text) are shown for the 6-channel array. For the 4-channel array, the array axis is tilted northward by 8°, and the aperture zone is slightly smaller than shown. The visual observation perch is located 190m from the northernmost MARU (Site-7), too close to be shown separately at this map scale.

Table 1

Locations, depths, deployment and retrieval dates, for MARUs deployed near the visual observation perch in 2011. Approximate depths were obtained from Google Earth.

Site	Latitude (°)	Longitude (°)	Depth (m)	Deployment date	Recovery date
1	71.332717	–156.818367	37	12/04/11	29/07/11
2	71.341383	–156.780300	40	12/04/11	29/07/11
3	71.355267	–156.763767	44	12/04/11	29/07/11
4	71.364067	–156.716650	37	12/04/11	27/07/11
5	71.318367	–156.828800	26	12/04/11	Not recovered
6	71.330967	–156.795800	37	02/05/11	27/07/11
7	71.354533	–156.742783	31	01/05/11	27/07/11

The 4-element MARU array, which provided data for analysis from 0:00[4] on 13 April through 14:59 on 2 May had an array aperture of 4,725m, with distances between adjacent elements of 1,638 to 1,671m. The 6-element array, which recorded from 15:00 on 2 May through 12:00 on 27 July, had an array aperture of 5,065 m, with distances between adjacent elements of 755 to 1,659m. Given the rule of thumb that reliable acoustic locations can be calculated with a linear, sparse array out to ranges four times the array aperture (Carter, 1993), these aperture values support our working assumption that acoustic locations calculated with these arrays are reliable out to approximately 20km from the centre of the arrays.

Array synchronisation

All of the MARUs were synchronised at the start and end of the deployment, and at repeated intervals during the recording period. Synchronisation is required because the algorithm used for computing an acoustic location depends on precise and accurate measurements of the times at which the same sound was recorded by each MARU. Although the quartz-based oscillators that control the audio sampling rates in the MARUs operate at the same nominal frequency, small variations between individual oscillators lead to 'clock drift' among MARUs in the array, which can substantially degrade the accuracy of the relative time-of-arrival measurements.

After recovery of the MARUs a two-step method was used to correct the digital audio files for the effects of MARU-specific clock drift. First, data from onboard temperature loggers were used to compensate for changes in clock frequency that occurred as a result of variations in temperature inside the MARU. Prior to deployment, the oscillator frequency of each MARU was characterised in the laboratory over a wide range of temperatures, yielding a MARU-specific curve of oscillator frequency as a function of temperature. During the deployment period an onboard logger recorded the internal temperature at 15-minute intervals. After the MARUs were recovered, data from each unit's temperature log and its characteristic temperature-frequency curve were used to correct the stream of audio data so that the number of samples in each 15-minute temperature-logging interval matched the value predicted by the nominal sampling rate (Marchetto *et al.,* 2012; see Appendix 3).

The second step in synchronising recordings from MARUs relied on the use of synchronisation sounds played into the water from known locations near the array at intervals of 1 to 8 days (mean = 5) during the deployment period. Because the times of the sync sound playbacks, the speed of sound (1,439m/s), and the distances between the playback speaker and all of the MARUs are known, the expected arrival-times for the sync sound could be calculated for each MARU. After the MARUs were recovered and their data streams were temperature compensated, the observed arrival times of the sync sounds were compared to their expected arrival-times. The number of audio samples between successive recorded sync sounds was adjusted by uniformly inserting or removing samples from the sound stream as necessary to bring the recorded sync sounds to the expected times. Once all of the individual extracted audio data streams were time-compensated in these two ways, they were merged into synchronised, multi-channel audio files for subsequent analysis.

Analysis of acoustic data

Location analysis of the acoustic data was a four-stage process. First, experienced analysts inspected multi-channel spectrograms for selected sample periods and logged bowhead whale sounds that were recorded on three or more MARUs for later location estimation. Sounds recorded on fewer than three MARUs cannot be located and were not logged. Second, an automated localisation algorithm was run as a batch process on the logged whale sounds. Third, the acoustic locations (henceforth 'locations') were screened by a combination of manual and automated processes to eliminate locations that were definitely or probably erroneous. Fourth, locations that were likely to be from the same whale were flagged by an automated algorithm in order to reduce bias from over-represented, acoustically active whales.

The selection of sample periods and the stages in the analysis process are explained in further detail below.

Selection of sample periods

Two sets of sample periods were chosen for location analysis. For the first set, the season was divided into early (13–17 April), gap (18–21 April), core (21 April–15 May), and late (16 May–1 June) time blocks based on major changes in visual sighting rates apparent in the visual field data logs. The gap period corresponds to about three days when no visual watch was possible due to storm conditions. A total of 230 hours of acoustic sample periods was selected within the early, gap, core and late time blocks, with 25, 15, 135 and 55 hours allocated to the early, gap, core and late blocks, respectively. Acoustic sample periods were

---

[4] All times are given in Alaska Daylight Time.

chosen semi-systematically: taking samples when there was simultaneous visual effort was the highest priority, followed by sampling when the observed whale passage rate was high, and finally ensuring at least some acoustic data had been collected during each time block. Aside from the gap period, all acoustic sampling periods were wholly contained within (potentially longer) periods with visual effort.

The second set of sampling periods was chosen after completing location analysis of the first set of sampling periods and after preliminary analysis of the combined visual and acoustic data from those sample periods. In the analysis of Givens *et al.* (2016), availability (the proportion of whales swimming within 4km of the perch: visual detection range) is estimated from the acoustic data as a smooth function of time. By looking at the preliminary estimated curve, it was possible to identify periods of time when the standard error of the availability estimate was comparatively large. If during this time period, the estimated number of whales passing the perch was also high, then these two factors together could produce an undesirably large contribution of variance to the overall abundance estimate. To reduce this effect, an additional 98 acoustic sampling hours (essentially the maximum the project could fund) were selected in such periods, both within and outside intervals of visual effort. Finally, two additional hours were sampled during visual watch on the first day (13 April) and one additional hour on the last day (1 June) of the analysed season. These were added for purely computational reasons since they enabled estimation of the availability curve over the entire season so that no extrapolation was needed. In sum, 331 hours of acoustic data were sampled. This means that acoustic location analysis was performed for about 28% of the total time acoustically monitored during the analysed visual census period as defined by Givens *et al.* (2016). A complete list of sample periods is provided in Appendix 1.

Manual examination of data and annotation of bowhead sounds

Experienced acoustic analysts used a customised, MATLAB-based software system (XBAT) to examine multi-channel spectrograms of the recorded audio data from each sample period, typically viewing data in the 20–600Hz frequency band, one minute at a time. For the 4-channel array, audio data from MARU sites were assigned channel numbers in the multi-channel sound files from south to north. Thus, channel 1 in the 4-channel spectrograms displayed data from the southernmost MARU, and channel 4 displayed data from the northernmost MARU. For the 6-channel array, audio data from MARU sites were assigned channels in a south to north sequence such that the sequence of sites was 1, 2, 6, 3, 4, 7.

Sounds that were recorded by three or more MARUs were potentially locatable, and were annotated by using a cursor to draw a box around the sound in the one channel that recorded the clearest arrival of the call (i.e. the *reference channel*). Data on the time and frequency boundaries of marked calls were stored in XBAT log files for later processing by the locator algorithm. Calls that were received on fewer than three channels were not logged because they cannot be located.

Three categories of bowhead sounds were marked by analysts (Clark and Johnson, 1984; Würsig and Clark, 1993):

- **Individual calls** (Fig. 2a)**:** Each individual bowhead call that was not part of a call sequence or song (see below) was logged.
- **Call sequences** (Fig. 2b)**:** A call sequence is a sequence of calls, typically frequency-modulated and of similar shape, at regular intervals (typically 1.5–3s) apparently from the same source. Call sequences typically last 20–30s. When call sequences occurred, analysts logged one individual call from each sequence, rather than each individual sound, in order to reduce over-representation of an individual whale in the final data set.

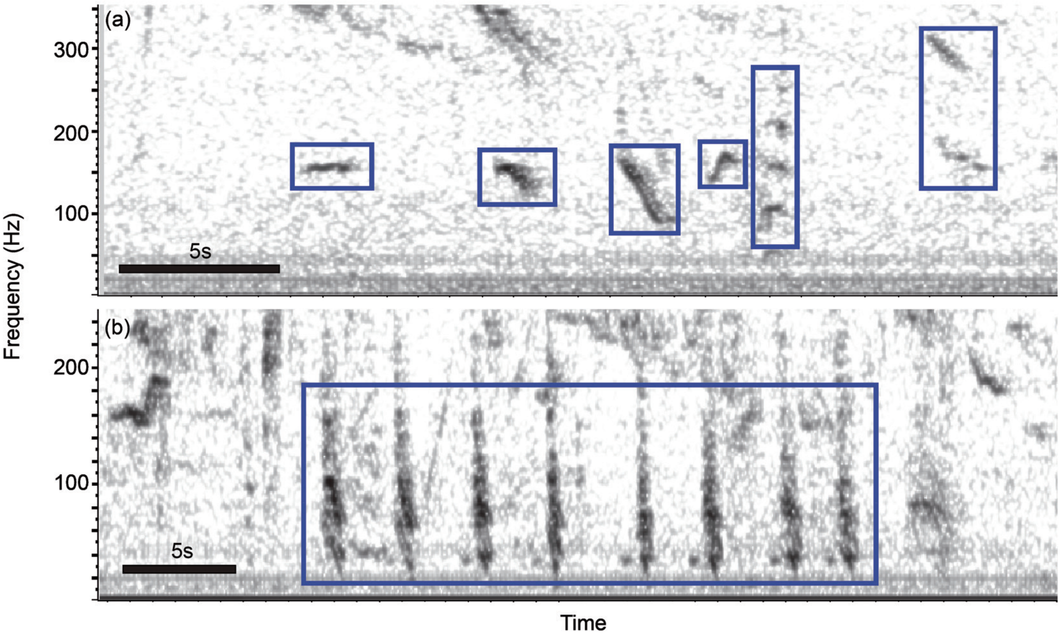


Fig. 2. Examples of individual bowhead whale sounds. Only a single channel of audio recording is shown. (A) Individual calls recorded at 13:49 on 8 May. Note variability of call shapes. (B) A call sequence containing eight calls recorded from a bowhead whale at 23:10 on 29 April. Note the similar shape and regular time intervals of calls within the sequence.

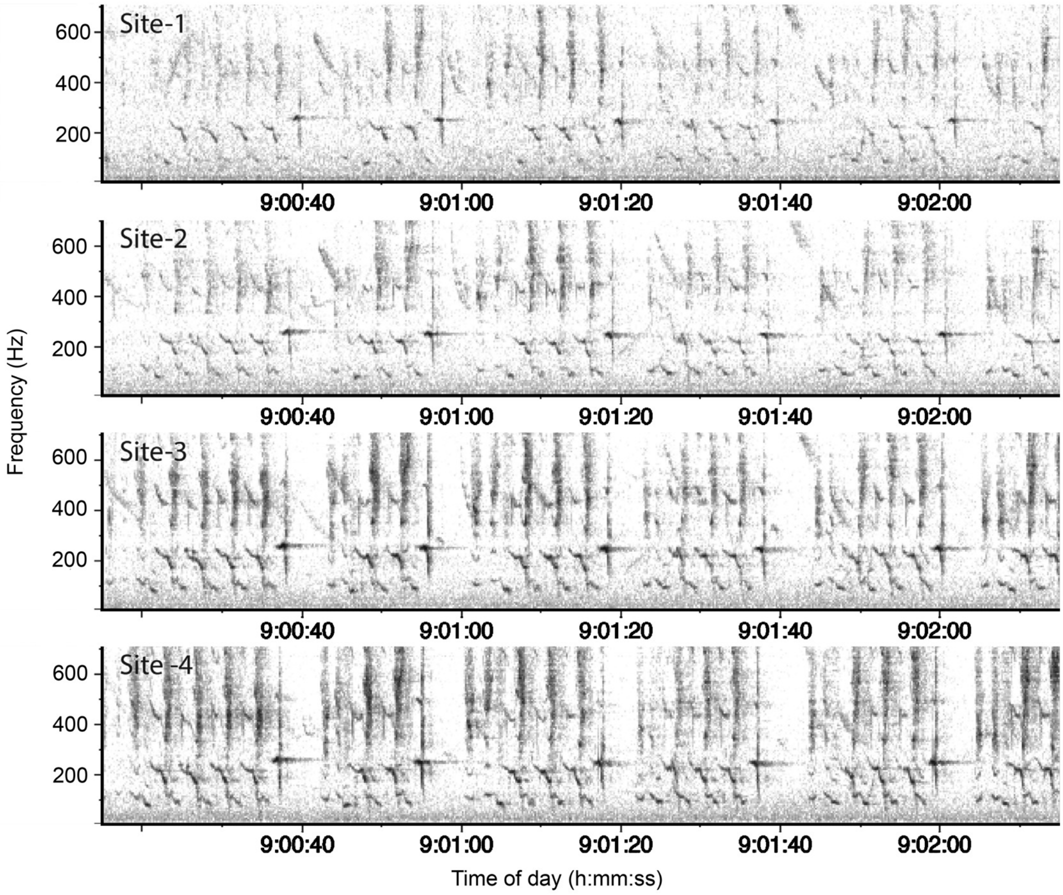


Fig. 3. Example of bowhead whale song recorded at 9:00 on 13 April 2011. Two minutes of the recording are shown from all four MARUs in the recording array. Site-1 is the southernmost recording site in the array (Fig. 1). The highly repetitive structure typical of song is clearly visible.

- **Song (**Fig. 3**):** When bowhead song (Würsig and Clark, 1993; Stafford *et al.,* 2008; Delarue *et al.,* 2009, Tervo *et al.,* 2009) was detected, a single song note was logged once per clock hour. Individual bowhead songs may contain many tens of individual notes within the span of one to two minutes, and individual whales may sing continuously for many tens of minutes or hours at a time. Logging every song note or even a single note from every song could thereby result in orders of magnitude more locations for singing whales than non-singing whales.

In all but the first few sample periods analysed, analysts excluded sounds where the first arrival was on channel 1 (corresponding to the southernmost MARU), because whales producing these sounds would have been to the south of the visual observation perch, and well outside of the rectangular aperture zone used for the abundance estimate (Givens *et al.,* 2016).

Calculation of acoustic locations

When a sound is received on three or more sensors at known positions and in water of known sound velocity, the location of the sound source can be determined from the unique set of pairwise differences in sound's time of arrival at multiple sensors in an array (Clark *et al.,* 1986; Clark *et al.,* 1996; see Fig. 4). In practice, sound source location accuracy and precision are compromised by several sources of uncertainty including sensor position, speed of sound, sound bandwidth and duration, and background noise (see Carter, 1993).

The positions of vocalising bowhead whales were calculated using a custom correlation sum estimation (CSE) algorithm (Urazghildiiev and Clark, 2013), which determines the most likely set of pairwise time-of-arrival differences in order to determine the most likely source location. The CSE locator estimates the most likely set of time delays by finding the pairwise time lags which maximise the sum of filtered waveform cross-correlation values over all sensor pairs. This approach is equivalent to using near-field beamforming spatial energy maximisation to estimate the location of an acoustic source (Appendix 2). The CSE locator software was configured to search for locations out to distances of 20km from the centre of the array. Acoustic locations returned by the locator are expressed in Cartesian coordinates relative to the centroid of the sensor positions. The y-axis of the coordinate system is oriented to geographic (true) North. The locator also returns heuristic estimates of the 95% confidence intervals for x and y coordinates (Appendix 3).

The location algorithms used in previous bowhead censuses determined pairwise arrival-time differences for the same sound recorded on different sensors by finding the maximum in the cross-correlations of, originally, the spectrogram images (Clark *et al.,* 1986), and later, the filtered waveforms (Clark *et al.,* 1996) of the recorded audio. In this approach, time delays are determined independently for each pair of hydrophones, based only on the peak value from the cross-correlation for the corresponding pair of audio channels. The pairwise arrival-time differences were then used as input to an algorithm that calculated the acoustic location (see Clark

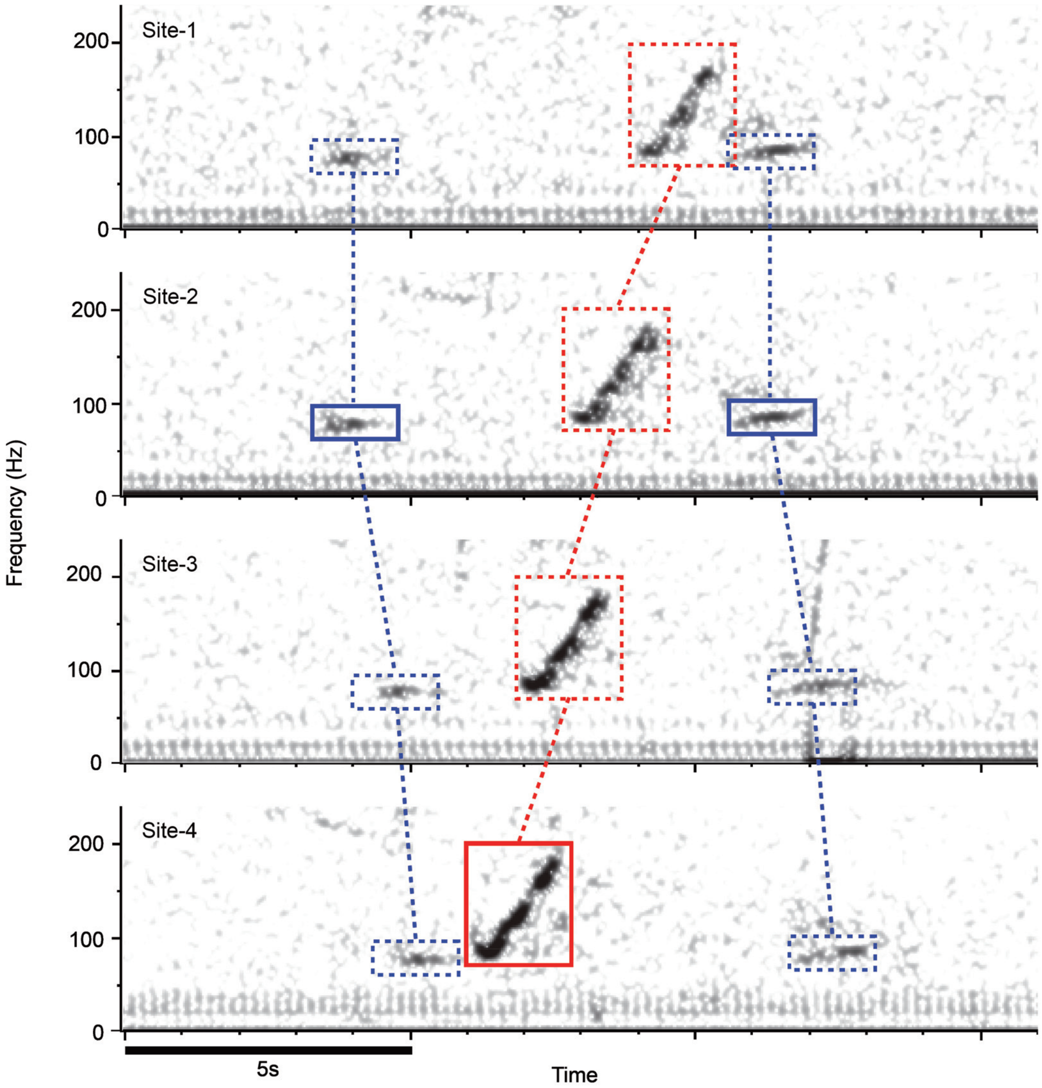


Fig. 4. Time-of-arrival delays for three different bowhead whale calls (boxes) received on the 4-channel recording array at 00:31 on 27 April. The four spectrograms represent synchronised audio streams from four MARU sites, where Site-1 is the southernmost recorder (see Fig. 1). Solid outlines around calls were manually drawn in the 'reference' channel for each call. Dashed outlines around calls in non-reference channels were drawn by the localisation algorithm. Dashed lines link the same call as recorded on the four recorders. The order in which each call was recorded by the four MARUs is determined by the whale's distance from each recorder. The time delays of the first and third calls indicate that they came from approximately the same bearing, nearly equidistant between Site-1 and Site-2. The time delays for the middle call indicate that it came from a different bearing, to the north of the array.

et al., 1996 for a more detailed description). In contrast, the CSE locator determines the most likely time delays by using all of the complete cross-correlation functions for all sensor pairs as an ensemble. This approach is more robust in the presence of noise than traditional peak-picking methods (Birchfield and Gillmor, 2001, 2002).

Review and filtering of automated locations

After all potentially locatable calls in a sample period were manually logged, locations were generated for the logged sounds. One of the outputs of the CSE locator is a prediction of the time at which the logged sound is expected to appear in all channels other than the reference channel, based on the estimated location. XBAT visualises these predicted times of occurrence of secondary arrivals by displaying a coloured rectangular box overlaid on the spectrogram image in each non-reference channel (Fig. 4). If the computed location estimate is correct, these predicted time-delay boxes are properly aligned with the visible arrivals of the whale call in the non-reference channels. Faulty alignment of time delay boxes indicates that the computed location is incorrect, most commonly as a result of poor signal-to-noise ratio on one or more channels. Analysts reviewed each location for faulty time-delays by inspecting the alignment between the predicted time-delay boxes and the images of the whale sound in the non-reference channels. No attempt was made to manually adjust faulty arrival times, and locations that included faulty time-delays were marked in the logs as unreliable and removed from the final data files in a later post-processing step.

After locations with faulty arrival-times were removed, the following additional automated processing was performed via an Excel spreadsheet:

- Locations that fell outside of the 120° sector centered on the line perpendicular to the array axis were excluded from the data set (Clark *et al.,* 1996). In general, with a nearly linear array, location estimates within 30° of the array axis tend to be unreliable with respect to range, hence are excluded from further analysis. These 30° sectors are called the 'endfire zones' (Fig. 1).

- Range and bearing errors from the centroid of the hydrophone array were calculated for all locations based on the heuristic 95% CIs for x and y. The x and y CIs define a rectangular uncertainty area centered on the estimated location. For range error, the difference in range between the estimated location and the farthest corner of this rectangle is used. For bearing error, half the difference between the bearings to the second and third nearest corners of this rectangle is used (Fig. 5). With a linear array, range error generally increases with increasing range; bearing error is largely unaffected by range.
- Locations with bearing errors > 22.5° were flagged as unreliable and excluded from further analysis.
- Offshore distances and minimum and maximum offshore distances were calculated for all locations. The offshore distance for a location is the perpendicular distance from the location to the nominal ice edge (Fig. 1). The minimum and maximum offshore distances are the perpendicular distances from the array axis to the nearest and farthest corners, respectively, of the location's uncertainty rectangle.
- Upon inspection of the complete set of located calls, it became apparent that, in some sample periods, many individual sounds had erroneously been logged for the same song and same call sequences, contrary to the planned protocol. As a result, a few sample periods contained inflated numbers of locations that were probably produced by the same individual whale in a small spatial area and a short period of time. In order to identify these redundant 'duplicate' acoustic location events in the data set without a prohibitively time-consuming manual review of all events, a simple algorithm was developed and applied that identified sequences of events that occurred within 10s of each other and that had overlapping range and bearing errors. Extensive spot-checking of the data marked by this algorithm indicated that most of the events erroneously logged in call sequences and songs were found by this process, with very few cases of properly logged events being identified. Events identified by this algorithm as duplicates were eliminated from further analysis and reporting.

RESULTS

A total of 484 hours of audio data were recorded with the 4-channel array, from 11:00 on 12 April through 15:00 on 2 May. A total of 2,067 hours of audio data were recorded with the 6-channel array from 15:00 on 2 May through 18:00 on 27 July.

A total of 331 hours of data were analysed in 155 sample periods. In total, analysts marked 22,426 sounds that yielded locations in the 120° sector in front of the array. Of these, 3,195 were considered unreliable because their bearing errors were > 22.5°, and 4,393 were identified as likely 10-second duplicates. After removal of the latter two categories of events, a total of 15,647 locations remained. Of these, 6,944 were within the rectangular aperture zone directly in front of the array.

Fig. 6 illustrates the temporal distribution of bowhead acoustic activity over the course of the monitoring season, showing the number of potentially locatable bowhead whale sounds (i.e. sounds that were recorded on ≥3 channels of the acoustic array) per hour for each of the 155 sampling periods. Across all 331 hours analysed, the mean rate of potentially locatable vocalisations was 51.2 sounds/h, including sounds for which locations were deemed unreliable because of excessive bearing error. The figure excludes redundant acoustic location sounds that occurred within 10 s of each other and that had overlapping range and bearing errors; most such 'duplicate' sounds were part of a song or call sequence. The peak rate of vocal activity, 274 sounds/h, occurred between 8:00 and 10:00 on 2 May. The interquartile range of dates in the cumulative distribution of locatable bowhead sounds was between 29 April and 9 May.

Recordings after 1 June have thus far not been systematically sampled to quantify bowhead acoustic activity. However, a few scattered bowhead calls were observed in casual inspection of recordings during the period of 2–10 June, indicating that some bowheads did pass through the census area after the conclusion of the visual census.

Fig. 7 shows the geographic distribution of the 15,647 bowhead sounds located in the 120° sector in front of the array, from the 331 hours of data analysed. Fig. 8 shows the distribution of offshore distances of the 6,944 locations that were within the rectangular aperture zone.

DISCUSSION

Overall, in comparison to recordings from previous censuses, the array recordings made in 2011 had extremely high levels of bowhead whale acoustic activity. Table 2 compares mean rates of occurrence of locatable bowhead sounds in recordings analysed from the 2011 census to data from

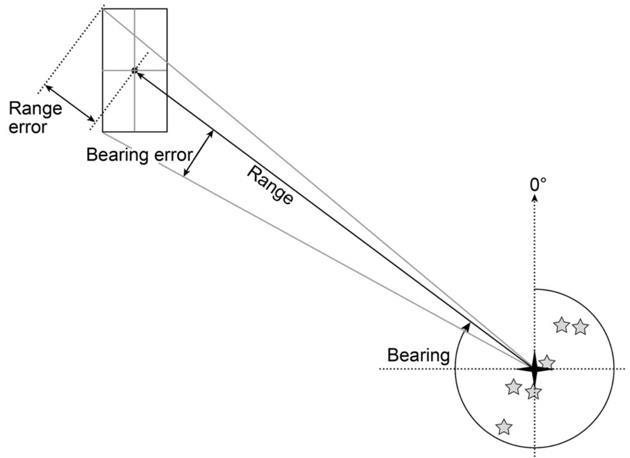


Fig. 5. Schematic illustration of range and bearing to an acoustic location, and their respective errors. The grey stars represent the locations of the MARUs. The black cross represents the centroid of the recording array. The locator algorithm calculates the x and y coordinates of a vocalising whale (black dot), and the heuristic 95% CIs for x and y, which define a rectangular uncertainty area. The range and bearing are calculated by converting the x and y to geographic polar coordinates. The range error is the difference between the range to the location and the farthest corner of the uncertainty rectangle. Bearing error is the difference between the bearing to the location and to either the second or third farthest corners of the uncertainty area.

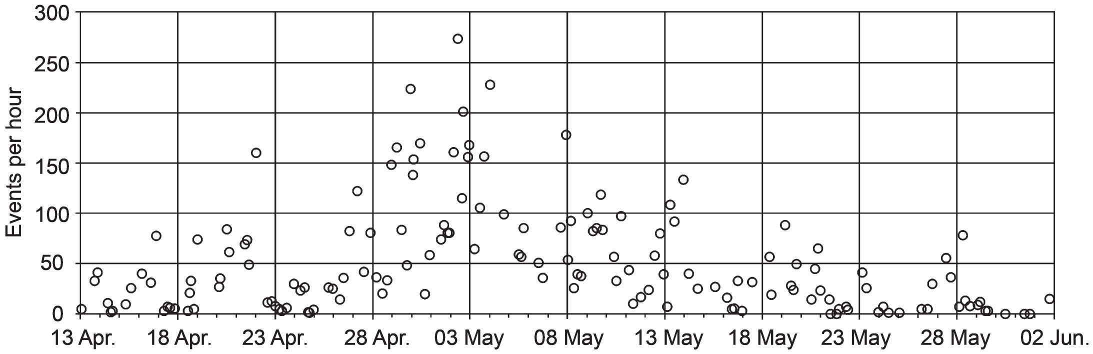


Fig. 6. Mean rate of potentially locatable bowhead whale vocalisations for 155 sample periods between 13 April and 1 June 2011. Each point represents one sample period. Mean length of sample period = 2.16h. Vocalisations that were recorded on < 3 channels of the acoustic array, and could not be located, are not included in these data. In order to convey the seasonal distribution of vocal activity, all vocalisations that were recorded on ≥3 channels of the acoustic array were included in this plot regardless of whether or not they were excluded from location analyses and figures due to excessive bearing error. 'Duplicate' sounds that occurred within 10s of another sound with overlapping range and bearing errors are omitted. The total number of sounds included here = 18,033.

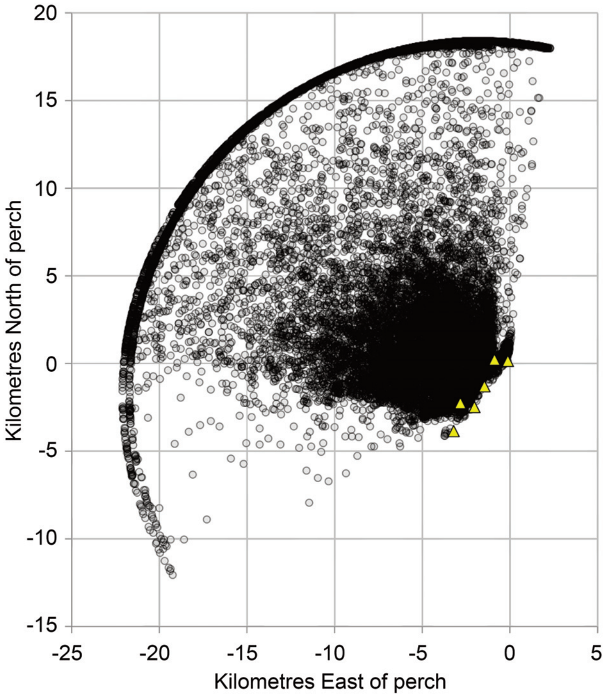


Fig. 7. Acoustic locations of 15,647 bowhead sounds, from 155 sample periods totaling 331 hours of recording between 13 April and 1 June 2011. The origin of the coordinate system is the location of the primary visual perch. Triangles indicate locations of hydrophones in the 6-element recording array. As a whale's true location becomes farther away from the array, range errors inevitably increase. The locator software was configured to search for locations out to 20km, which gives rise to the circular edge in the location distribution. Locations at or close to this 20km boundary represent whales that were probably beyond the 20km search limit.

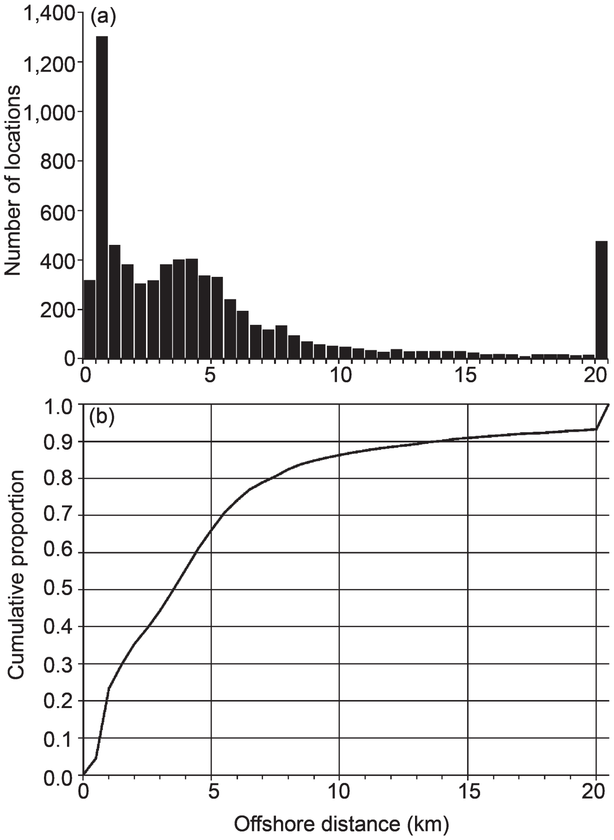


Fig. 8. Offshore distance distribution for the 6,944 locations inside the rectangular aperture zone. (a) Number of locations in 0.5km distance bins. (b) Cumulative proportion of locations ≤ a given distance. In both plots, the greatest value represents all locations at distance > 20km.

1993 and 2001 (Clark and Johnson, 1984; George *et al.,* 2004). Overall, between 1993 and 2011, the mean rate of acoustically located events increased by approximately 570%.

The 2011 recordings also appeared to have much higher occurrence rates of call sequences and songs compared to past censuses, although quantitative comparisons are not presently available.

There were some differences between the methods used in 2011 and in previous years, but it is not believed that these differences account for the increase in acoustic activity or the number of reliable locations. These differences include the use in 2011 of autonomous recorders suspended 2–3m from the seafloor rather than cabled hydrophones deployed over the ice edge or through the ice as in all previous years. For the 2011 data the depths of hydrophones below the surface were 29–42m, while in previous years, hydrophone depths were typically 20–40m. Recorder sensitivity in 2011 was less than that in previous years because MARUs were sampling at 2kHz with a dynamic range of approximately 66dB, while earlier systems were sampling at a minimum of 10kHz with a dynamic range of 90dB. If anything, lower numbers of sound detections would then be expected and fewer acoustic locations from the 2011 system compared to previous years. Array aperture differences were minimal

Table 2

Comparison of numbers of locatable bowhead whale sounds processed from censuses in 1993, 2001 and 2011.

	1993	2001	2011
Hours analysed	732	757	331
Reliable locations	6,042	26,606	15,647
Locations/h	8.3	35.1	47.3

between 2011 and previous years, where array aperture influences the range out to which locations are reliable. In 2011 array apertures were 4,725m (4-channel) and 5,065m (6-channel); in 1993 apertures of the 25 separate arrays used were typically around 4,425m. Thus, the 4- and 6-channel arrays used in 2011 were around 7% and 14% longer than those used in 1993.

This paper is the final cornerstone of the 2011 BCB bowhead ice-based abundance estimate (Givens *et al.*, 2016). Although that estimate is quite complex, its essence is that it scales up counts of sighted whales by adjusting for detection probability (sighting a whale given that it is available to be sighted; see Givens *et al.,* 2014) and availability (whether a whale passing the perches is available to be sighted, i.e. within 4km of the ice edge). The acoustic analyses presented here provide the sole basis for the availability correction and hence are essential for estimating abundance. In particular, the availability correction is estimated as a time-varying smooth function of the probability that animals pass within visual range of the observation stations, where those probabilities are derived from the data presented here. Uncertainty is estimated using the bootstrap.

Abundance estimates for the BCB bowhead population are required for IWC management of subsistence hunting by Alaska Natives. Sustainable quotas are estimated using the IWC's Bowhead *Strike Limit Algorithm* (*SLA*; IWC, 2003) which requires updated abundance estimates every 10 years or, ideally, much more frequently. The prior two abundance estimates were for 2001 (Zeh and Punt, 2005) and 2004 (Koski *et al.,* 2010); the next is planned for 2019.

Our acoustic results suggest that BCB bowhead abundance has markedly increased in the last two decades, and it is not believed that any of the differences in field data collection and/or data processing methods can account for the almost 6-fold increase in rates of locatable bowhead sounds observed in 2011 in comparison to 1993. Moreover, the past four fully corrected abundance point estimates have been 7,778 (1993), 10,470 (2001), 12,631 (2004) and 16,820 (2011). This also suggests that the bowhead population is growing relatively rapidly despite the small subsistence harvest and profound changes in the arctic habitat.

ACKNOWLEDGEMENTS

The many researchers who worked on the ice-based visual and acoustic survey collecting the data required for the abundance estimate are gratefully acknowleged. In particular, people recognised are Jason Michalec, Jason Herreman, Kate Stafford, and Billy Adams who helped deploy and retrieve the acoustic recorders under very dangerous conditions. The Whaling Captains Association at Barrow and the Alaska Eskimo Whaling Commission are thanked for their support and patience, allowing us to conduct these studies near Utqiagvik (formerly Barrow) during the whaling season. Kristin Hodge, Maureen Loman, Clara MacCarald, Elizabeth McDonald, and Kaitlin Palmer are thanked for painstaking analysis of the acoustic data. We thank Mike Pitzrick for software tools and consultation on post-processing of the location data. We also thank the North Slope Borough, NOAA, BOEM, and BP Exploration, Alaska, Inc. for funding by which to collect and analyse the acoustic data used for the abundance estimate.

REFERENCES

Birchfield, S.T. and Gillmor, D.K. 2001. Acoustic source direction by hemisphere sampling. Presented to the IEEE International Conference on Acoustics, Speech, and Signal Processing (ICASSP*)*, 7–11 May 2001, Salt Lake City, UT, USA. 4pp.

Birchfield, S.T. and Gillmor, D.K. 2002. Fast Bayesian acoustic localization. Presented to the IEEE International Conference on Acoustics, Speech, and Signal Processing (ICASSP), 13–17 May 2002, Orlando, FL, USA. 4pp.

Carter, G.C. (Ed.) 1993. *Coherence and Time Delay Estimation: An Applied Tutorial for Research, Development, Test, and Evaluation Engineers*. IEEE Press. 518pp.

Clark, C.W., Brown, M.W. and Corkeron, P. 2010. Visual and acoustic surveys for North Atlantic right whales, *Eubalaena glacialis*, in Cape Cod Bay, Massachusetts, 2001–2005: Management implications. *Mar. Mamm. Sci.* 26: 837–54.

Clark, C.W., Charif, R.A., Mitchell, S. and Colby, J. 1996. Distribution and behavior of the bowhead whale, *Balaena mysticetus*, based on analysis of acoustic data collected during the 1993 spring migration off Point Barrow, Alaska. *Rep. int. Whal. Commn* 46: 541–52.

Clark, C.W., Ellison, W.T. and Beeman, K. 1986. Acoustic tracking of migrating bowhead whales. *Oceans 86*: 341–6. [Available from IEEE Oceanic Engineering Society]:

Clark, C.W. and. Johnson, J.H. 1984. The sounds of the bowhead whale, *Balaena mysticetus*, during the spring migrations of 1979 and 1980. *Can. J. Zool.* 62: 1,436–41.

Delarue, J., Laurinolli, M. and Martin, B.. 2009. Bowhead whale (*Balaena mysticetus*) songs in the Chukchi Sea between October 2007 and May 2008. *J. Acoust. Soc. Am.* 126: 3,319–28.

George, J.C., Zeh, J., Suydam, R.S. and Clark, C.W. 2004. Abundance and population trend (1978–2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. *Mar. Mam. Sci.* 20: 755–73.

Givens, G.H., Edmondson, S.L., George, J.C., Suydam, R., Charif, R.A., Rahaman, A., Hawthorne, D.L., Tudor, B., Delong, R.A. and Clark, C.W. 2016. Horvitz-Thompson whale abundance estimation adjusting for uncertain recapture, temporal availability variation and intermittent effort. *Environmetrics*, 26: 1–16.

Givens, G.H., Edmondson, S.L., George, J.C., Tudor, B., DeLong, R.A. and Suydam, R. 2014. Weighted likelihood recapture estimation of detection probabilities from an ice-based survey of bowhead whales. *Environmetrics*, 26: 1–16.

International Whaling Commission. 2003. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 5:1–92.

Koski, W.R., Zeh, J. Mocklin, J., Davis A.R., Rugh, D.J., George, J.C. and Suydam, R. 2010. Abundance of Bering-Chukchi-Beaufort bowhead whales (*Balaena mysticetus*) in 2004 estimated from photo-identification data. *J. Cetacean Res. Manage.* 11(2): 89–99.

Marchetto, P., Strickhart, A., Mack, R. and Cheyne, H. 2012. Temperature compensation of a quartz tuning-fork clock crystal via post-processing. Presented to the IEEE International Frequency Control Symposium (FCS), 20–24 May 2012. Baltimore, MD, USA. 4pp.

Stafford, K.M., Moore, S.E., Laidre, K.L and Heide-Jorgensen, M.P. 2008. Bowhead whale springtime song off West Greenland. *J. Acoust. Soc. Am.* 124: 3,315–23.

Tervo, O.M., Parks, S.E. and Miller, L.A. 2009. Seasonal changes in the vocal behavior of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western Greenland. *J. Acoust. Soc. Am.* 126: 1,570–80.

Urazghildiiev, I.R. and Clark, C.W. 2013. Comparative analysis of localization algorithms with application to passive acoustic monitoring. *J. Acoust. Soc. Am.* 134: 4,418–26.

Würsig, B. and Clark, C.W. 1993. Behavior. pp.157–199. *In*: J. J. Burns, J. J. Montague and C. J. Cowles (ed.) *The Bowhead Whale*. Chapter 5, Special Publication No. 2. The Society for Marine Mammalogy.

Zeh, J. and Punt, A. 2005. Updated 1978–2001 abundance estimates and their correlations for the Bering-Chukchi-Beaufort Seas stock of bowhead whales. *J. Cetacean Res. Manage.* 7(2): 169–75.

Appendix 1. Sample periods for acoustic analysis

Date	Start time	End time	Duration (h)
13/04	0:00	2:00	2.0
13/04	15:44	18:30	2.8
13/04	20:00	22:00	2.0
14/04	8:32	10:32	2.0
14/04	12:38	13:38	1.0
14/04	14:34	16:34	2.0
15/04	6:38	8:38	2.0
15/04	13:12	15:12	2.0
16/04	3:00	4:00	1.0
16/04	13:30	15:30	2.0
16/04	20:30	22:30	2.0
17/04	6:15	8:15	2.0
17/04	11:00	12:00	1.0
17/04	13:00	16:17	3.3
17/04	20:03	21:00	0.9
18/04	12:00	13:00	1.0
18/04	14:00	15:00	1.0
18/04	16:00	17:00	1.0
18/04	18:00	21:00	3.0
19/04	0:00	1:00	1.0
20/04	2:00	3:00	1.0
20/04	4:00	5:00	1.0
20/04	12:00	13:00	1.0
20/04	14:00	17:00	3.0
21/04	10:00	11:00	1.0
21/04	13:00	14:00	1.0
21/04	14:55	16:05	1.2
22/04	0:00	1:00	1.0
22/04	10:30	18:00	7.5
22/04	19:00	21:00	2.0
23/04	0:00	0:15	0.3
23/04	5:00	6:00	1.0
23/04	8:00	9:00	1.0
23/04	10:10	18:00	7.8
23/04	22:00	23:59	2.0
24/04	6:00	8:00	2.0
24/04	10:00	14:00	4.0
24/04	15:00	18:00	3.0
24/04	18:00	19:00	1.0
24/04	22:00	23:59	2.0
25/04	16:00	19:00	3.0
25/04	22:00	23:59	2.0
26/04	7:00	9:00	2.0
26/04	10:17	14:00	3.7
26/04	18:00	21:00	3.0
9/05	10:03	14:00	4.0
9/05	15:57	17:51	1.9
9/05	18:30	21:00	2.5
10/05	9:00	10:20	1.3
10/05	10:20	14:00	3.7
10/05	16:00	20:00	4.0
11/05	3:00	5:00	2.0
11/05	8:30	10:00	1.5
11/05	16:00	21:00	5.0
12/05	3:00	5:00	2.0
12/05	9:00	14:00	5.0
12/05	16:00	20:00	4.0
12/05	22:00	23:59	2.0
13/05	2:00	4:00	2.0
13/05	6:00	8:00	2.0
13/05	10:02	14:00	4.0
13/05	22:00	23:59	2.0
14/05	5:00	6:00	1.0
14/05	16:00	18:00	2.0
15/05	14:00	14:40	0.7
16/05	4:00	5:00	1.0
16/05	10:02	10:50	0.8
16/05	12:45	14:00	1.3
16/05	16:00	20:00	4.0
16/05	23:00	23:59	1.0
17/05	10:02	14:00	4.0
18/05	8:00	10:00	2.0
18/05	11:00	12:00	1.0
19/05	4:00	5:00	1.0
19/05	10:00	13:00	3.0
19/05	14:00	15:00	1.0
19/05	17:00	19:00	2.0
20/05	12:00	13:00	1.0
27/04	4:00	7:00	3.0
27/04	10:18	16:18	6.0
27/04	20:00	22:00	2.0
28/04	4:00	6:00	2.0
28/04	10:00	14:00	4.0
28/04	16:00	20:00	4.0
28/04	22:00	23:59	2.0
29/04	4:00	7:00	3.0
29/04	10:00	14:00	4.0
29/04	16:00	20:00	4.0
29/04	22:00	23:59	2.0
30/04	1:00	2:00	1.0
30/04	2:00	3:30	1.5
30/04	8:30	12:30	4.0
30/04	14:30	18:30	4.0
30/04	21:00	23:00	2.0
1/05	12:00	13:00	1.0
1/05	14:08	18:12	4.1
1/05	20:00	21:00	1.0
1/05	22:00	23:59	2.0
2/05	2:00	5:00	3.0
2/05	8:00	10:00	2.0
2/05	13:00	14:59	2.0
2/05	15:00	16:00	1.0
2/05	21:00	22:00	1.0
2/05	22:00	23:59	2.0
3/05	4:00	7:00	3.0
3/05	10:00	14:00	4.0
3/05	15:00	19:50	4.8
4/05	0:00	1:00	1.0
4/05	17:00	18:00	1.0
5/05	10:10	14:00	3.8
5/05	14:40	15:15	0.6
5/05	16:17	20:00	3.7
6/05	10:10	14:11	4.0
6/05	16:01	20:00	4.0
7/05	14:00	17:00	3.0
7/05	21:00	23:59	3.0
8/05	0:00	2:00	2.0
8/05	3:00	5:00	2.0
8/05	7:00	9:00	2.0
8/05	10:49	14:03	3.2
8/05	16:00	18:17	2.3
9/05	0:00	2:00	2.0
9/05	7:00	9:00	2.0
20/05	16:00	18:00	2.0
20/05	20:00	22:00	2.0
20/05	23:00	23:59	1.0
21/05	10:00	11:00	1.0
21/05	12:00	13:00	1.0
21/05	19:00	21:00	2.0
21/05	21:30	23:30	2.0
22/05	7:00	8:00	1.0
22/05	9:00	10:00	1.0
23/05	3:00	4:00	1.0
23/05	8:00	8:59	1.0
23/05	23:00	23:59	1.0
24/05	5:00	6:00	1.0
24/05	10:00	14:00	4.0
25/05	0:00	2:00	2.0
26/05	4:00	5:00	1.0
26/05	11:00	12:00	1.0
26/05	17:00	18:00	1.0
27/05	10:00	12:00	2.0
27/05	16:00	17:00	1.0
28/05	2:00	3:00	1.0
28/05	7:00	8:00	1.0
28/05	10:00	11:00	1.0
28/05	15:00	17:00	2.0
29/05	1:00	2:00	1.0
29/05	4:00	5:00	1.0
29/05	11:00	12:00	1.0
29/05	14:00	15:00	1.0
30/05	11:00	12:00	1.0
31/05	10:00	12:00	2.0
31/05	17:00	18:00	1.0
1/06	17:00	18:00	1.0
1/06	18:00	19:00	1.0

Appendix 2. The Correlation Sum Estimation (CSE) algorithm

The correlation sum estimation (CSE) locator employs near-field beamforming spatial energy maximisation to estimate the location of an acoustic source. The formulation here is mathematically similar to that employed by Birchfield and Gillmore (2001, 2002) to study the localisation of acoustic sources in a room, although here bearing and range are computed, rather than azimuth and elevation as computed by those authors. Given N sensors, the average power output of an M sample record of a conventional delay and sum beamformer with a narrow band signal at frequency ω emitted from spatial location $\vec{x}$ is given by

$$P(\vec{x}) = \frac{1}{M}\sum_{k=1}^{M}\sum_{n=1}^{N}\sum_{m=1}^{N} y_n(k)\, y_m^*(k)\, e^{i\omega(\tau_n(\vec{x})-\tau_m(\vec{x}))}$$

where $\tau_n(\vec{x})$ is the propagation time from location $\vec{x}$ to sensor *n*, and $y_n(k)$ is the signal received at sensor *n* at discrete sample time *k*. Observing that in the phasor domain, the complex exponential represents a time shift operator, and exchanging the order of the summations, it may be written

$$P(\vec{x}) = \frac{1}{M}\sum_{n=1}^{N}\sum_{m=1}^{N}\left[\sum_{k=1}^{M} y_n(k)\, y_m^*\left(k - \frac{\tau_n(\vec{x})-\tau_m(\vec{x})}{T}\right)\right]$$

The quantity in brackets is observed as the M point cross-correlation of $y_n(k)$ and $y_m(k)$ evaluated at discrete sample time $\frac{\tau_n(\vec{x})-\tau_m(\vec{x})}{T}$.That is,

$$P(\vec{x}) = \frac{1}{M}\sum_{n=1}^{N}\sum_{m=1}^{N} Corr(y_n y_m)\big|_{\frac{(\tau_n(\vec{x})-\tau_m(\vec{x})}{T}}$$

where *T* is the temporal sample period. It is physically intuitive that the value of $\vec{x}$, which maximises this sum, corresponds to the location of the source. One advantage to this technique is that the entire set of pair-wise cross-correlation functions may be pre-computed in the frequency domain using the Fast Fourier Transform (FFT), which is much more computationally efficient than computation in the time domain. When searching space for the point of maximum power, the correlation values in a series of tables are merely looked up, requiring no further correlation computation. If the maximum value of a pair-wise cross-correlation function does not exceed a prescribed threshold value, then that pair is excluded from the sum. If the number of remaining channels does not exceed a prescribed number, then failure is indicated and the calculation is aborted.

The remainder of the algorithm consists of a stochastic search over space to find the point of maximum average power. Initially, 30,000 points are randomly chosen inside a circle of radius R centred at the origin. The average power is calculated at each point and the point $\hat{\vec{x}}$ of maximum power is located. The centroid of the set $\sum\vec{x}_i$ is also computed. The procedure is iterated with the circle centered at the point of maximum power observed over all previous iterations and a radius equal to the centroid magnitude of the previous iteration. The procedure continues until the magnitude of the centroid is less than a prescribed value.

Appendix 3. Error estimation in the Correlation Sum Estimation (CSE) locator v2.3

Estimation of standard errors and confidence intervals for the location estimates produced by the CSE locator is extremely complex. Below, a heuristic approach is decribed. An advantage of this approach is that it allows us to incorporate more sources of uncertainty, including statistical ‘process errors’ beyond standard sampling/estimation error. A disadvantage is that there is no assurance that the resulting confidence interval actually has 95% coverage. Due to this concern, the intervals are referred to as ‘heuristic 95% confidence intervals’ to distinguish them from 95% confidence intervals derived directly from statistical theory.

Although the true coverage probability of these CIs may be only approximately correct, a relatively large degree of coverage rate error can be tolerated for the present purpose. Specifically, for the population abundance estimate of Givens *et al.* (2013), the CIs produced here are used only to estimate weights for time-smoothing probabilities that offshore distances exceed 4km. The estimated smooth probability is fairly insensitive to the choice of weights. Furthermore, in any time interval (say, 1h), let us suppose that the CI coverage probabilities are relatively inaccurate but such inaccuracies are not correlated with offshore distance. Admittedly this may be a strong assumption, but to the extent that it is true, the errors in the weights employed at the local smooth fit for this time interval would tend to cancel each other out, thereby leaving the smooth fit relatively unbiased.

Now for the discussion of the components of uncertainty reflected in our heuristic estimates of standard errors and confidence intervals for locations.

(1) Sources of location error
The major sources of error in the CSE locator algorithm are:

(a) Statistical error
The CSE locator operates by maximisation of the sum of pair-wise correlations of the array’s sensors. The acoustic data from each sensor include noise. The statistical error measures how much the noise affects the location estimate.

(b) Error due to sensor positional uncertainty
The CSE locator algorithm assumes that the locations of the sensors are known exactly; in reality, this is never true.

(c) Error due to variation in the speed of sound
Like the sensor positions, the CSE locator algorithm assumes that the speed of sound is known with great accuracy. In marine environments this could become a significant source of error.

(d) Error due to uncertainty in the sensors’ clock rates
Clock rate uncertainty can be mitigated to some degree by aligning the sensor recordings with respect to a bang or an FM sweep, and amortising the error uniformly across the sensor recordings between the

start and end markers. De-convolving the sensor unit's oscillator crystal temperature history can also mitigate temperature-induce clock rate drift.

2. Error estimation

(a) Statistical location error

The question here is 'Given the (noisy) sensor data, how accurately is the location of the energy maximum known?' Accordingly, our goal is to compute the variance of the energy maximum location estimator $\hat{\vec{x}}$. While searching for an energy maximum, the CSE locator maintains a list of the top 1,000 highest candidate energies and coordinates. The location estimator variance was estimated by computing the sample variance of this set.

$$\sigma_x^2 = \frac{1}{N-1}\sum (x_i - \bar{x})^2$$

The same approach is used for σ_y^2 and (optionally) σ_z^2.

Confidence intervals for x, y, and z are constructed independently using Gaussian assumptions. (The possible alternative approach based on a histogram of the 1,000 candidates is a topic for future work.) This study has not yet implemented a non-independent approach based on a multivariate Gaussian approach for the three coordinates jointly.

(b) Systematic location error due to sensor position uncertainties

Systematic error due to sensor position uncertainty is estimated using numerical sensitivities of the error maximum with respect to small changes in the sensor positions. To obtain the coordinate confidence limits, this study employs a first order Taylor expansion of the energy as a function of location vector $\vec{x}$:

$$E = E(\vec{x}^{\max}) + \delta\vec{x}\cdot\nabla_{\vec{x}'}E(\vec{x}')\,|_{\vec{x}'=\vec{x}^{\max}} + \text{higher order terms}$$

Taking, for example, the x component, to first order it is

$$E = E(\vec{x}^{\max}) + \delta x \frac{\partial}{\partial x'} E(\vec{x}')\,|_{\vec{x}'=\vec{x}^{\max}}$$

Unfortunately, for a true maximum of the energy function, the derivative $\frac{\partial}{\partial x'} E(\vec{x}')|_{\vec{x}'=\vec{x}^{\max}}$ is zero. However, the first order representation is linear in δx, approximating the energy surface as a cone with a constant slope along each coordinate axis. Therefore, if a suitable point away from the energy maximum at the apex of the cone was chosen, the partial derivative can be numerically estimated $\frac{\partial}{\partial x'}E(x)$. Conveniently, the CSE locator supplies us with an appropriate distance scale, the median centroid distance, d. The choice was made to compute the numerical derivative at distances $\Delta x = \Delta y = \Delta z = \frac{d}{2}$ from the energy maximum.

Numerical calculations of the derivatives can be very difficult to compute; the simple two point $\frac{\Delta y}{\Delta x}$ is frequently not accurate enough and it gives no bounds on the accuracy. Ridder's method was chosen to compute the derivatives and a bound on their errors. Conceptually, Ridder's method computes the ratio $\frac{\Delta y}{\Delta x}$ for a decreasing series of Δx and extrapolates to $\Delta x = 0$. If the error bound returned by Ridder's method is larger than the derivative estimate, the CSE locator displays a warning message, but does not signal failure.

It was sought to compute the sensitivity of the source location with respect to the change in sensor position location $\vec{s}_i$. Concentrating on the x component of the i^th^ sensor position vector and invoking the chain rule for partial derivatives

$$\frac{\partial x}{\partial s_{i,x}} = \frac{\partial E}{\partial s_{i,x}} \frac{\partial x}{\partial E}$$

$$\frac{\partial x}{\partial s_{i,x}} = \frac{\frac{\partial E}{\partial s_{i,x}}}{\frac{\partial E}{\partial x}}$$

This is the sensitivity of location coordinate, x, with respect to the i^th^ sensor position coordinate $s_{i,x}$. The partial derivatives appearing in the numerator and denominator are estimated using Ridder's method. For a finite uncertainty in the i^th^ sensor position's coordinate, $\Delta s_{i,x}$, the change is computed in x, Δx, to be

$$\Delta x = \frac{\frac{\partial E}{\partial s_{i,x}}}{\frac{\partial E}{\partial x}} \Delta s_{i,x}$$

which is the error estimate that is sought. Assuming the input of 95% confidence limit of $\Delta s_{i,x}$, The 95% confidence limit of Δx was obtained. The CSE locator repeats this calculation for the x, y and (optionally) z position components for each sensor used in the calculation of the energy (i.e. the correlation sum). A similar calculation is performed to obtain an estimate of the uncertainty in the location coordinates due to uncertainty in the speed of sound. Finally, the errors are summed coherently by components to obtain an estimate of the upper bound of the uncertainty in the energy maximum location.

(c) Systematic location error due to speed of sound uncertainty

The systematic error due to the uncertainty in the speed of sound is estimated using the same methodology used to estimate the systematic error due to uncertainties in the sensor locations.

(d) Clock drift error

Due to temperature changes and aging of the crystal oscillators, MARU clocks may drift over time by rates of several seconds per day. MARU data extraction software mitigates the error in two ways: (1) oscillator temperatures are logged during the duration of the deployment and acoustic data are compensated for temperature drift using a function measured in the laboratory, and (2) any residual error is amortised over the interval between synchronisation points. Amortisation of a few seconds per day is actually a very small correction. For example, assume the clock drift was –3 sec/day. Since there are 86400 sec/day, one audio frame must be inserted every $\frac{86400}{3}$ = 28800 frames, a minor correction. By amortising the error this way, it is never more than one sample period away from the correct absolute time. Therefore, it is believed that it is justified to ignore clock drift error.

Cue rates and surfacing characteristics of sei whales (*Balaenoptera borealis*) in the Falkland Islands

CAROLINE R. WEIR, MARIA TAYLOR, PAMELA A.Q. JELBES AND ANDREW STANWORTH

Falklands Conservation, Jubilee Villas, Ross Road, Stanley, Falkland Islands

Contact e-mail: whales@conservation.org.fk

ABSTRACT

The cue rate (CR: blows per whale per hour), surfacing characteristics and swim speeds of sei whales (*Balaenoptera borealis*) were quantified from focal follows carried out at Berkeley Sound (East Falkland) between January and May 2017 and off the west coast of West Falkland between February and April 2018. In Berkeley Sound, focal follows were conducted from Cape Pembroke lighthouse and from a small boat. In West Falkland all focal follows were conducted from a yacht. Thirty-seven focal follows of sei whale individuals or groups (2–5 individuals) were analysed to produce CRs ranging from 21.99 to 46.73, with a mean of 31.46 (SD = 5.12). There was no significant difference in the CRs observed from shore vs. boat platforms or between the two study areas. Maximum submergence times exceeding 13min were recorded from both individuals and groups. The durations of 51 whale surfacing events had a mean of 6.4s (SD = 1.7). The average swim speed during boat-based sei whale focal follows was 5.7kmh−1. The inter-breath intervals (IBIs) recorded from 13 solitary individuals ranged from 77.2 to 180.1s, with an overall mean of 118.6s (SD = 137.6). A combined approach incorporating IBI parameters and sequence pattern was used to classify 270 IBIs into surface dives (mean = 37.2s), intermediate dives (mean = 113.7s) and true dives (mean = 332.6s). Individuals showed marked variation in dive pattern, with some exhibiting clear cycles of true dives interspersed with surface bouts while others routinely took intermediate-duration dives interspersed by single surfacings. Sei whales in Berkeley Sound exhibited a higher proportion of surface dives than whales in West Falkland, and those surface dives were of lower mean and median IBI. Individual sei whales had surface bouts comprising a mean of 3.8 blows and a mean IBI of 33.4s. These are the first quantifiable data on surfacing-dive patterns and CRs for sei whales in the Falkland Islands and across the wider range of the species. The data have conservation and management relevance, including addressing availability bias for line transect and cue count abundance estimates, incorporation into vessel strike modelling, and understanding foraging behaviour.

KEYWORDS: CUE RATES; DIVING; FALKLAND ISLANDS; SOUTH ATLANTIC; SOUTHERN HEMISPHERE; SURVEY – AERIAL; SURVEY – SHORE-BASED; SURVEY – VESSEL; SWIM SPEED

INTRODUCTION

The collection of data on cetacean dive duration and surfacing behaviour is relevant to several aspects of their management and conservation including assessing energetic costs (Sumich, 1983; Acevedo-Gutiérrez *et al.,* 2002), investigating responses to anthropogenic disturbance (Ljungblad *et al.,* 1988; Argüelles *et al.,* 2016), and producing estimates of the amount of time that animals are at the surface and thus available for visual detection during abundance and cue-counting surveys (Øien *et al.,* 1990; Hiby, 1992; Heide-Jørgensen and Simon, 2007). In addition, knowledge of the breath frequency, dive interval, surfacing behaviour and swim speed of whales is important for understanding the conditions in which whale encounters can lead to vessel strikes (Nowacek *et al.,* 2001; Argüelles *et al.,* 2016). Consequently, the dive behaviour of most large baleen whale species has been studied, including the North Atlantic right whale (*Eubalaena glacialis*: Nowacek *et al.,* 2001), southern right whale (*E. australis*: Argüelles *et al.,* 2016), bowhead whale (*Balaena mysticetus*: Würsig *et al.,* 1984; 1985; Ljungblad *et al.,* 1988), blue whale (*Balaenoptera musculus*: Lagerquist *et al.,* 2000; de Vos *et al.,* 2013), fin whale (*B. physalus*: Stone *et al.,* 1992; Jahoda *et al.,* 2003; Heide-Jørgensen and Simon, 2007), Bryde's whale (*B. brydei*: Alves *et al.,* 2010), common minke whale (*B. acutorostrata*: Stockin *et al.,* 2001; Heide-Jørgensen and Simon, 2007), Antarctic minke whale (*B. bonaerensis*: Friedlaender *et al.,* 2014), humpback whale (*Megaptera novaeangliae*: Heide-Jørgensen and Simon, 2007; Witteveen *et al.,* 2008) and the gray whale (*Eschrichtius robustus*: Sumich, 1983).

The duration and surfacing behaviour of cetaceans has been monitored using various techniques including satellite telemetry (Lagerquist *et al.,* 2000), time-depth recorders (TDRs) attached by suction-cups (e.g. Friedlaender *et al.*, 2014; Argüelles *et al.,* 2016) and visual observations (e.g. Stone *et al.,* 1992; Heide-Jørgensen and Simon, 2007; de Vos *et al.,* 2013). It has been monitored from a wide variety of platforms including aircraft (e.g. Würsig *et al.,* 1984; Ljungblad *et al.,* 1988), boats (e.g. Jahoda *et al.,* 2003; de Vos *et al.,* 2013) and shore vantage points (e.g. Stone *et al.,* 1992; Heide-Jørgensen and Simon, 2007).

The dive behaviour of the sei whale (*Balaenoptera borealis*) has been little studied in comparison with other baleen whales, perhaps primarily due to the offshore, pelagic habitat usually occupied by the species and its unpredictable occurrence in many areas (Horwood, 1987). During a small number of sightings in the Magellan Strait (Chile) sei whales were reported to take 5–7min dives, followed by four or five blows at the surface (Acevedo *et al.,* 2017), although systematic recording of dive times was not reported. Some respiration intervals were also recorded from whale watching vessels in the Gulf of Maine in 1986, where sei whales mostly undertook shorter dives (≤ 90s) consistent with observations of surface feeding but also exhibited longer dives of 6–11min duration (Schilling *et al.,* 1992). Two sei whales were tagged with acoustic time-depth transmitters off Japan in 2013, providing data for 10 and 32hr respectively and revealing overall mean dive durations of around 3min and a maximum dive of 12.2min (Ishii *et al*., 2017).

During 2017 and 2018, research was conducted on sei whales in the Falkland Islands to collect baseline information on their distribution, ecology and behaviour (Weir, 2017; 2018). This paper presents data on the cue rate, swim speed, and the dive and surfacing characteristics of sei whales in coastal areas off East and West Falkland. The data were primarily collected to generate correction factors for an aerial abundance survey carried out in Berkeley Sound in 2017, but also because of their relevance to ongoing work including foraging behaviour and understanding vessel interactions.

METHODS

Data collection

A sei whale survey was carried out between January and May 2017 in the Berkeley Sound candidate Key Biodiversity Area (cKBA) on the east coast of the Falkland Islands (Fig. 1). A second study occurred off West Falkland between February and April 2018, focussing on the King George Bay and Queen Charlotte Bay cKBAs (Fig. 1). Both study areas were located in coastal waters with depths of ≤ 60m.

Whale surfacing behaviour was monitored from shore and boat platforms. In Berkeley Sound, shore-based observations were conducted from the Cape Pembroke lighthouse at 28m eye height. The lighthouse provided unrestricted views over Port William and across a wide expanse of open Atlantic Ocean (Fig. 1). A single observer conducted standardised visual watches for whales during favourable weather conditions (Beaufort sea state ≤ 3, visibility ≥ 5km) using the naked eye and *Bushnell Marine* 7 × 50 binoculars with a

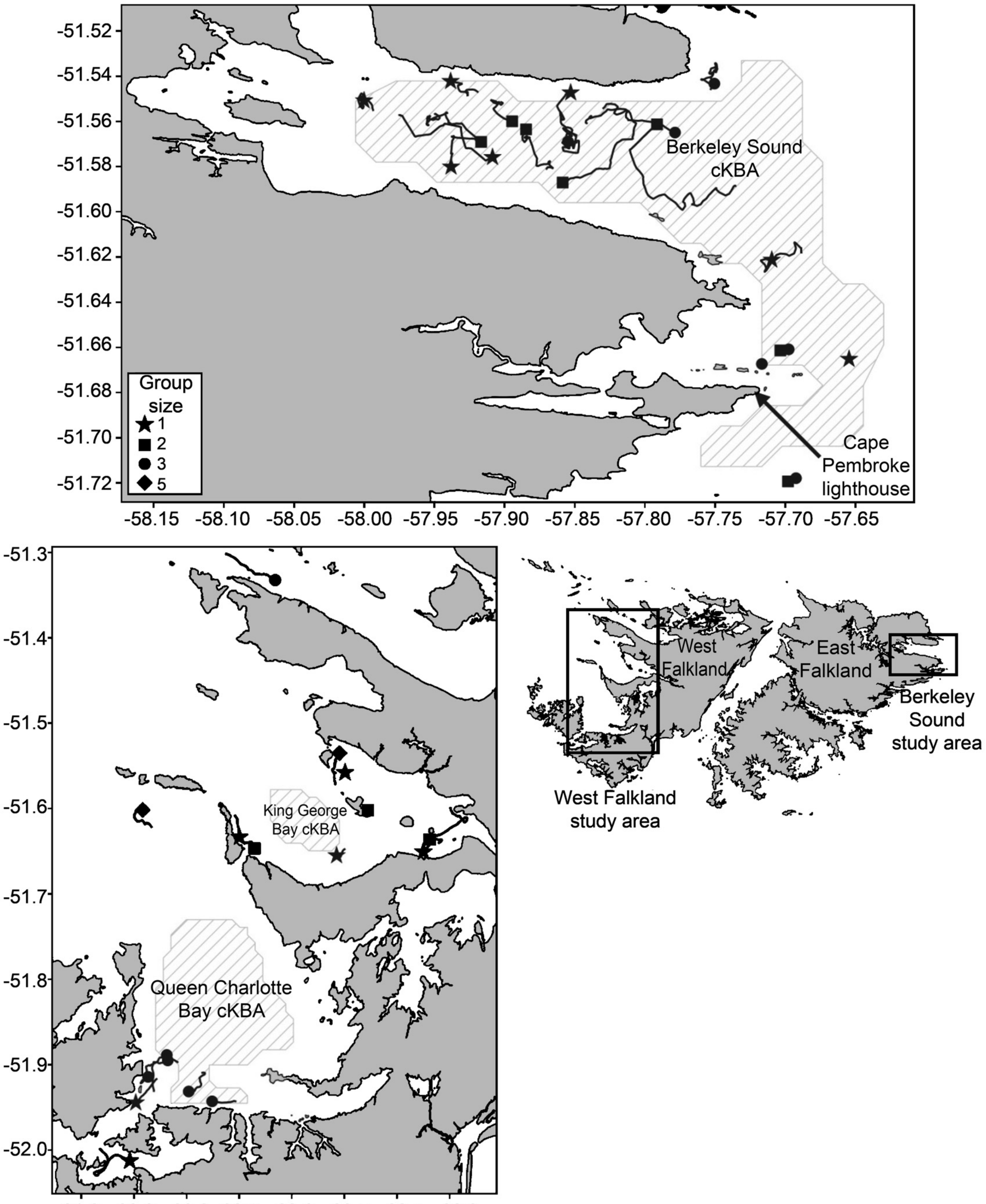


Fig. 1. Location of the Berkeley Sound and West Falkland study areas in the Falkland Islands, showing the spatial extent of the candidate Key Biodiversity Areas, the initial sighting locations for the 37 sei whale focal follows included in the study, and the tracks of the boat-based focal follows.

vertical reticle. Boat surveys were conducted in Berkeley Sound using a 6.5m rigid-hulled inflatable boat (RHIB) with twin 125-hp engines. A 19.5m motor-sailing vessel, providing a 5.1m observation eye height, was used throughout the West Falkland survey. At least two dedicated observers searched for whales continuously with the naked eye during boat surveys. More information on the general methods implemented during the surveys is available in Weir (2017; 2018).

Standardised information including group size, position and behaviour was logged for all sei whale sightings. A whale group was defined as a number of associated animals moving in the same direction and separated from one another by no more than three body lengths. Group size was visually estimated and, during small boat work, confirmed using photo-identification whenever possible. A dedicated focal follow (FF; Altmann, 1974) to collect surfacing data was initiated when the following criteria were met: (1) the sighting was at sufficient proximity that the observer was confident of detecting all blows; (2) the group size and spacing were stable so that the target animal(s) could be confidently tracked over time; and (3) prevailing light and sea conditions were favourable for detecting blows. Each focal follow ceased either: (1) when at least one hour of data had been collected; (2) if the focal animal or group was lost; or (3) immediately that group composition changed.

During each FF, whale surfacing events or ‘cues’ were logged verbally into a time-calibrated digital voice recorder (DVR) by the observer or directly into a laptop by a second person using a custom-designed Excel spreadsheet with an automatic timestamp (1s accuracy). A cue was defined as any appearance of a whale at the surface; this predominantly comprised the blow, but also included a small number ($n = 7$; 0.6%) of surfacings where the head, back or dorsal fin broke the surface without a visible blow being observed (consistent with Heide-Jørgensen and Simon, 2007).

A distance of at least 200m was usually maintained between the whales and the boat to minimise disruption to behaviour. At the end of each surfacing bout the vessel relocated to the position where the whales had submerged to maximise the detection of the subsequent surfacing. During RHIB surveys the engines were often switched off so that surfacing animals could be detected audibly as well as visually. Photo-identification data were collected using a 100–400mm zoom lens, either prior to commencing the behavioural work or opportunistically during the focal follow. Short video clips of sei whales were taken on an opportunistic basis using *GoPro* cameras (14–30fps) during 2017 and using a *DJI Phantom 4* drone (24–30fps) during 2018.

Data analysis

Only FFs that commenced when animals were < 5km from the lighthouse were included in the shore-based dataset, since it becomes difficult to accurately monitor behaviour when whales are ≥ 5km from a shore vantage point (Würsig *et al.,* 1985). For all datasets, FFs of < 20min duration were omitted from the analysis to reduce potential bias from long dives being under-recorded. A total of six shore-based FFs and 31 boat-based FFs were suitable for data analysis after this initial quality control.

The time (1s accuracy) of every whale cue logged verbally using the DVR method was extracted from the recordings using the software Audacity 2.1.2 (*http://www.audacityteam.org*). The cue rate (CR), defined as the number of cues per whale per hour, was calculated for each focal follow as: CR = $(B/D*60)/G$. Where, B is the total number of cues during D, minus 1; D is the total duration (min) of the FF, from the time of the first cue recorded to that of the last; and G is the number of individuals in the FF.

Since it was not possible to assess accurate dive duration of individual whales within a group (due to lack of overt natural markings that would make individuals recognisable at distance), a minimum dive duration (MDD) was produced for each FF. The MDD was defined as the maximum amount of time when all individuals within a focal group were submerged and provides an indication of the minimum dive duration of any individual within the focal group. A minimum average swim speed was calculated for boat-based FFs, by calculating the distance travelled by the boat during each FF using a QGIS (*https://qgis.org*) script. This definition produces a straightline horizontal swim speed across the surface and does not account for vertical movements or finer-scale spatial movements.

The duration of whale surfacing events (WSE; i.e. the time taken for an individual’s body to complete a surfacing) was assessed from the video clips. Only WSEs where exact emergence and submergence times were evident were included in the analysis. Each WSE was analysed frame by frame, and the start time was extracted for the emergence of the rostrum or splashguard, or the appearance of a surge of water such as the bow-wave from the head or exhalations that commenced subsurface (i.e. any cue at the surface of the emerging whale). The completion of the WSE was defined as the total disappearance of the whale’s body below the surface (usually ending with the dorsal fin tip).

Only FFs conducted on solitary sei whales ($n = 13$; see Table 1) were used for detailed investigation of dive types and cycles. Inter-breath intervals (IBIs) were calculated as the time elapsed between two consecutive surfacings by an individual. Only data from complete dive cycles were used to ensure adequate representation of longer dives. A complete dive cycle was defined as a long, deeper dive (i.e. true dive) followed by a full surfacing bout, or vice versa (depending on where in the dive cycle the focal follow had commenced). Initial examination of IBIs against dive sequence number for each whale revealed obvious inter-individual differences in sei whale dive pattern (Fig. 2). Consequently, it was not considered useful to define dive types by merging the IBIs from all whales and determining a single IBI cut-off point via a log-survivorship analysis (e.g. Stone *et al.,* 1992; Kopelman and Sadove, 1995; Jahoda *et al.,* 2003). Rather, a combined approach was developed that allowed for inter-individual variation in dive pattern and dive type duration. Firstly, the dive sequences for each individual were visually-inspected to determine whether or not differentiated dive types (i.e. dives that were clearly surface or true) were apparent based on duration and pattern of occurrence. For individuals that clearly exhibited differentiated dive types ($n = 9$), each dive was visually-categorised as surface, true or intermediate based solely on examination of that individual’s dive sequence and prioritising pattern over IBI

Table 1

Sei whale cue rates recorded during 37 focal follows (FF) in the Berkeley Sound (BS) and West Falkland (WF) study areas using shore, rigid-hulled inflatable boat (RHIB) and yacht platforms. Behaviour is abbreviated as: T = Travel, F = Forage, M = Milling.

FF No.	Date	Start time (UTC)	Platform	Photo-ID no.	FF durn. (min)	Group size	Average speed (kmh^{-1})	Overall behaviour	Total no. of blows	Cue rate (cues/whale/hr)
BS–1	07/02/17	15:45	Shore	–	33.1	1	–	T	16	27.2
BS–2	07/02/17	19:05	Shore	–	39.2	2	–	T	42	31.4
BS–3	08/02/17	12:41	Shore	–	123.8	2	–	T	113	27.1
BS–4	14/02/17	17:31	Shore	–	58.2	3	–	T	108	36.8
BS–5	19/03/17	14:00	RHIB	BS–55	60.4	1	3.5	F	48	46.7
BS–6	02/04/17	13:27	RHIB	BS–62, 72	93.3	2	7.2	T	96	30.5
BS–7	09/04/17	17:54	RHIB	BS–62	21.6	1	7.5	T	12	30.5
BS–8	09/04/17	13:48	RHIB	BS–74	40.3	1	7.1	F	27	38.8
BS–9	09/04/17	15:46	RHIB	BS–73	51.3	1	7.3	F	36	41.0
BS–10	17/04/17	17:46	Shore	–	54.0	3	–	F	105	38.5
BS–11	17/04/17	19:15	Shore	–	46.2	3	–	T	72	30.8
BS–12	23/04/17	16:35	RHIB	BS–62, 88	21.9	2	8.1	T	23	30.1
BS–13	23/04/17	15:12	RHIB	BS–85, 86, 87	48.1	3	6.1	F	80	32.8
BS–14	08/05/17	15:47	RHIB	BS–97	49.5	1	3.8	F	20	23.0
BS–15	08/05/17	17:10	RHIB	BS–82, 89, 94	42.0	3	7.1	N/K	73	34.3
BS–16	16/05/17	13:59	RHIB	BS–82, 89	74.4	2	6.9	T	95	37.9
BS–17	16/05/17	16:05	RHIB	BS–95, 99	47.1	2	6.1	N/K	51	31.9
BS–18	16/05/17	17:07	RHIB	BS–94	83.0	1	4.7	T	34	23.8
BS–19	22/05/17	14:50	RHIB	BS–97, 99	68.8	2	5.5	F	52	22.2
BS–20	29/05/17	14:38	RHIB	BS–89, 97, 99	56.3	3	6.4	T	79	27.7
WF–1	25/02/18	15:08	Yacht	WF–2, 3, 5	84.7	3	5.4	F	137	32.1
WF–2	03/03/18	09:45	Yacht	–	90.0	1	–	F	44	28.7
WF–3	03/03/18	13:03	Yacht	WF–9, n/a	96.8	2	6.0	T	104	31.9
WF–4	03/03/18	17:51	Yacht	WF–12, n/a	53.5	2	4.8	T	55	30.3
WF–5	03/03/18	18:46	Yacht	WF–12	38.2	1	4.6	T	15	22.0
WF–6	05/03/18	13:02	Yacht	–	22.2	3	8.3	T	37	32.4
WF–7	06/03/18	12:09	Yacht	WF–15, n/a	109.2	3	4.1	T	165	30.0
WF–8	06/03/18	17:06	Yacht	WF–16, 17, 18	61.4	3	4.3	N/K	90	29.0
WF–9	06/03/18	18:37	Yacht	WF–19, 20, 21	23.8	3	3.7	T	40	32.7
WF–10	10/03/18	16:51	Yacht	WF–24, 25, 26, 27, 28	66.4	5	4.6	T	171	30.7
WF–11	15/03/18	14:16	Yacht	–	24.6	1	4.8	N/K	14	31.7
WF–12	15/03/18	15:50	Yacht	WF–39	72.2	1	3.6	M	37	29.9
WF–13	16/03/18	10:48	Yacht	WF–55, 56, 57, 58, 59	38.1	5	5.3	T	111	34.7
WF–14	19/03/18	19:43	Yacht	WF–61, 88	34.3	2	–	M	41	35.0
WF–15	24/03/18	19:52	Yacht	WF–15, 97, 98	62.1	3	6.0	T	105	33.5
WF–16	25/03/18	18:08	Yacht	WF–100	85.7	1	7.7	T	43	29.4
WF–17	26/03/18	14:40	Yacht	–	54.1	1	5.9	T	25	26.6

duration. For example, dives 13 and 32 during BS-18 were classified as surface dives based on the consistent sequence of true dives interspersed by shorter surface dives (Fig. 2g), even though their IBIs were more than double those of most other surface dives exhibited by that individual.

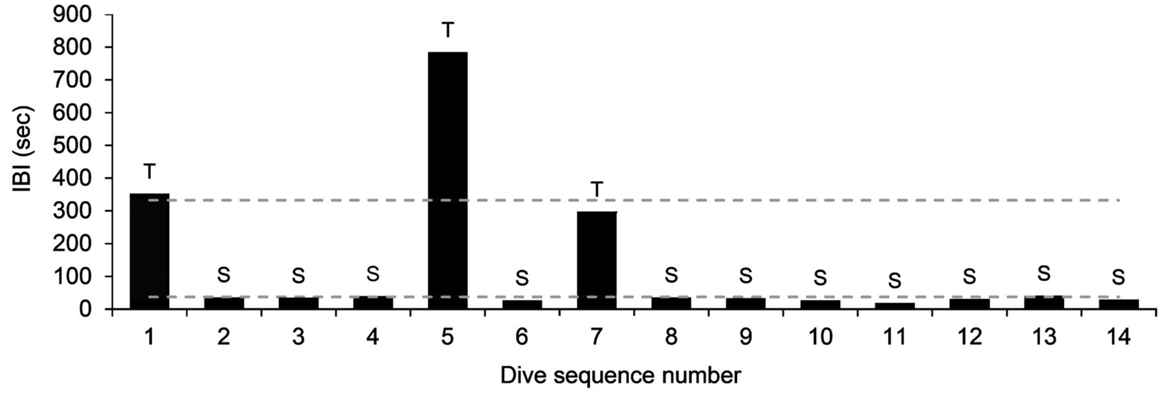
Secondly, the percentage difference of each IBI (pcIBI) from the overall mean IBI of all dives combined was calculated separately for each individual whale, as a method to incorporate intra-individual variation in the classification of the dive types. The pcIBI values were ranked in order for the nine individuals that exhibited differentiated dive types to assess whether they comprised non-overlapping categories with respect to the visually-identified dive types. All pcIBI values of ≤ 55.8 related to visually-identified surface dives. All pcIBI values of > 147 were related to true dives. All pcIBI values of 72.7 to 140.4 had been visually-classified as intermediate dives. However, a small number of dives that had been visually-allocated to surface or intermediate types ($n = 23$) occurred in a zone of overlapping pcIBI value (56.1 to 72.6) and therefore remained uncategorised using this method.

The third method incorporated inter-individual variation in the duration of dive types, by ranking the IBIs of the nine whales that exhibited differentiated dive types to assess the cut-off values that distinguished between the visually-identified dive types. All dives with an IBI of ≤ 64s related to visually-identified surface dives. All IBI's > 169.7s were related to true dives, while IBI's of 117.2 to 126s formed a non-overlapping group of intermediate dives. However, there were areas of overlap in IBI duration between visually-identified surface and intermediate dives ($n = 40$; 64.7–116s) and between intermediate and true dives ($n = 13$; 126.1–165s), and those dives therefore remained uncategorised.

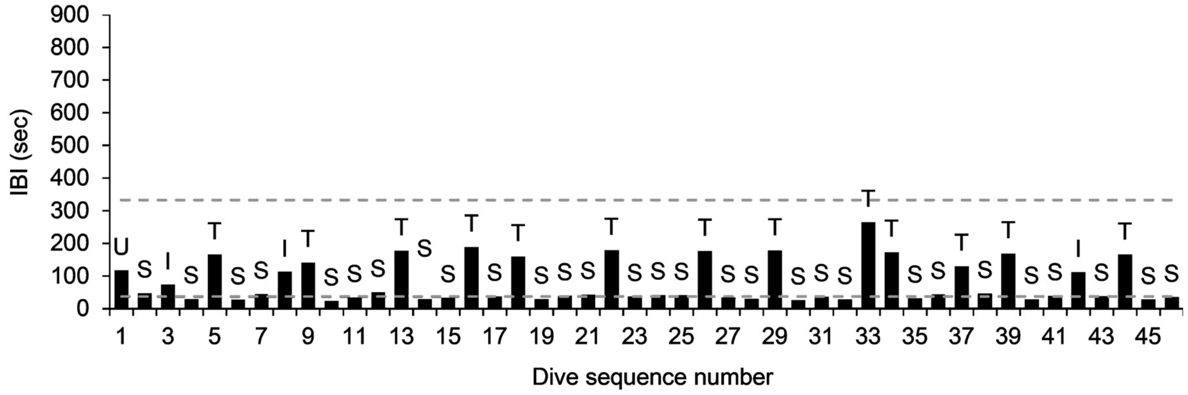
The pcIBI and IBI cut-off values identified for each dive type using the above methods were then applied to categorise the dives recorded in the four non-differentiated focal follows. An overall dive type was then assigned. For the nine whales with differentiated dive patterns, a final dive type was allocated only when at least two of the three methods produced the same dive type category (thus potentially allowing the visually-identified dive type to be over-ruled by the IBI approaches). For the four whales with undifferentiated dive patterns, a final type was allocated only when the pcIBI and IBI methods produced the same dive type.

For the nine individuals with differentiated dive patterns, complete dive cycles were extracted to examine surface bout parameters. Surfacing bouts that included intermediate dives were omitted. The surfacing bout duration (SBD) was

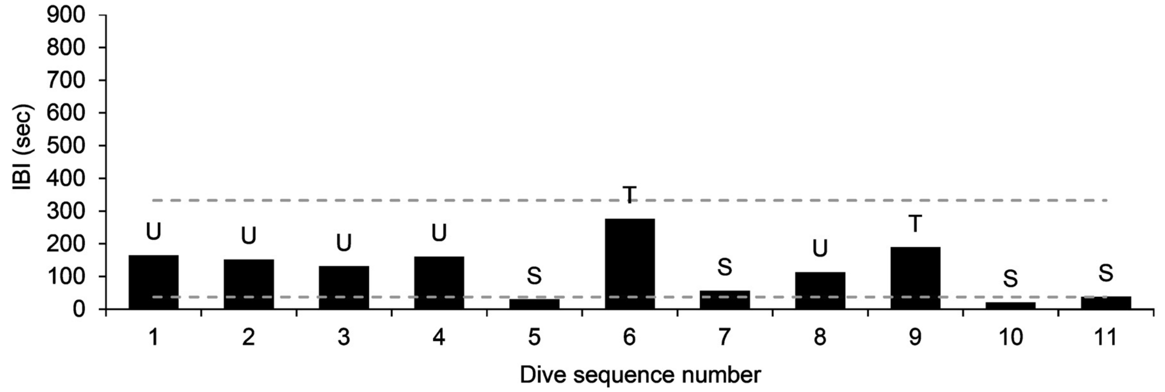
(a) BS–1



(b) BS–5



(c) BS–7



(d) BS–8

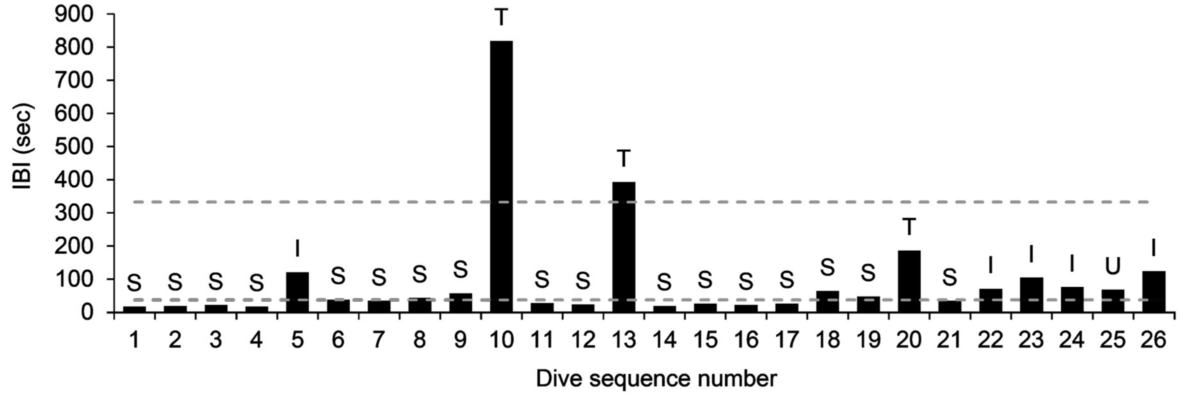
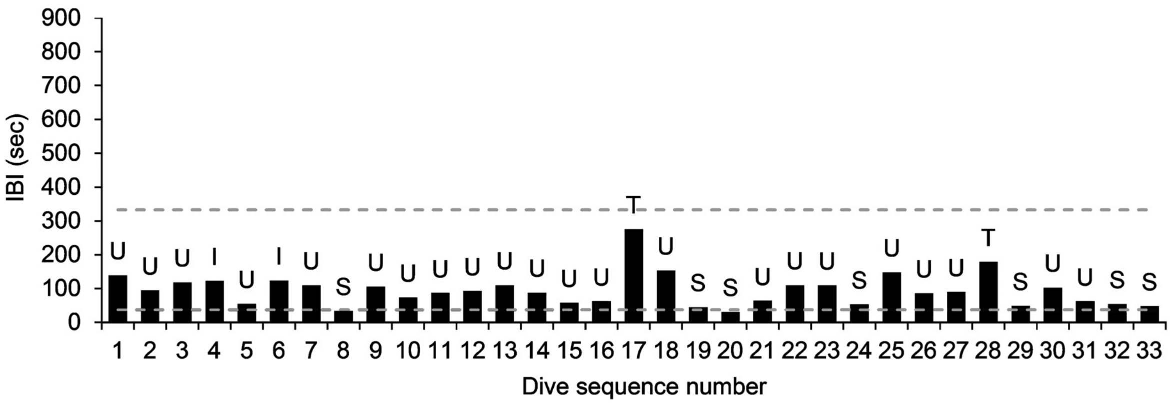
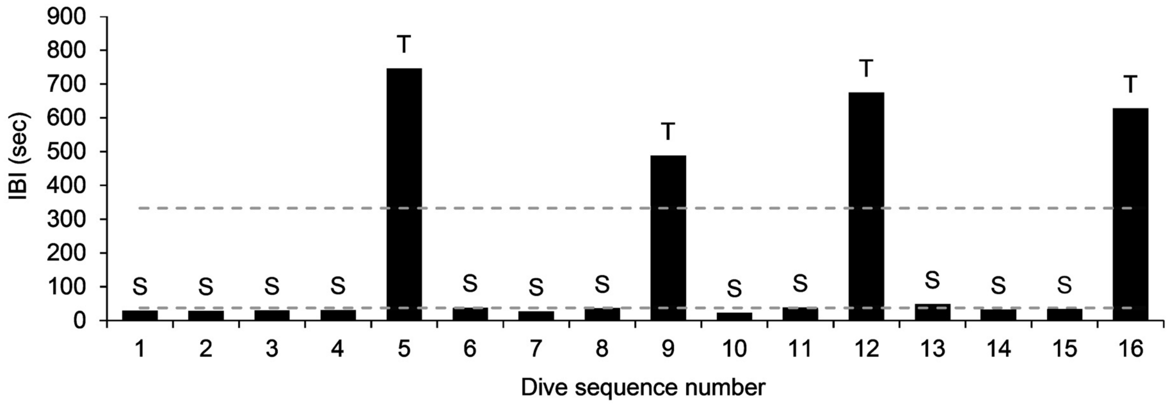


Fig. 2. Inter-breath intervals (IBIs) for complete dive cycles recorded during focal follows (FF) of 13 individual sei whales (a–m). Dashed lines show the mean IBI for surface and true dives for the combined dataset. Dive types assigned during the analysis are labelled: S – Surface, I – Intermediate, T – True, U – Unclassified.

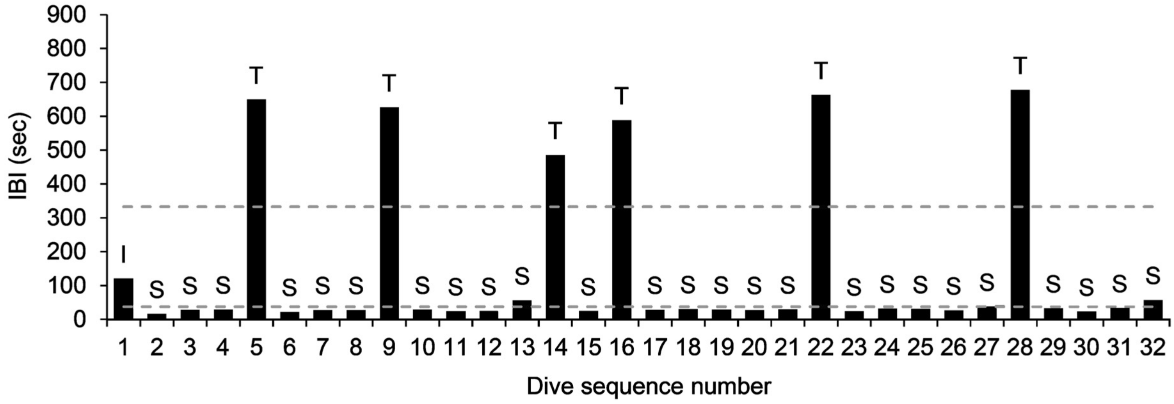
(e) BS–9



(f) BS–14



(g) BS–18



(h) WF–2

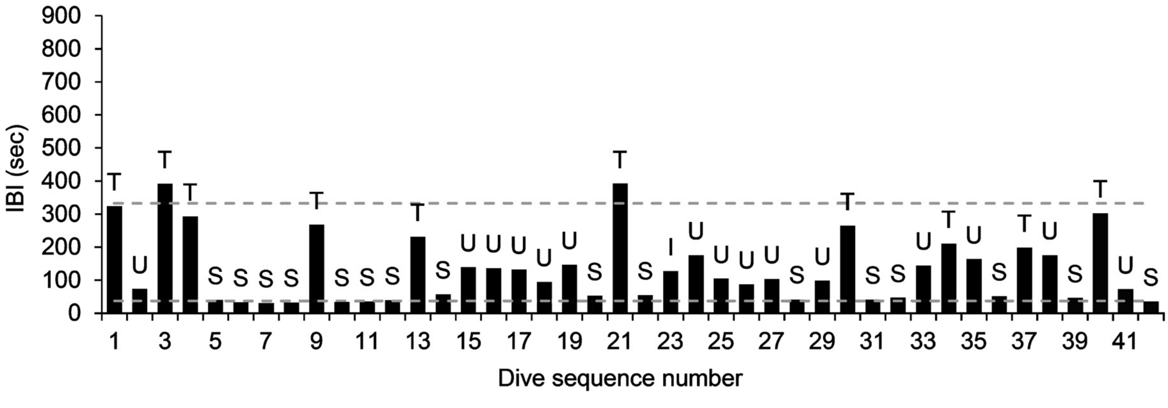
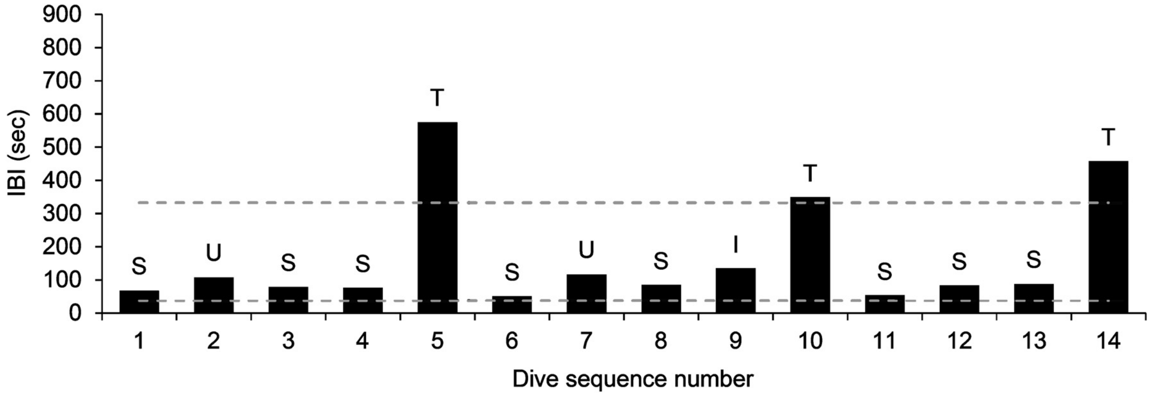
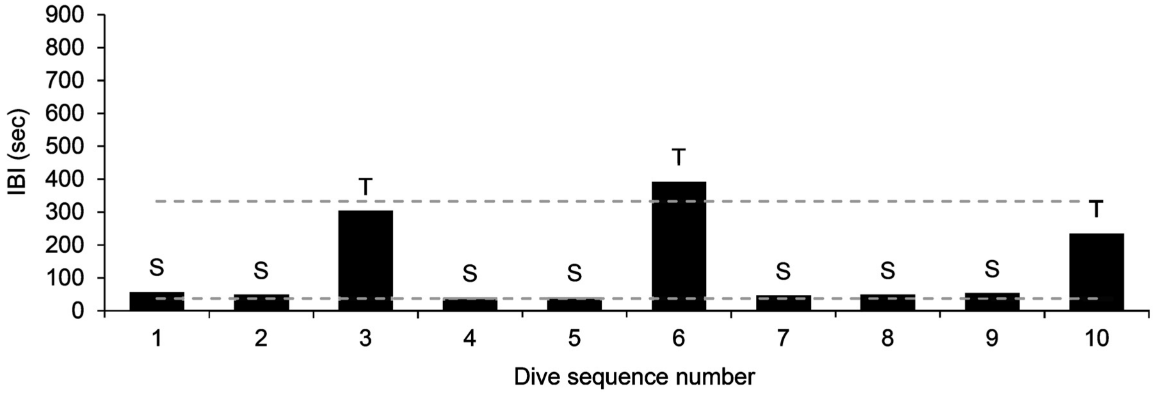


Fig. 2. Continued.

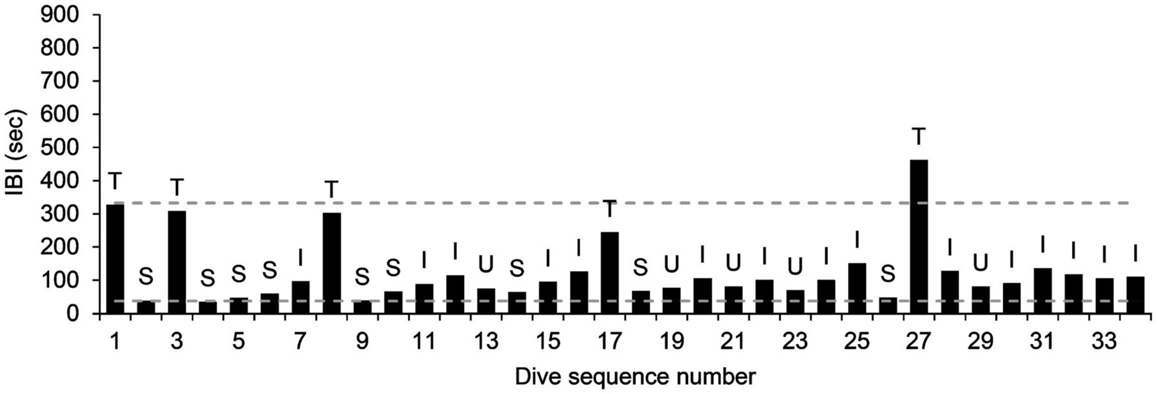
(i) WF–5



(j) WF–11



(k) WF–12



(l) WF–16

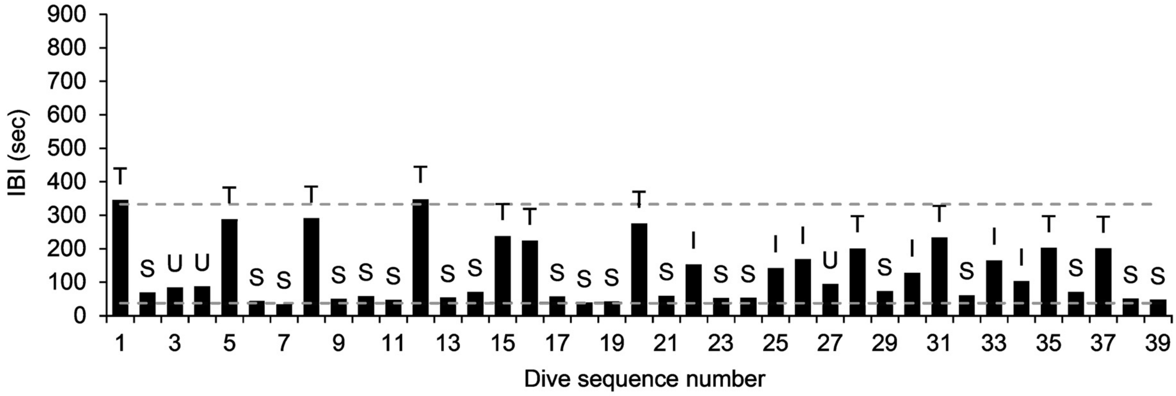


Fig. 2. Continued.

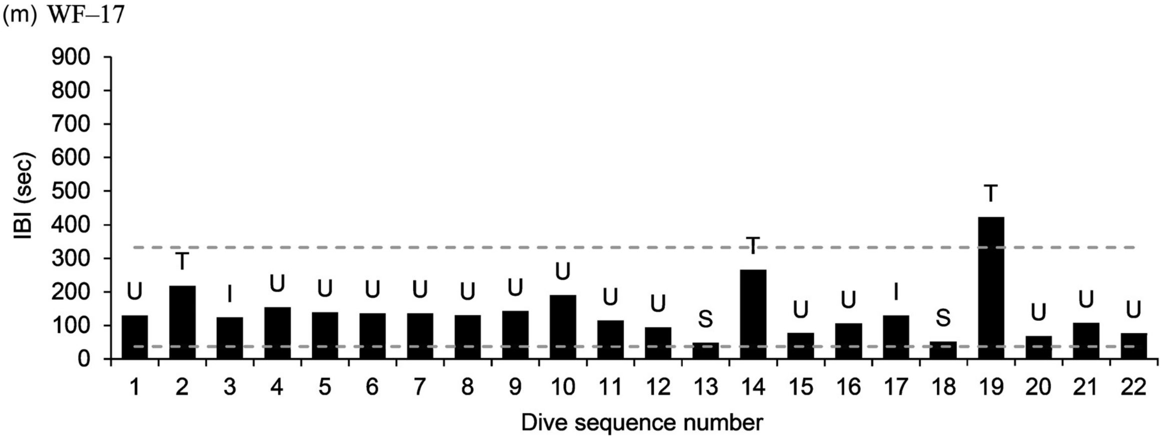


Fig. 2. Concluded.

defined as the sum of consecutive IBIs that were classified as surface dives. The true dive time (TDT) was defined as the IBI of longer true dives, i.e. dives between surfacing bouts. The number of blows per surface bout (BSB) was defined as the number of breaths per surfacing bout.

RESULTS

Cue rates

A total of 37 FFs were carried out on sei whale individuals or groups, including 20 in Berkeley Sound and 17 in West Falkland (Fig. 1). The CR ranged from 22 to 46.7 (Table 1), with an overall mean of 31.5 (SD = 5.12) and a median of 30.8. Mean CRs of 32.3 (n = 20, SD = 6.4, median = 31.1, range = 22.2–46.7s) and 30.6 (n = 17, SD = 3.1, median = 30.7, range = 21.9–35s) were recorded in Berkeley Sound and West Falkland respectively. Following Anderson-Darling Tests for normality, a two sample t-test of CR between Berkeley Sound and West Falkland was not significant (p = 0.346). Two sample t-tests also showed no significant difference between the CRs obtained from shore versus boat platforms, either using only the Berkeley Sound dataset (p = 0.924) or also including the West Falkland dataset (p = 0.781). The mean CR for each of the recorded group sizes was 30.7 (n = 13, SD = 7.3, median = 29.4) for single animals, 30.8 (n = 10, SD = 4.2, median = 31) for pairs, 32.6 (n = 12, SD = 3.1, median = 32.6) for groups of three whales, and 32.7 (n = 2, SD = 2.8, median = 32.7) for groups of five whales.

Dive and surfacing durations

There were 57 occurrences of submergences exceeding 300s (5mins), including 29 accurate dive times recorded from individuals and 28 MDDs recorded from groups of 2 or 3 whales. In Berkeley Sound the longest dive recorded from an individual of 815.2s (13.6mins) was similar to the longest group MDD of 800.1s (13.3mins). In West Falkland, the longest submergences were 574s (9.6mins) by an individual and 363s (6.1mins) as a group MDD. Altogether there were 20 dives recorded from single individuals or groups of whales (2 or 3 individuals) that exceeded 480s (> 8mins) duration, with the majority occurring during eight focal follows in Berkeley Sound and only a single occurrence in West Falkland.

A total of 51 WSEs were extracted from 11 different sei whale encounters on nine dates (Table 2). The durations ranged from 4.1 to 12.1s, with a mean of 6.4s (SD = 1.7) and a median of 6.1s. Mean durations per encounter varied from 5.1 to 9.9s (Table 2). The WSEs were of longer duration in West Falkland (n = 14, mean = 8s, SD = 1.8) than in Berkeley Sound (n = 37, mean = 5.8s, SD = 1.1).

Swim speed

The average linear swim speed during boat-based sei whale focal follows was 5.7kmh^{-1} (Table 1; n = 29, SD = 1.4, median = 5.9, range = 3.5–8.3kmh^{-1}). Swim speed was higher in Berkeley Sound (n = 14, mean = 6.2kmh^{-1}, median = 6.7) than in West Falkland (n = 15, mean = 5.3kmh^{-1},

Table 2

Number and mean duration of whale surfacing events (WSE) per sei whale encounter.

					WSE			
WSE No.	Date	Area	Method	Group size	n	Mean durn. (s)	SD	Range (s)
1	23/02/17	Berkeley Sound	GoPro	3	7	5.1	0.8	4.1–6.3
2	23/02/17	Berkeley Sound	GoPro	4	3	5.4	1.5	4.4–7.1
3	27/02/17	Berkeley Sound	GoPro	4	5	5.4	0.6	4.9–6.1
4	28/03/17	Berkeley Sound	GoPro	3	6	5.1	1.0	4.3–6.9
5	08/05/17	Berkeley Sound	GoPro	6	5	6.1	0.7	5.1–7.1
6	13/05/17	Berkeley Sound	GoPro	4	10	6.8	1.1	5.5–8.6
7	16/05/17	Berkeley Sound	GoPro	2	1	6.6	n/a	6.6–6.6
8	24/03/18	West Falkland	Drone	3	4	7.1	1.1	6.1–8.3
9	26/03/18	West Falkland	Drone	3	4	6.6	1.7	6.1–7.5
10	26/03/18	West Falkland	Drone	4	1	8.2	–	8.2–8.2
11	27/03/18	West Falkland	Drone	5	5	9.9	1.6	7.6–12.1

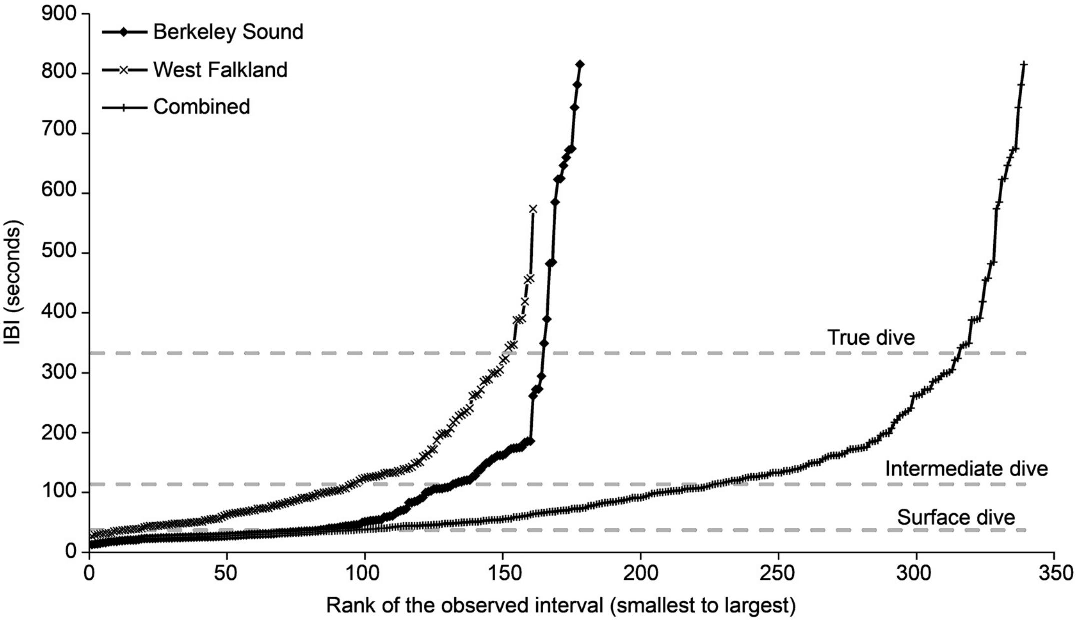


Fig. 3. Ranked order of Inter-breath intervals (*n* = 339) for complete dive cycles recorded from 13 individual sei whales, showing the mean values for surface, intermediate and true dives from the combined dataset.

Table 3

Inter-breath intervals (IBIs, *n* =339) recorded during full dive cycles of 13 sei whale focal follows (FF) in Berkeley Sound (BS) and West Falkland (WF).

	Dive pattern	All combined (s)						Surface (s)			Intermediate (s)			True (s)			Unclassified (s)		
FF No.	type	*n*	Min	Max	Mean	SD	Median	*n*	%	Mean IBI	*n*	%	Mean IBI	*n*	%	Mean IBI	*n*	%	Mean IBI
BS–1	Diff.	14	15.2	781.2	124.3	217.0	31.6	11	78.6	28.7	0	0	–	3	21.4	475	0	0	–
BS–5	Diff.	46	20.0	261.1	77.2	64.8	39.1	29	63.0	32.2	3	6.5	95.4	13	28.3	170.7	1	2.2	113.82
BS–7	Undiff.	11	17.4	272.9	117.9	79.3	127.9	4	36.4	32.8	0	0	–	2	18.2	229.4	5	45.5	141.31
BS–8	Diff.	26	13.9	815.2	92.9	166.7	37.5	17	65.4	28.4	5	19.2	95.9	3	11.5	463	1	3.8	64.65
BS–9	Undiff.	33	27.5	271.9	91.6	48.7	86.2	7	21.2	41.4	2	6.1	120.1	2	6.1	223.8	22	66.7	92.9
BS–14	Diff.	16	19.6	743.2	180.1	273.4	31.4	12	75.0	29.8	0	0	–	4	25.0	631.1	0	0	–
BS–18	Diff.	32	12.8	674.4	139.1	233.1	25.9	25	78.1	26.5	1	3.1	117.2	6	18.8	611.7	0	0	–
WF–2	Undiff.	42	27.0	388.0	128	102.6	97.5	16	38.1	38.6	1	2.4	124	10	23.8	284	15	35.7	119.7
WF–5	Diff.	14	48.0	574.0	163.7	167.4	84	8	57.1	70.3	1	7.1	132	3	21.4	458.3	2	14.3	111.5
WF–11	Diff.	10	38.0	391.0	124.6	132.4	48.5	7	70.0	45.7	0	0	–	3	30.0	308.7	0	0	–
WF–12	Diff.	34	32.0	458.0	119.5	95.5	93	9	26.5	48.7	15	44.1	108.5	5	14.7	325.4	5	14.7	74.2
WF–16	Diff.	39	31.0	347.0	125.4	93.7	81	19	48.7	51.3	6	15.4	140.3	11	28.2	256.1	3	7.7	85.3
WF–17	Undiff.	22	45.0	419.0	136	81.6	126.5	2	9.1	46.5	2	9.1	123	3	13.6	299.7	15	68.2	116.9

median = 4.8). It was also slightly higher for FFs in which overall behaviour was considered to be travel (*n* = 17, mean = 6kmh^{-1}, median = 6) compared with foraging (*n* = 7, mean = 5.5kmh^{-1}, median = 5.5).

Dive types and cycles by individual whales

Accurate dive cycle timings were available for 13 solitary sei whales; those for which photo-identification images had been successfully obtained each comprised a unique individual (Table 1). The mean IBIs for individuals ranged from 77.2 to 180.1s (Table 3), producing an overall combined mean IBI of 118.6s (*n* = 339, SD = 137.6). Nine individuals were considered to have differentiated dive patterns (Fig. 2, Table 3). When ranked in order, the majority of the 339 IBIs recorded from full dive cycles occurred along a continuum, with little indication of distinct dive types based on IBI duration alone (Fig. 3). Using the combined-method approach a total of 270 (79.6%) IBIs were assigned to a dive type, while the other 69 (20.4%) dives remained unclassified (Table 3).

Using the combined dataset, the majority of IBIs (49%) comprised surface dives with a mean IBI of 37.2s and a median of 34.3s (Table 4). True dives with a mean IBI of 332.6s and a median of 278.9s comprised 20.1% of the dives. A relatively small number of dives (10.6%) were categorised as intermediate dives, with a mean IBI of 113.7s and a median of 116.1s. The remaining dives were unclassified, but their mean and median IBIs of 106.2s and 102.5s respectively indicated that they would be most-appropriately categorised as intermediate dives. The combined dataset contained overlapping IBI ranges between surface (12.8–86s) and intermediate (67.5–165s) dives, and between intermediate and true (126.1–815.2s) dives (Table 4). Within the Berkeley Sound and West Falkland study sites the surface, intermediate and true dives had non-overlapping IBI values, but the range of values differed between the sites. In particular, the mean and median IBIs of surface dives were notably higher in West Falkland than in Berkeley Sound (Table 4).

The nine individuals with differentiated dive patterns were, in most cases, characterised by a higher proportion (> 48%) of surface dives, a low proportion (< 15%) of unclassified dives, and median IBIs of < 85s (Table 3). The

Table 4

Inter-breath intervals (s) for sei whale dive types in Berkeley Sound and West Falkland.

	Combined dataset					Berkeley Sound					West Falkland				
Dive type	*n*	%	Mean	Range	Median	*n*	%	Mean	Range	Median	*n*	%	Mean	Range	Median
Surface	166	49.0	37.2	12.8–86.0	34.3	105	59.0	30.2	12.8–60.8	27.9	61	37.9	49.3	27.0–86.0	48.0
Intermediate	36	10.6	113.7	67.5–165.0	116.1	11	6.2	102.1	67.5–120.5	108.4	25	15.5	118.8	87.0–165.0	120.0
True	68	20.1	332.6	126.1–815.2	278.9	33	18.5	367.6	126.1–815.2	271.9	35	21.7	299.5	195.0–574.0	288.0
Unclassified	69	20.4	106.2	51.5–187.0	102.5	29	16.3	101.0	51.5–162.0	102.5	40	24.8	110.0	65.0–187.0	103.0
TOTAL	339	100.0	118.6	12.8–815.2	69.0	178	100.0	108.8	12.8–815.2	40.6	161	100.0	129.6	27.0–574.0	94.0

exception was WF-12 (Fig. 2k), which was considered to have a differentiated dive pattern but had a far higher proportion (44.1%) of intermediate dives and a lower proportion of surface dives (26.5%) compared with the other eight individuals. Four whales (BS-1, BS-14, BS-18 and WF-11) exhibited strikingly-differentiated dive patterns characterised by > 96.9% of their dives being either surface or true dives (Fig. 2). However, WF-11 had a higher mean IBI for surface dives and a lower mean IBI for true dives than the other three individuals (Table 3). The dives of BS-5 were generally consistent in pattern but with a less pronounced difference between surface and true dives than the other individuals with differentiated dive patterns; this individual had the lowest mean IBI for true dives (170.7 sec) and the smallest difference between the mean IBI of true and surface dives (Table 3; Fig. 2b). The dive patterns of BS-8, WF-5 and WF-16 were more variable (Fig. 2). While over 76% of the dives of these three individuals could be attributed to surface or true dives, they exhibited a higher proportion of intermediate or unclassified dive types (> 21%) compared with the other whales with differentiated dive patterns. Three individuals (BS-8, WF-12 and WF-16) appeared to alter their dive patterns over the duration of the focal follow, in all cases changing from defined sequences of true and surface dives to a more variable pattern of intermediate dives (Fig. 2).

All four individuals with undifferentiated dive patterns were characterised by high proportions (35.7–68.2%) of unclassified dive types, low proportions (9.1–38.1%) of surface dives and median IBIs of > 85s (Table 3). The mean IBIs of true dives for those whales were < 300s. All four individuals exhibited periods of successive intermediate or unclassified dive types (Fig. 2), with the majority (> 72%) of dives by BS-9 and WF-17 comprising those types.

Surfacing bout parameters were extracted for six individuals that exhibited regular dive patterns (BS-5, BS-8, BS-14, BS-18, WF-5 and WF-11). The BSB varied from 1 to 7 with a mean of 3.8 (n = 28, SD = 1.3). The mean IBI during surfacing bouts was 33.4s (n = 27, SD = 10.5, range = 20.8–72s) and the SBD had a mean of 97.1s (n = 27, SD = 45.7, range = 20.8–216s). The TDT had a mean of 387.7s (n = 28, SD = 226.3, range = 126.1–815.2s).

DISCUSSION

Cue rates and surfacing times

The overall mean CR of 31.5 obtained for Falkland sei whales was notably lower than the CRs published in other studies for baleen whales including minke (46.1), fin (52) and humpback (71) whales in Greenland (Heide-Jørgensen and Simon, 2007), fin whales in the Gulf of Maine (48 without boats and 51 with boats present; Stone *et al*., 1992), and minke whales in Norway (44; Øien *et al*., 1990). No differences in CR were apparent between shore and boat platforms or between different study areas. Additionally, the dataset included multiple FFs carried out in different years (but in similar seasons), dates, time of day and with different individuals. Consequently, we conclude that Falkland sei whales produce genuinely lower CRs than those published for minke and fin whales, highlighting the limitations of inferring data from other, even closely-related, species. The CR range for Falkland sei whales (22–46.7) was well within the range of variability reported for other baleen whales, for example minke whales (16–66; Øien *et al*., 1990), fin whales (17.4–90; Heide-Jørgensen and Simon, 2007) and humpback whales (22.1–156; Heide-Jørgensen and Simon, 2007).

The mean WSE recorded for Falkland sei whales (6.4s) was longer than that reported for minke (3.5s) or fin (4s) whales in Greenland (Heide-Jørgensen and Simon, 2007). While the difference from minke whales may be the result of the greater body size and stronger blow of sei whales, the longer WSE compared with the larger fin whale is less explainable. Heide-Jørgensen and Simon (2007) did report WSE variation of 2–11s for fin whales which is similar to that noted for sei whales. Possibly the shallower-surfacing behaviour and taller dorsal fin (which protrudes above the water for longer) of sei whales may account for them being visible longer above the surface even though their body size is smaller, or these differences may simply reflect variation in the behaviours of the sampled individuals. The WSE durations measured in this study should be treated as a minimum indication of ‘availability’ during a visual survey, since sei whales were certainly also visible from the air while submerged within the upper water column (as demonstrated by drone footage; Weir, 2018). Similar is true for Icelandic minke whales, with the WSE from boats (3.5s) being doubled when visible submergence time was included from aircraft (7.2s) (Heide-Jørgensen and Simon, 2007). It is likely that the apparent variation in WSE between the Falkland study areas was the consequence of small sample sizes, variation in method, and the differences in behaviour of whales during the video footage. Moreover, six surfacings in the West Falkland dataset related to two individuals that each surfaced three successive times, which may have biased the dataset (one of these animals produced the three highest WSE values).

Dive types and cycles by individual whales

Many visual observation studies of baleen whale diving behaviour have defined only two dive types based on an IBI cut-off. For example, several fin whale studies used log-survivorship analysis of merged datasets to define cut-off IBI durations between surface and true dives of 25–28s (e.g. Stone *et al.,* 1992; Kopelman and Sadove, 1995; Jahoda *et al.,* 2003). However, the duration of dives considered as 'true' or 'surface' may vary between individuals. Øien *et al.* (1990) noted that Norwegian minke whales exhibited considerable intra- and inter-individual variation in surfacing behaviour, and in the Falklands it was evident that the dive durations that comprised surface and true dives for one sei whale (e.g. BS-18) were different from the durations that comprised the same dive types for other individuals (e.g. WF-11). Moreover, a continuum of dive durations was exhibited, and the overlapping IBI ranges between dive types in the combined Falkland dataset indicated that IBI duration alone was not a clear indicator of dive type. Incorporating dive sequence pattern and the pcIBI into the classification of sei whale dives allowed variables such as behavioural context (i.e. occurrence in the dive sequence pattern) and inter-individual variation to be factored in to what constituted a particular dive type.

Although sei whales in Berkeley Sound and West Falkland exhibited similarities in their overall range of dive behaviour, the proportions and parameters of dive types varied between the regions. The mean and median IBIs of intermediate, true and unclassified dives were broadly comparable, indicating that the differences between the sites were best explained by surface dive parameters and by the overall dive type ratios. Sei whales in Berkeley Sound exhibited a higher proportion of surface dives than whales in West Falkland (59 vs. 37.9%), and those surface dives were of much shorter mean and median IBI than in West Falkland. As a consequence, individuals in Berkeley Sound undertook far fewer intermediate dives than those in West Falkland (15.5 vs. 6.2% of the total dives, increasing to 40.4 vs 22.5% if unclassified dives are also included as intermediate dives).

The underlying reasons for these differences are unclear, but could relate to variation in foraging conditions and behaviour between the two regions. The larger numbers of sei whales encountered in West Falkland compared with Berkeley Sound (Weir, 2017; 2018), could be considered to reflect higher prey densities or enhanced foraging conditions (for example, prey located closer to the surface resulting in reduced energetic demands) in that area. It is feasible that although the overall durations of true dives were similar between the two sites, whales in Berkeley Sound may have been diving deeper to reach their prey resulting in the necessity to take a greater number of breaths at the surface between foraging dives. Alternatively, whales in West Falkland may have been foraging less during daylight hours than those in Berkeley Sound and spending more time resting or travelling, with the differences in dive parameters reflecting different overall behaviour during the focal follows. In Japan, the mean dive durations of two tagged sei whales were significantly longer during the day than at night, and the whales also dove deeper during the day (Ishii *et al*., 2017). The changes were related to the depth of the dense scattering layer (which migrated closer to the surface at night), suggesting that sei whales altered their diving depth and sequence in response to changes in the depth distribution of their prey (Ishii *et al*., 2017). In the Falklands, initial indications from faecal sampling work are that sei whales target lobster krill (*Munida gregaria*: Weir, 2017; 2018), the shoals of which vary considerably in their horizontal and vertical spatial distribution according to environmental factors (Diez *et al*., 2016).

Lunge-feeding in baleen whales is a very energetically-costly behaviour (Goldbogen *et al*. 2008, 2011). In general, baleen whales maximise their energetic gains by increasing the number of lunges per dive with increasing depth and prey density (e.g. Friedlaender *et al*., 2016). Therefore, surfacing bouts after long and deep dives should include increased surface times and ventilation rates to recover used oxygen stores. Shallower feeding however, in which whales perform a single or fewer number of lunges could be difficult to discern from a travelling dive based on dive time alone, as whales can maximise feeding rates by incorporating breathing into the cycle of prey processing (Ware *et al*., 2011). In these situations, the whales are likely conserving oxygen, unlike in deep feeding when foraging rates could lead to oxygen debts (Hazen *et al*., 2015). The surfacing patterns found in this study suggest a substantial amount of shallow diving behaviour and determining the proportion of feeding occurring during this time would help shed light on the ecological interactions between sei whales and their prey around the Falkland Islands.

Unfortunately, it proved difficult to unequivocally assign behavioural categories to sei whales in the study areas to determine whether the regional differences in dive pattern reflected the sampling of different behaviours, since the animals were generally cryptic and exhibited little overt behaviour at the surface. Consequently, their behaviour was mostly judged in the field from their dive pattern and by the extent and speed of their spatial movements, which essentially voided any objective assessment of whether the dive patterns varied according to behaviour.

Intra-specific comparisons

The surfacing behaviour reported for Falkland sei whales broadly overlaps with the limited information available for the species elsewhere; however, the inconsistencies in methods used to describe dive types hinders intra-specific comparisons. For example, Avecedo *et al*. (2017), Schilling *et al*. (1992) and Ishii *et al*. (2017) did not describe IBI parameters or dive cycles either due to the more generalised nature of the studies (which were not specifically assessing behaviour) or due to limitations inherent to the methods used (e.g. tag data resolution and detection range). The 5–7min dives noted by Avecedo *et al*. (2017) for Chilean sei whales do fall within the Falkland dive duration range. The maximum dive times recorded for sei whales in the Gulf of Maine (11min; Schilling *et al*., 1992) and off Japan (12.2mins; Ishii *et al*., 2017) are similar to those recorded in the Falklands (13.6mins), despite being recorded in different habitats including open shelf waters (Gulf of Maine), nearshore shallow waters (Falklands) and open ocean of around 5,000m depth (Japan). These likely reflect longer foraging dives since all three of these regions are considered to represent sei whale feeding areas. The shorter dive times (≤ 90s) recorded regularly by Schilling *et al*. (1992) were correlated with numerous observations of surface-feeding during that study, whereas the whales monitored in the

Falklands and Japan were predominantly feeding sub-surface (Ishii *et al*., 2017; Weir, 2017; 2018).

The average swim speeds recorded for Falkland sei whales were inherently limited by methods, since the GPS positions reflect the locality of the boat rather than the movements of the whales themselves. These estimates therefore reflect minimum average speeds. The Falkland results (3.5–8.3kmh^{-1}) are lower than those recorded during two boat-based focal follows in Japan (8.1 and 10kmh^{-1}; Ishii *et al*., 2017), but comparable to the mean speeds of 6.2 and 7.4kmh^{-1} (for migration and non-migration) reported by Prieto *et al*. (2014) from satellite-tracking in the Azores. It is likely that different methods, varying focal follow duration, and behaviour of the animals in different studies will affect the results. Fast bursts exceeding 22kmh^{-1} were recorded by Falkland sei whales on occasion (Weir, 2017), and the species may therefore vary its speed and surfacing characteristics according to behaviour.

CONCLUSION

This study of Falkland sei whale cue rates and surfacing behaviour provides novel systematic information that will be useful to inform abundance estimates and to better understand differences in behaviour between habitats around the Islands. Other baleen whale species vary their diving behaviour according to factors including prey type, group size, time of day, geographic area, season, behaviour and habitat (Würsig *et al.,* 1985; Stone *et al.,* 1992; Kopelman and Sadove, 1995; Stockin *et al.,* 2001; Alves *et al.,* 2010), and consequently the most appropriate datasets for correcting whale abundance estimates are those collected on the same species, in the same geographic area and at the same time of year as the abundance survey is carried out (Heide-Jørgensen and Simon, 2007). The collection of cue rate, dive cycle and WSE data are relevant to addressing availability bias for line transect and cue count methods, and the data presented here should therefore be directly applicable to future sei whale abundance surveys in the Falklands. In addition, understanding the natural surfacing behaviour of sei whales is an integral component of vessel strike modelling, assessing potential disturbance from human activities, and maximising fieldwork approaches for photo-identification, tagging and biopsy sampling. While visual methods have produced useful initial data, they are restricted to daylight hours and periods of favourable weather. The collection of full diurnal datasets (i.e. including the hours of darkness) and information on the underwater behaviour of sei whales via the use of tags would be useful for generating ethograms of behaviour over spatio-temporal scales relevant to the whales around the Falklands to better inform future management decisions.

ACKNOWLEDGEMENTS

Funding was provided by the European Union BEST 2.0 Programme, Falklands Conservation (FC), the Royal Society for the Protection of Birds (RSPB), and the Falkland Islands Government (FIG). Fieldwork was carried out under FIG research licences R23/2016 and R11/2017. The Falkland Islands Museum and National Trust provided access to Cape Pembroke lighthouse. We are grateful to the vessel skippers Steve Cartwright and Jérôme Poncet. The study of dive behaviour was encouraged by Daniel Pike. The Marine Research Institute in Iceland kindly loaned digital voice recorders during 2017. Thanks to several FC volunteers for helping to collect some of the data presented here. Our thanks to Ari Friedlaender for his useful comments on a draft, and also to the manuscript reviewers for their helpful feedback.

REFERENCES

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49: 227–67.

Alves, F., Dinis, A., Cascão, I. and Freitas, L. 2010. Bryde's whale (*Balaenoptera brydei*) stable associations and dive profiles: new insights into foraging behavior. *Mar. Mam. Sci*. 26: 202–12.

Argüelles, M.B., Fazio, A., Fiorito, C., Pérez-Martínez, D., Coscarella, M. and Bertellotti, M. 2016. Diving behavior of southern right whales (*Eubalaena australis*) in a maritime traffic area in Patagonia, Argentina. *Aquat. Mamm*. 42: 104–08.

Acevedo-Gutiérrez, A., Croll, D.A. and Tershy, B.R. 2002. High feeding costs limit dive time in the largest whales. *J. Exp. Biol*. 205: 1747–53.

Acevedo, J., Aguayo-Lobo, A., González, A., Haro, D., Olave, C., Quezada, F., Martínez, F., Garthe, S. and Cáceres, B. 2017. Occurrence of sei whales (*Balaenoptera borealis*) in the Magellan Strait from 2004–2015, Chile. *Aquat. Mamm*. 43: 63–72.

de Vos, A., Christiansen, F., Harcourt, R.G. and Pattiaratchi, C.B. 2013. Surfacing characteristics and diving behaviour of blue whales in Sri Lankan waters. *J. Exp. Mar. Biol. Ecol*. 449: 149–53.

Diez, M.J., Cabreira, A.G., Madirolas, A. and Lovrich, G.A. 2016. Hydroacoustical evidence of the expansion of pelagic swarms of *Munida gregaria* (Decapoda, Munididae) in the Beagle Channel and the Argentine Patagonian Shelf, and its relationship with habitat features. *J. Sea Res*. 114: 1–12.

Friedlaender, A.S., Goldbogen, J.A., Nowacek, D.P., Read, A.J., Johnston, D. and Gales, N. 2014. Feeding rates and under-ice foraging strategies of the smallest lunge filter feeder, the Antarctic minke whale (*Balaenoptera bonaerensis*). *J. Exp. Biol*. 217: 2851–4.

Friedlaender, A.S., Johnston, D.W., Tyson, R.B., Kaltenberg, A., Goldbogen, J.A., Stimpert, A.K., Curtice, C., Hazen, E.L., Halpin, P.N., Read, A.J. and Nowacek, D.P. 2016. Multiple-stage decisions in a marine central-place forager. *R. Soc. Open Sci*. 3(5): 160043.

Goldbogen, J.A., Calambokidis, J., Croll, D.A., Harvey, J.T., Newton, K.M., Oleson, E.M., Schorr, G. and Shadwick, R.E. 2008. Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. *J. Exp. Biol*. 211: 3712–19.

Goldbogen, J.A., Calambokidis, J., Oleson, E., Potvin, J., Pyenson, N.D., Schorr, G. and Shadwick, R.E. 2011. Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *J. Exp. Biol*. 214: 131–46.

Hazen, E.L., Friedlaender, A.S. and Goldbogen, J.A. 2015. Blue whales (*Balaenoptera musculus*) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. *Science Advances* 1(9): e1500469.

Heide-Jørgensen, M.P. and Simon, M. 2007. A note on cue rates for common minke, fin and humpback whales off West Greenland. *J. Cetacean Res. Manage*. 9(3): 211–14.

Hiby, L. 1992. Fin whale surfacing rate as a calibration factor for cue-counting abundance estimates. *Rep. int. Whal. Commn* 42: 707–09.

Horwood, J. 1987. *The Sei Whale: Population Biology, Ecology and Management*. Croom Helm, London. 375pp.

Ishii, M., Murase, H., Fukuda, Y., Sawada, K., Sasakura, T., Tamura, T., Bando, T., Matsuoka, K., Shinohara, A., Nakatsuka, S., Katsumata, N., Okazaki, M., Miyashita, K. and Mitani, Y. 2017. Diving behavior of sei whales *Balaenoptera borealis* relative to the vertical distribution of their potential prey. *Mammal Study* 42: 191–199. [Available at: *https://doi.org/10.3106/041.042.0403*].

Jahoda, M., Lafortuna, C.L., Biassoni, N., Almirante, C., Azzellino, A., Panigada, S., Zanardelli, M. and di Sciara, G.N. 2003. Mediterranean fin whale's (*Balaenoptera physalus*) response to small vessels and biopsy sampling assessed through passive tracking and timing of respiration. *Mar. Mam. Sci*. 19: 96–110.

Kopelman, A.H. and Sadove, S.S. 1995. Ventilatory rate differences between surface-feeding and non-surface-feeding fin whales (*Balaenoptera physalus*) in the waters off eastern Long Island, New York, U.S.A., 1981–1987. *Mar. Mam. Sci*. 11: 200–08.

Lagerquist, B.A., Stafford, K.M. and Mate, B.R. 2000. Dive characteristics of satellite-monitored blue whales (*Balaenoptera musculus*) off the central California coast. *Mar. Mam. Sci*. 16: 375–91.

Ljungblad, D.K., Würsig, B., Swartz, S.L. and Keene, J.M. 1988. Observations on the behavioral responses of bowhead whales (*Balaena mysticetus*) to active geophysical vessels in the Alaskan Beaufort Sea. *Arctic* 41: 183–94.

Nowacek, D.P., Johnson, M.P., Tyack, P.L., Shorter, K.A., McLellan, W.A. and Pabst, D.A. 2001. Buoyant balaenids: the ups and downs of buoyancy in right whales. *P. Roy. Soc. Lond. B* 268: 1811–16.

Øien, N., Folkow, L. and Lydersen, C. 1990. Dive time experiments on minke whales in Norwegian waters during the 1988 season. *Rep. int. Whal. Commn* 40: 337–41.

Prieto, R., Silva, M.A., Waring, G.T. and Gonçalves, J.M.A. 2014. Sei whale movements and behaviour in the North Atlantic inferred from satellite telemetry. *Endang. Species Res*. 26: 103–13.

Schilling, M.R., Seipt, I., Weinrich, M.T., Frohock, S.E., Kuhlberg, A.E. and Clapham, P.J. 1992. Behavior of individually-identified sei whales *Balaenoptera borealis* during an episodic influx into the southern Gulf of Maine in 1986. *Fish. Bull*. 90: 749–55.

Stockin, K.A., Fairbairns, R.S., Parsons, E.C.M. and Sims, D.W. 2001. Effects of diel and seasonal cycles on the dive duration of the minke whale (*Balaenoptera acutorostrata*). *J. Mar. Biol. Assoc. UK* 81: 189–190.

Stone, G.S., Katona, S.K., Mainwaring, A., Allen, J.M. and Corbett, H.D. 1992. Respiration and surfacing rates of fin whales (*Balaenoptera physalus*) observed from a lighthouse tower. *Rep. int. Whal. Commn* 42: 739–45.

Sumich, J.L. 1983. Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. *Can. J. Zool*. 61: 647–52.

Ware, C., Friedlaender, A.S. and Nowacek, D.P. 2011. Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. *Mar. Mamm. Sci.* 27: 587–605.

Weir, C.R. 2017. Developing a site-based conservation approach for sei whales *Balaenoptera borealis* at Berkeley Sound, Falkland Islands. Falklands Conservation report. 120pp. [Available at: *http://www.ketosecology.co.uk/PDF/FC_SeiWhale_Report.pdf*].

Weir, C.R. 2018. A preliminary assessment of endangered sei whales (*Balaenoptera borealis*) in two candidate Key Biodiversity Areas in West Falkland. Falklands Conservation report. [Available from the first author, CW, *caroline.weir@ketosecology.co.uk*].

Witteveen, B.H., Foy, R.J., Wynne, K.M. and Tremblay, Y. 2014. Investigation of foraging habits and prey selection by humpback whales (*Megaptera novaeangliae*) using acoustic tags and concurrent fish surveys. *Mar. Mam. Sci*. 24: 516–34.

Würsig, B., Dorsey, E.M., Fraker, M.A., Payne, R.S., Richardson, W.J. and Wells, R.S. 1984. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: surfacing, respiration and dive characteristics. *Can. J. Zool*. 62: 1910–21.

Würsig, B., Dorsey, E.M., Fraker, M.A., Payne, R.S. and Richardson, W.J. 1985. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: a description. *Fish. Bull.* 83: 357–77.

Large mass strandings of selected odontocete species: statistics, locations, and relation to earth processes

L.J. Hamilton

Defence Science and Technology Group, Department of Defence, Australia

Contact e-mail: hamiltonles@hotmail.com

ABSTRACT

Larger mass strandings of open ocean odontocetes (toothed whales) of 10+ animals are examined with a compilation of 710 worldwide events. Six species form 96% of events (false killer, long-finned pilot, melon-headed, short-finned pilot, sperm and white whales), with beaked, killer, and pygmy killer whales forming 4%. Site type was determined for 630 events – three-quarters (76%) are in bays, 14% in shallow topographically complex areas (estuarine environments, straits, keys, reef and coastal lagoons), 8% on relatively unindented coasts, with ice entrapment (of killer whales) and miscellaneous categories being 2%. For the 76% of events in bays, sites with headland-bay character make up 42%, spit-bays 20% (even though there are only four of them), indented bays 9% and unspecified bay types 5%. Headland-bays and spit-bays become stranding sites through the properties endowed them by their mechanisms of formation and maintenance, but these mechanisms differ greatly for the two. Breakwaters, groyne series, tides, partial burial, and violent storms also appear as themes. Nearshore slopes are less than 1° for 94 of 105 sites having bathymetry information, with only two reaching or exceeding 3°. Some types of potential stranding sites can be identified by simple quantitative specifications for planform, sediment size, and seabed slope, although strandings will not necessarily occur there. There is an indication that larger strandings are globally correlated with areas of higher oceanic primary productivity near landmasses and oceanic islands, but quantitative studies are needed to clarify any such possible relationship. There is also an indication that larger strandings are associated with plate tectonics, with few events being seen on the steeper swell resistant active western margins of South America and South Island (New Zealand) in particular. In contrast several larger events are recorded for the relatively older passive margins of the south-eastern sides of these two landmasses, putatively because waves and swell have had time to construct stranding sites on them. Similarly, few larger events are seen for steeper shores adjacent to coastal highlands, such as those of South Africa and Brazil. These observations indicate previously unsuspected relations between the phenomenon of odontocete mass strandings and global scale earth and ocean processes, but they are essentially hypotheses in need of more quantitative examination.

KEYWORDS: STRANDINGS; TRENDS; BAIRD'S BEAKED WHALE; BLAINVILLE'S BEAKED WHALE; CUVIER'S BEAKED WHALE; FALSE KILLER WHALE; GRAY'S BEAKED WHALE; KILLER WHALE; LONG-FINNED PILOT WHALE; MELON-HEADED WHALE; PYGMY KILLER WHALE; SHORT-FINNED PILOT WHALE; SPERM WHALE; WHITE WHALE

INTRODUCTION

Hamilton and Lindsay (2014a) found that Australian mass stranding events of open ocean odontocetes (toothed whales) involving 10+ animals occurred dominantly in bays (63 of 66 events and 33 of 36 locations), especially bays with fine sandy sediments and offshore seabed slopes deeper than the wave base of less than 0.5º (this is a 1m vertical change over 100m horizontal distance). These conditions were observed to occur particularly in mature headland-bays. These have a distinctive half-heart or log-spiral shape (Fig. 1) sculpted behind headlands by waves and swell, with the shape forming to lessen wave action at the bay shore (Silvester and Ho, 1972). The striking geometrical regularity of mature headland-bay planforms enables ready identification of these coastal features. Most Australian headland-bays were sited south of 25°S on coastlines influenced by strong persistent Southern Ocean swell. The dominance of bays in Australian mass strandings of odontocetes had not previously been noted, nor had headland-bays been formally recognised in the stranding literature. These remarks exemplify just how little is known about mass strandings and possible relations to stranding site properties.

Remarkably, Hamilton and Lindsay (2014a) were able to express their findings quantitatively. They first used indentation ratio and planform to class stranding bays as having indented or headland-bay character. Strong similarities were noted between quantitatively defined ranges of site properties (coastal indentation, sediment size, seabed slopes) for Australian headland-bays which were attributed to their common mode of geomorphological origin and similar state of maturity. Developing headland-bays do not have all these property ranges. The similarities imply that particular site properties may be directly related to strandings. Possible reasons advanced were the gradually shallowing depths in headland-bays, which odontocetes may not be able to readily comprehend, sonar termination (Dudok Van Heel, 1962; 1966) in the low slopes and fine sands of mature headland-bays, the effect of the headland in then influencing odontocetes to turn onshore to danger or offshore to safety if unexpectedly encountered, and lesser wave action at the shore in times of calms in headland-bays compared to other bay types to alert whales to land. Whether or not these factors are involved in strandings is moot, but for Australia the observed correlation of particular site properties with larger live mass strandings provides predictive power in indicating other potential stranding sites, although this does not mean that strandings will occur there. In effect, the 'where' of strandings can be known without a perfect knowledge of the behavioural 'why', and if the 'where' is known, then the 'why' may follow.

An examination of worldwide sites of larger mass strandings was made using the quantitative framework of Hamilton and Lindsay (2014a) to see if they are also associated with particular geomorphologies or other physical factors. The data also provide indicative statistics on numbers of larger events for regions and species. Ultimately

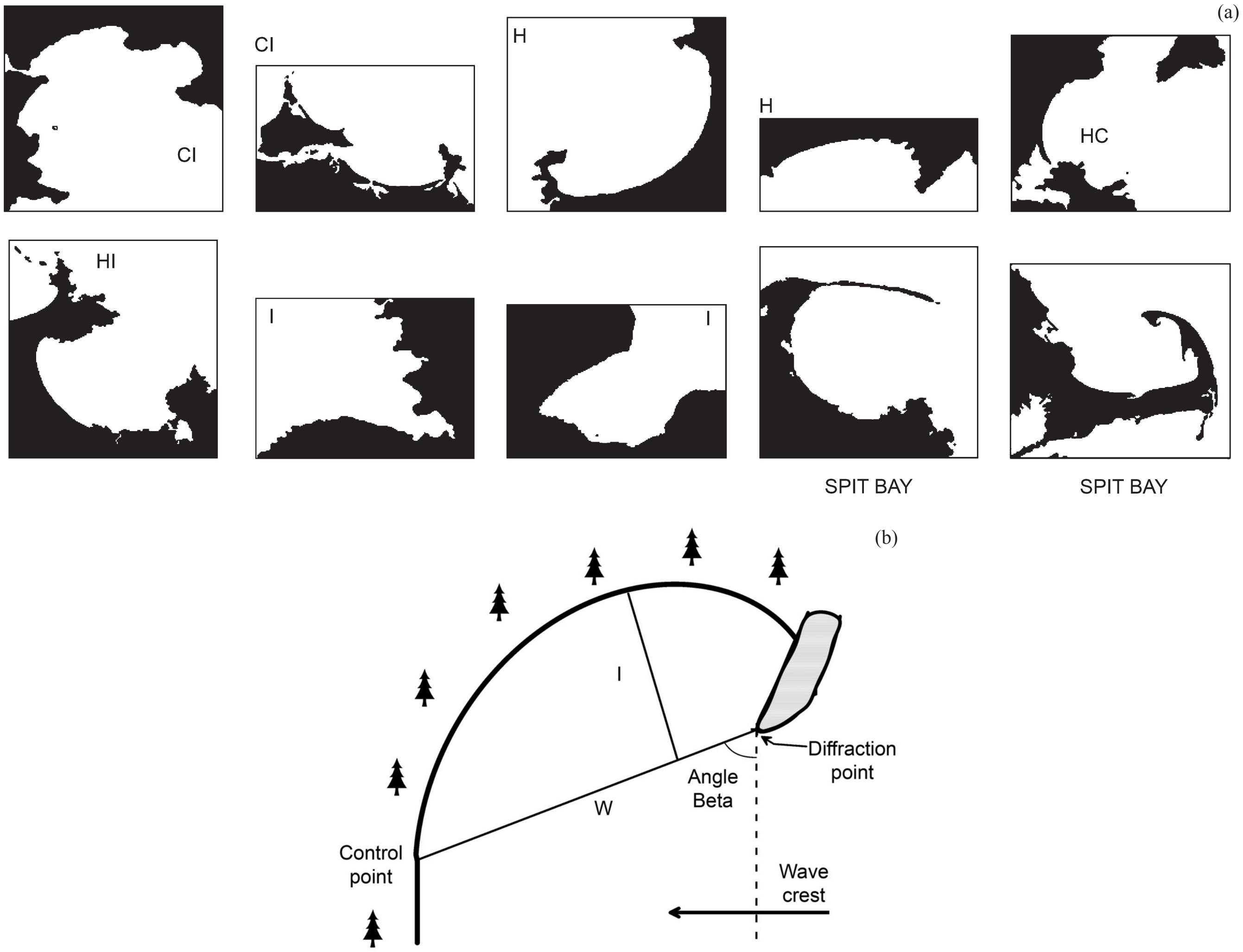


Fig. 1. Bay types (CI, H, HC, HI, I) and definitions. Coastal outlines from: *http://gadm.org/country*.

(a) Top panel: Bremer Bay – indented bay with complex character (three internal bays) (CI), Perkins Bay – indented bay with complex character (islands and channels in the west) (CI), Mason Bay – headland-bay (H), Wreck Bay – headland-bay (H), Marion Bay – headland-bay with complex character (HC) caused by northern island and channel. Lower panel: Doubtless Bay – headland-bay with indented character (HI), Doughboy Bay – indented bay (I), The Wash – indented bay (I), Golden Bay and Cape Cod Bay (spit-bays).

(b) Log-spiral headland-bay planform and characteristics. The control point is taken where the beach straightens from the log-spiral. W is headland-bay width. I is indentation distance. Bay indentation ratio (W:I) for classic log-spiral headland-bays is > 2. Swell direction is from right to left.

there are intriguing indications that many larger mass strandings are related to global earth and ocean processes in a rather straightforward but previously unrealised manner.

MATERIALS AND METHODS

Data

Details of larger mass strandings (10+ odontocetes per event) were sourced from online national databases, scientific papers and reports, newspapers, and internet sources (Table 1). The number 10 is chosen to reduce statistical noise, to obtain unequivocal examples of mass stranding events, and to obtain events expected to be active or live strandings, rather than passive. Active strandings are those where cetaceans are not impaired by factors such as injury or disease, which is unlikely for all animals in larger strandings. Passive strandings are those where sick, impaired, or dead individuals simply drift into shore under the action of wind, wave, and current. Active strandings are required if correlations of animal behaviour with properties of stranding locations are to be investigated.

A mass stranding is usually defined as two or more animals, excluding a single mother-calf pair (Brabyn, 1990; d'Amico *et al.,* 2009). Larger events are expected to provide more reliable statistics than this usage, because many smaller events will not be reported, an unknown number will not be live events, and details of larger events are typically better noted and verifiable. Whale drives, and cases where cetaceans entered bays or constricted waters, channels, or shallow coastal areas but did not actually strand are not included.

Dolphin and porpoise strandings are not examined, as these smaller cetaceans are often resident or semi-resident in ports and coastal areas, and may not have the same stranding patterns as other odontocetes, such as Physeteridae, Kogiidae, Ziphiidae, and selected species of Delphinidae (melon-headed, pygmy killer, false killer, killer, long-finned pilot and short-finned pilot whales) (Brabyn, 1990). The Arctic species, white whale (*Delphinidae leucas*) and Narwhal (*Monodon monoceras*) are included as dominantly being open ocean cetaceans, although both spend time in estuaries. Baleen whales are not examined because they seldom mass strand in larger numbers.

Table 1.

Summary of information on sites with large mass strandings of 10 or more animals per event.

COUNTRY / SITE NAME	DISTRICT	SITE TYPE	WIDTH (m)	INDENT (m)	W:I	SLOPE1 (Degrees)	SLOPE2 (Degrees)	SLOPE3 (Degrees)	SUBSTRATE	LARGE EVENTS
ALASKA										
Knik Arm		E	0	0	0.0				M	
Susitna River		E	0	0	0.0				M	2
Turnagain Arm		E	0	0	0.0				M	20
ARGENTINA										
Bahia Bustamante		I	5522	4682	1.2	0.11			Sa	
Bahia San Sebastian		Spit-bay	17192	22945	0.8	0.063			M	5
Caleta Malaspina		I	4495	9150	0.4				R, St	
Caleta San Mauricio, Peninsula Mitre		HC	2026	1105	1.8				m.Sa	
Comodoro Rivadavia		X	0	0	0.0					
Mar del Plata		HB	2473	432	5.7	0.26	0.16	0.06	f.Sa, Sa.Sh	
Punta Norte, Peninsula Valdes		Small indent south of peninsula	1068	342	3.1					
Punta Tafor		HC	1532	512	3.0					
Punta Tombo, 2km south of		HB	1068	342	3.1				R, Sa, St	
AUSTRALIA										
Arthurs Bay, Flinders Island	Tas	HB	7801	2660	2.9					
Aurukun	NT	X	0	0	0.0					
Blackman Bay	Tas	HB	877	365	2.4					
Blooming Beach, Maria Island	Tas	HI	3800	1810	2.1	0.3				
Butlers Beach, Bruny Island	Tas	HB	709	161	4.4					
Cape Grim	Tas	I	600	750	0.8		0.4	0.2	R	
Cheynes Beach, Albany	WA	HB	1100	524	2.1	0.3	1.1	1.5		
Cloudy Bay, Bruny Island	Tas	CI	5400	6000	0.9		0.7	0.2	Sa	
Crowdy Head	NSW	S	0	0	0.0	1.9	1.1	0.1	Sa	2
Darlington Bay, Maria Island	Tas	HB	800	333	2.4	1.2	0.5	0.3		
Doubtful Island Bay	WA	HB	23600	9440	2.5	0.2	0.1	0.03		6
Dundowran	Qld	HB	21000	7241	2.9	0.06			Sa	
Elcho Island, eastern end	NT	X	0	0	0.0					
Flinders Bay, Augusta	WA	HB	30088	7510	4.0	0.14	0.06		Sa	2
Eurong Beach, Fraser Island	Qld	S	0	0	0.0					
Friendly Beaches	Tas	HB	10358	2164	4.8					
Geographe Bay	WA	HB	63000	24231	2.6	0.2	0.08	0.07	Sa	4
Greens Pt Beach, Marrawah	Tas	HI	2900	1526	1.9					
Gunnamatta Beach	Vic	S	0	0	0.0	0.8	0.6	0.4	f.Sa	
Hamelin Bay	WA	HC	4650	1560	2.2	0.24	0.2		Sa	2
Jigaimara Point, Howard Island	NT	X	0	0	0.0					
Koombana Bay, Bunbury	WA	HB	0	0	0.0					
Lighthouse Beach, Seal Rocks	NSW	HI	2200	917	2.4	1.3	0.9	0.6		
Mann's Beach	Vic	E	0	0	0.0					
Marion Bay	Tas	HC	14800	6435	2.3	0.5	0.2		f.Sa	6
McIntyre's Beach, Falmouth	Tas	HB	1700	607	2.8	0.5	0.5	0.3		
Merdayerrah to Eucla	SA	HB	0	0	0.0				S	
Moreton Island, SW corner	Qld	HI	5700	2280	2.5	0.2	0.9	0.1	M.Sa,Sa	
Naracoopa Beach, King Island	Tas	HB	0	0	0.0					
Newman's Beach, Koonya, Tasman Peninsula	Tas	I	1700	1545	1.1	0.24	0.08		M, Sa	
Ninety Mile Beach, near Port Albert	Vic	E	0	0	0.0					
North Bay, Two Mile Beach, Dunalley	Tas	HB	4600	2875	1.6	1.6	1	0.7		2
Ocean Beach	Tas	HB	18500	6852	2.7	0.4	0.2	0.5	S	7
Pardoe Beach, Devonport	Tas	HB	4700	1880	2.5	0.4	0.3	0.2	Sa	
Parry Inlet, Walpole	WA	HB	7634	2441	3.1					
Patriarch Beach (NE Flinders Island)	Tas	HB	31664	7505	4.2					4
Perkins Bay, Stanley	Tas	CI/Spit-bay	18000	12000	1.5	0.17	0.03		Sa	8
Petrel Point to Island Point (Port Hicks beach)	Vic	S	0	0	0.0	0.8	1.3	2	Sa, Sa.Sh	
Picanniny Point, north of Seymour	Tas	HB	0	0	0.0					
Pieman River Heads	Tas	I	2000	1176	1.7					
Point Charles	WA	HB	0	0	0.0					
Point Hibbs	Tas	HI	5000	2632	1.9	0.3	0.07	0.07	R	
Port Prime, St Vincent Gulf	SA	HB	7600	4471	1.7	0.07	0.2	0.04	Sa, M	
Port Welshpool	Vic	E	0	0	0.0				Sa	
Rheban Beach	Tas	HB	2811	853	3.3				Sa	
Richardsons Beach, Coles Bay, Great Oyster Bay	Tas	I	0	0	0.0	0.9	0.7	0.4		
Sandy Cape	Tas	HB	10600	3028	3.5				R	2
Sawyer Bay, Stanley	Tas	HB	11435	3932	2.9	0.2	0.2	0.1	Sa	5
Sea Elephant Beach, King Island	Tas	HB	10400	3852	2.7	0.5	0.1	0.13	Sa.Sh	2
Seal Bay, King Island	Tas	HB	339	178	1.9					
Seal Rocks	NSW	HI	0	0	0.0					
Sellar Point, Flinders Island	Tas	HB	21000	5676	3.7	0.14	0.07	0.05	S	
Small rocky island near Centre Island	NT	X	0	0	0.0					
St Alban's Bay, Bridport	Tas	HB	5600	3111	1.8	0.4	0.35	0.12	Sa	
Stephen's Beach, Port Davey	Tas	HI	3300	1941	1.7	1				
Stokes Pt, Barrow Island	WA	X	0	0	0.0					
Treachery Beach, Seal Rocks	NSW	HI	2200	579	3.8	1.7	1.1		Sa.Sh	2
Wreck Bay	NSW	HB	9111	3822	2.5	0.3	0.25	0.3	Sa	
Yabooma Island	NT	X	0	0	0.0					

Table 1 (*continued*).

COUNTRY / SITE NAME	DISTRICT	SITE TYPE	WIDTH (m)	INDENT (m)	W:I	SLOPE1 (Degrees)	SLOPE2 (Degrees)	SLOPE3 (Degrees)	SUBSTRATE	LARGE EVENTS
BRAZIL										
Bojuru beach, Rio Grande de Sul		S	0	0	0.0					
Piracanga		S	6048	1138	5.3	0.4	0.5	0.3	Sa, Rf	
Rio Grande Do Sul, 51 km Of Beach Opp. Lagoa Mangueira		X	0	0	0.0					
Sao Miguel do Gostoso		Salient-Island	0	0	0.0					
Upanema, Areia Branca		HB	8195	1757	4.7	0.3	0.4	0.2		
BRITISH VIRGIN ISLANDS										
East End, Anegada Island		X	0	0	0.0					
CANADA										
Bayfield, Antigonish	Nova Scotia	HB	4322	2267	1.9	0.11	0.08	0.12		
Beach between Boulder Pt and Estevan Pt		S	0	0	0.0				Bo	
Bedeque Bay, Lower Bay, Near Summerside, PEI		HB	0	0	0.0					
Bonavista Bay, Charleston		CI	0	0	0.0					
Borden, Prince Edward Island (PEI)		X	0	0	0.0					
Cape Kildare (near to), PEI		HB	0	0	0.0					
Cow Head, St Pauls Bay		B	0	0	0.0					
Cumberland Sound, saltwater lake at head of		I	77722	220860	0.4					
Ellesmere Island, near to	Nunavut	X	0	0	0.0					
Fortune Bay, Burin Peninsula	Newfoundland	B	0	0	0.0					
Glace Bay, Cape Breton Island		X	0	0	0.0					
Grand Beach, Burin Peninsula		HB	0	0	0.0					
Grand Etang, Breton Island	Nova Scotia	HB	7118	2290	3.1					
Grant Suttie Bay, Foxe Basin		Ice	0	0	0.0					
Guysborough County	Guysborough	X	0	0	0.0					
Lamaline Bay, Point au Gaul beach, Burin Peninsula		HB	0	0	0.0					
Malpeque Bay, Cabot Beach and south side of Hog Island, PEI		E	0	0	0.0					
Metis to Riviere Blanche, St Lawrence Estuary		E	0	0	0.0					
Miquelon Island, Between Goulet De Langlade & Pointe Aux Alouettes		X	0	0	0.0					
Musgrave Harbor	Newfoundland	I	0	0	0.0					
Near Inukjuak, eastern shore of Hudson Bay	Quebec	Ice	0	0	0.0				Ice	
Notre Dame Bay		I	0	0	0.0					2
Percival (and Enore) River, PEI		B	29050	13578	2.1					
Port Maitland		HB	4724	1004	4.7					2
Sable Island region		Island crescent	35479	6135	5.8					2
Saint Mary's Bay	Newfoundland	I	0	0	0.0					
Saint Pierre		X	0	0	0.0					
St Georges Bay, Judique, Cape Breton Island		HB	4945	1172	4.2				R	
Sturgess Bay, beach across Masset Sound from Old Masset (Haida Gwaii, BC)	BC	I	44733	13588	3.3	0.08	0.03	0.01	R	
Trinity Bay, New Melbourne	Newfoundland	Ice	0	0	0.0					
Trois Pistoles, S Shore of St. Lawrence opp. Saguenay River		E	0	0	0.0					
Yarmouth, Pinkney, South Point	Nova Scotia	X	0	0	0.0					
CANARY ISLANDS										
Ginijinamar	Fuerteventura Island	HI	730	362	2.0					
Las Colorados, Playa Blanca, Lanzarote		HI	798	357	2.2				St, Sa	
SE Fuerteventura		X	0	0	0.0					
CAPE VERDE										
Bahia de Sal Rei		HB	3671	1254	2.9	1	0.25		Sa	2
Calheta Funda (and Praia de Jorge Fonseca), Sal		I	412	260	1.6				R	
Maio (northern shore of)		X	0	0	0.0					
Parda to Kite Beach, Sal		HB	233	103	2.3					
Pedra de Lume (south of)		HI	0	0	0.0					2
Ponta Rica (de Porto Cais), Maio		X	0	0	0.0					
Ponta Sino, Sal		HB	3304	1011	3.3					
Praia de Abrolhal & Praia de Carvao, Boa Vista		HB	0	0	0.0				Sa	2
Praia de Boa Esperanca, Boa Vista		S	12488	3086	4.0					
Praia de Monte Leao, Sal		B	0	0	0.0					
Praia do Canto, Boa Vista		HB	6021	1537	3.9				Sa	
Praia do Coqueiro, Cancelo, Santa Cruz, Ilha de Santiago		B	1110	653	1.7				Pb, St	
Praia dos Achados, Santa Luzia		HB	3038	971	3.1				Sa, R	
Praia dos Balejos, Boa Vista		HB	1450	348	4.2					
Santa Maria beach, Sal Island		HB	2180	567	3.8					
CHILE										
Bahia Posesion, Rio Duck to Rio Butterfly		B	0	0	0.0					
Bahia Windhond, Isla Navarino		I	11900	12687	0.9					
Holger Islets, Beagle Channel		E	0	0	0.0					
Isla San Clemente, a small bay		I	1020	916	1.1				Sa.M	
Los Choros, Coquimbo		X	0	0	0.0					
Magellan Strait		E	0	0	0.0				M	3

Table 1 (*continued*).

COUNTRY / SITE NAME	DISTRICT	SITE TYPE	WIDTH (m)	INDENT (m)	W:I	SLOPE1 (Degrees)	SLOPE2 (Degrees)	SLOPE3 (Degrees)	SUBSTRATE	LARGE EVENTS
CHINA										
Shidao		X	0	0	0.0					
COLOMBIA										
San Andres Island		X	0	0	0.0					
COSTA RICA										
Playa Tambor		I	4531	4329	1.0					
CUBA										
Bahia de Nipe, Holguin (south of)		B	0	0	0.0					
Cayo Saetía		S	0	0	0.0					
DENMARK										
Bay Of Kiel Islands		X	0	0	0.0					
Jammerbugten, West Jutland		E	0	0	0.0				Sa	
Lakolk Beach, Romo Islands		E	0	0	0.0					2
ECUADOR										
Ancon, Santa Elena Peninsula	Guayas	HB	10592	2659	4.0					
Chanduy, provincia del Guayas	Guayas	HB	3040	755	4.0					
FALKLAND ISLANDS										
East Bay settlement, Philomel Harbor		E	0	0	0.0					
Fish Creek		X	0	0	0.0					2
Foul Bay		B	14379	9260	1.6					2
Pleasant Roads		I	1970	1913	1.0	0.4	0.5	0.1		
Ruggles Bay, Danson Harbour		I	1550	1162	1.3					
Speedwell Island, west side		I	708	530	1.3					
Teal Inlet, Bay of San Salvador		E	0	0	0.0					
FIJI										
Suva, beaches at		X	0	0	0.0					
FRANCE										
Anse de Cabestan, Rivage de Primelin		HI	1288	376	3.4				Sa	
Bay of St Vaast, Morsalines	Manche	HB	21366	6527	3.3					
Calais		S	0	0	0.0				Sa	
Carantec	Finistere	X	0	0	0.0					
Gulf of St Tropez		I	1986	1170	1.7					
Ker-Chalon beach, l'Ile-d'Yeu		B	1212	520	2.3					
L'estuaire du Jardy, La Roches-Derrien (Bois Du Renard)		E	0	0	0.0					
Paimpol	Cotes-Du-Nord	E	0	0	0.0					
Pleubian		X	0	0	0.0					
Port-la-Nouvelle, Aude (Le Barcares, Pyrenees Oriental)		Salient/Straight	0	0	0.0					
GALAPAGOS ISLANDS										
Puerto Villamil (near to), Isabela Island		HB	0	0	0.0				Sa	
Wreck Bay, Puerto Baquerizo beach, Moreno, San Cristobal		I	1498	956	1.6				Sa	
GERMANY										
Elbe river mouth, Neuwerk, Ritzebuttel		E	17227	22117	0.8				Sa	
GREECE										
Kypariassiakos Gulf		HB	57254	18883	3.0	0.6	0.6	1.2	Sa	
HAWAII										
Anini beach, Kauai		Reef lagoon	1422	348	4.1	0.13	1.2	2.9		
Kalihi beach, Kauai		I	1219	830	1.5	0.5	0.6	1.1		
Keomuku beach, Lanai		Reef lagoon	1049	107	9.8	0.3	0.3	3.5		
Waikiki, Oahu		HB	0	0	0.0				Sa	
HOLLAND										
Goeree beach, Sint Annaland, Zeeland		E	0	0	0.0					
Ouddorp, Goedereede Island		E	0	0	0.0				M	
Ter Heijde		E	0	0	0.0					
ICELAND										
Innri-Njar'vík (near to)		I	0	0	0.0					
Rif Harbour		Breakwater	4853	786	6.2					2
Thorlakshofn		HB	7673	2449	3.1	0.8	0.7		Sa.M	
INDIA										
Elizabeth Bay, Andaman Is		I	0	0	0.0				Sa	
Manapad		HB	0	0	0.0	0.1	0.04	0.4	Sa	2
Salt Lake (Serampore), Hooghly River, Calcutta		E	0	0	0.0				M	

Table 1 (*continued*).

COUNTRY / SITE NAME	DISTRICT	SITE TYPE	WIDTH (m)	INDENT (m)	W:I	SLOPE1 (Degrees)	SLOPE2 (Degrees)	SLOPE3 (Degrees)	SUBSTRATE	LARGE EVENTS
INDONESIA										
Ancol Beach, Banyuwangi, East Java		X	35578	15376	2.3					
Banyuwangi, East Java		S	0	0	0.0					
Deme Village, Savu Island, East Nusa Tenggara Timur		S	0	0	0.0				Sa	
Dringu, Gending, Bentar beaches, Probolinggo, East Java		B	0	0	0.0					
Kali River mouth, Besuki, Mllandingam, Madura Strait		E	0	0	0.0				Sa	
Kampong Nias, near Sabang, Weh Island		X	0	0	0.0					
Lhokseumawe, NE Sumatra		HB	10788	4320	2.5					
Ponggeran beach, Sulawesi		I	15811	11881	1.3					
Ujong Kareung beach, Aceh Besar		S	0	0	0.0					
IRELAND										
Ballyness beach, Falcarragh strand	Donegal	HB	0	0	0.0				cs.Sa	
Bay of Fethard, Fethard strand		HB	0	0	0.0					
Brandon Bay, Cloghane, Kerry		HI	6890	5575	1.2					
Dunfanaghy	Donegal	E	0	0	0.0					
Little Burrow, Fethard, Wexford		X	0	0	0.0					
Rutland Island, Donegal		X	0	0	0.0					
Tralee Bay		I	8693	7963	1.1				Sa	2
ITALY										
Calvi, Corsica		X	0	0	0.0					
Ligurian Sea		B	0	0	0.0					2
Near Mazaro del Vello, Sicily		X	0	0	0.0					
JAPAN										
Aoshima beach		HB	7902	1802	4.4					
Arikawa Bay, Shinkamigoto	Nagasaki-ken	I	0	0	0.0					
Beppu Bay, Oita City, Seto Inland Sea		I	13950	18150	0.8					
Choshi-shi, Chiba-ken		HB	72530	11040	6.6					3
Eshima Beach (between Kaedagawa & Aoshima)	Miyazaki	HB	0	0	0.0					
Fukuroi-shi, Shizuoka-ken		X	0	0	0.0					
Hannan-shi, Osaka-fu		I	0	0	0.0	0.7	0.2	0.1		
Ibaraki coast		HB	73064	11057	6.6					8
Ichinomiya-Cho, Chosei-gun, Chiba		HB	0	0	0.0					
Iioka coast, Asahi line, Chiba		HB	58667	15465	3.8					
Isumi-shi, Chiba-ken		X	0	0	0.0					
Kamakura-shi, Kanagawa-ken		I	2481	1188	2.1	0.08	0.7	0.6		
Kurikepura, Hirasawa-cho, Akita-ken		HB	0	0	0.0					
Menashi-Tomari, Esashi-Cho, Esashi-gun	Hokkaido	Ice	0	0	0.0	0.6	0.3	0.22		
Minamiboso-shi, Chiba-ken, Awa-gun		B	2511	1495	1.7					
Nachikatsuura-Cho, Higashimuro-gun, Wakayama-ken		X	0	0	0.0					
Nakatane town, Nagahama coast, Kagoshima-ken, Tanegashima Island		HB	23916	4348	5.5	0.7	0.25	0.9		
Near Aidomari Port, Rausu-Cho, Menashi-gun	Hokkaido	Ice	0	0	0.0					
Near Awa, Kagoshima		X	0	0	0.0					
Oura (dike), Minamisatsuma-shi, Kagoshima		HB	36798	17892	2.1					
Sado-shi, Niigata-ken		X	0	0	0.0					2
Sagami Bay, Odawara City, Kozu to Hayakawa		I	40500	20283	2.0					
Tanne-moy, Etorofu Island		Ice	0	0	0.0					
Tarama-Son, Minna island, Miyako-gun, Okinawa-ken		X	0	0	0.0					
Tatsugo-Cho, Oshima-gun, Kagoshima-ken		I	0	0	0.0					
Tsutsugajou beach, Iki-shi, Nagasaki-ken		X	0	0	0.0					
LESSER ANTILLES										
Butler's Area, NE Side Of Nevis island		S	0	0	0.0				R	
LOYALTY ISLANDS										
Saint-Joseph, Ouvea (Ohounou)		Reef lagoon	0	0	0.0					
MADAGASCAR										
Antsohihy, Loza Lagoon		E	0	0	0.0					
MEXICO										
Amortajada Bay, San Jose Island		HB	7490	2862	2.7	0.3	0.6	0.8	St, Sa	
Bahia de La Paz		HC	0	0	0.0					3
Bahia de San Rafael	BCN	HB	28098	9185	3.1					
Bahia Guadalupe, N of Bahia de los Angeles		HB	860	322	2.7					
Dzilam Bravo (24 km E of), Xpet Ha	Yucatan	X	0	0	0.0					
Holbox Island		X	64975	9482	6.9					
Huatabampito, Sonora		HB	16754	2446	6.8					
Punta Bufeo		HB	5704	1795	3.2					
Rio Lagartos, Yucatan	Yucatan	X	0	0	0.0					
San Bruno, 15km north of Mulege	BCS	X	0	0	0.0					
Tenabo, Campeche state	Campeche	X	0	0	0.0					
NEW CALEDONIA										
Baie d'Oro, sandy beach in front of a hotel		B	0	0	0.0				Sa	

Table 1 (*continued*).

COUNTRY / SITE NAME	DISTRICT	SITE TYPE	WIDTH (m)	INDENT (m)	W:I	SLOPE1 (Degrees)	SLOPE2 (Degrees)	SLOPE3 (Degrees)	SUBSTRATE	LARGE EVENTS
NEW HEBRIDES										
Ravallec Bay		HI	1713	1926	1.6	0.2	0.1	0.3	Sa	
NORWAY										
Brossoya (in a strait), north of Borgan, Vikna		E	0	0	0.0					
Laupstad, Austnesfjord (Ostnesfjord)		E	0	0	0.0					
NEW ZEALAND										
Aotea Harbour, north of		S	0	0	0.0					
Bay Of Plenty region		HB	29384	10329	2.8					4
Blind Bay, Great Barrier Island		CI	1736	2053	0.8					
Bream Bay		HI	20918	11386	1.8	0.22	0.04	0.2		11
Cape Campbell		HB	0	0	0.0					
Cloudy Bay		B	23181	10144	2.3	0.8	0.3	0.1		
Colville Beach, Coromandel Peninsula		I	0	0	0.0	0.03	0.09	0.1	M	
Dargaville		S	0	0	0.0					2
Doubtless Bay		HI	10600	13876	0.8	0.33	0.35	0.11		6
Doughboy Bay, Stewart Island		HI	6815	4980	1.4	0.16	0.34	0.86		2
Golden Bay		Spit-bay	0	0	0.0	0.4	0.04	0.13		37
Hanson Bay, Chatham Island		HB	28517	13509	2.1	0.6	0.9	0.2		14
Hawke Bay		HB	22139	6862	1.7	0.4	0.13	0.07	f.Sa	8
Houhora Bay, Northland		HB	1707	888	1.9					
Kaipara coast		S	0	0	0.0	0.3	0.1	0.15	Sa	4
Karepiro Bay, Wade River (Weiti River)		B	8758	1579	5.5				Sa	
Karikari Beach	North Island	S	0	0	0.0	0.9	0.2	0.3		2
Katherine Bay, Great Barrier Island		B	0	0	0.0					
Kawau Bay, Snells Beach	North Island	HB	1983	543	3.7					
Kuaotunu Bay, Matarangi Beach	North Island	HI	11848	3586	3.3					
Long Beach, Auckland		HI	24260	19874	1.2				Sa	
Lyall Bay, Cook Strait		I	1506	2170	0.7				Sa	
Mahurangi		X	0	0	0.0					
Mairangi, Wharekauri Beach, Chatham Island		HB	0	0	0.0					
Mangawhai Estuary		E	0	0	0.0					
Manukau Harbor, On Poutawa Bank		E	0	0	0.0					
Mason Bay, Stewart Island		HB	81505	7254	11.2	0.5	0.6	0.5		2
Maunganui, NW Chatham Island		HB	13787	4129	3.3	0.45	0.13	0.32		3
Muriwai		S	13439	4411	3.0	0.6	0.4	0.3		3
Napier Beach		X	0	0	0.0	0.5	0.1	0.1		
Ngawai Bay		HB	749	310	2.4					
Northland		X	0	0	0.0					
Ocean Beach, Old Sand Neck, Stewart Island		HI	728	338	2.2	0.8	0.9	0.5	Sa	
Paraparamau beach		HB	0	0	0.0	0.8	0.33	1	Sa	
Parengarenga, Northland		X	0	0	0.0					
Petre Bay, Long Beach, Chatham Island		HB	0	0	0.0	0.4	0.4	0.3		12
Port Levy, Banks Peninsula, South Island		CI	2085	6600	0.3	0.3	0.2	0.1		2
Radio Station beach, Pt Weeding, Chatham Island		HB	390	145	2.7					
Ruapuke Island, small beach near east end		HB	464	223	2.1					
Sandy Bay, Nelson		I	3262	2100	1.6					
Shipwreck Bay (near to) (Ahipara, Northland)		HB	77506	15229	5.1	0.9	0.26	0.13		
Spirits Bay		HB	16000	4050	4.0	0.9	0.3	0.2		
Stingray Bay, Great Mercury Is		B	0	0	0.0					
Tararewa River mouth, 2km east of		S	0	0	0.0					
Tasman Bay		B	0	0	0.0					
Te Paki, 90 Mile Beach		HB	2663	685	3.9					
Thames		I	10569	14035	0.8	0.02	0.03	0.04		
Titirangi Point, North Cape		X	0	0	0.0					
Tryphena Harbor, Great Barrier Island, Puriri Bay, Goosebury Flats		I	2638	3160	0.8	0.8	1	0.3		
Waianakarua River mouth, on rock platform		Reef, rock	0	0	0.0					
Waihau Bay, Orouiti Beach, Waihau Bay East		HB	4755	1639	2.9					
Waihere Bay, Pitt Island		HI	1871	1104	1.7					3
Waikuku Beach, North Cape		HB	11047	3120	3.5					
Wainui beach (Okitu), Tatapouri Point, Gisborne		HB	5480	917	6.0	0.8	0.5	0.14		
Waitangi West Beach, Chatham Island		HI	4820	2780	1.7					
Warrington (Okahau)		B	0	0	0.0	0.6	0.2	0.13		2
West Ruggedy Beach, Stewart Island		HB	2640	678	3.9	0.25	2.3	1.1		
Whale Bay/Hendersons Bay		HB	4425	1082	4.1					
Whangaparaoa Bay		HB	2944	982	3.0	0.24	0.1	0.08		2
Whangaumu Bay, Ngunguru		HI	1269	513	2.5					
Whatipu beach, West Auckland		S	608	365	1.7					
Whitianga Bay		CI	3645	5100	0.7					
Wooding Bay, Maori Beach, Stewart Island		HI	941	848	1.1	0.3	0.4	0.4		
OMAN										
Al Sawadi beach		HB	13649	1932	7.1	0	0.34	0.3		
PHILIPPINES										
Cadiz city, Negros Occidental province		X	11747	1946	6.0					

Table 1 (*continued*).

COUNTRY / SITE NAME	DISTRICT	SITE TYPE	WIDTH (m)	INDENT (m)	W:I	SLOPE1 (Degrees)	SLOPE2 (Degrees)	SLOPE3 (Degrees)	SUBSTRATE	LARGE EVENTS
PORTUGAL										
Albufeira, Algarve coast		HB	2590	555	4.7					
SCOTLAND										
Backaskaill Bay, Sanday, Orkney		HB	1950	828	2.4				Sa	
Bay Of Tafts, Twinness, Westray (South Side, Wastbis Farm)		HB	791	471	1.7					
Buddon Ness and Barry Sands east		E	0	0	1.5				Sa	
Dornoch Firth		E	0	0	0.0				M, Sa	
Isle Of Lewis		X	0	0	0.0					
Kyle of Durness		E	0	0	0.0	0	1	1.9		
Loch Carnan, South Uist		E	0	0	0.0					
Loch Torridon		E	0	0	0.0					
Pittenweem, Fife		S	0	0	0.0				Sa, R	
Point of Cott, Westray, Orkneys		I	0	0	0.0				St	
Staffin, Isle of Skye		HB	0	0	0.0					
Thorntonloch Beach, East Lothian		S	0	0	0.0					
Uyeasound, Shetland		I	0	0	0.0					
SENEGAL										
Yoff		HB	0	0	0.0	0.9	0.4	0.2		6
SEYCHELLES										
La Digue Island		X	0	0	0.0					
SOUTH AFRICA										
False Bay, Cape Peninsula		CI	0	0	0.0					
Grotto Bay, Seaspray, Mamre		HB	0	0	0.0				Sa	
Long Beach, Kommetjie		HB	1643	395	4.2				Sa	2
Melkboss Strand		S	0	0	0.0					
Morgan Bay		HB	1525	411	3.7					
Nordhoek beach		HB	4176	1049	4.0					
St Helena Bay		HB	53473	20284	2.6	0.14			Sa	3
Walkers Bay, Die Kelders		HI	22396	10809	2.1					
SPAIN										
Arbeyal beach, Gijon		B	1395	1580	0.9				Sa	
Bahia de Alcudia, Majorca		HI	16370	12830	1.3					
Bares Bay		HB	895	463	1.9					2
Burela (near to)		X	0	0	0.0					
La playa de Cobas, Vivero		I	1934	4860	0.4					
La playa de San Antonio, Nueva, Llanes		B	76	142	0.5					
La playa de Zumaya		B	750	393	1.9					
San Lorenzo beach, Gijon		HI	1039	562	1.8					
SRI LANKA										
Koddiyar Bay		HI	7934	9360	0.8				M	2
Shallow inlet near Kambanturai at Kayts, Velenai, Kayts Island		B	0	0	0.0				M, Sa	
TAIWAN										
Anping Harbour (near to), Tainan		Breakwater	0	0	0.0	0.4	0.4	0.1		
Chin-Shan fishing port (a beach near)		Breakwater	0	0	0.0	0.5	0.2	0		
Heng Chun		HB	12227	4723	2.6					
Tseng Wen River mouth		E	19722	3105	6.4	0.3	0.2	0.13		
Xingda port, Kaohsiung, Tainan		X	0	0	0.0					
THAILAND										
Batok Bay, Racha Yai Island		I	689	826	0.8				Sa	
TRINIDAD										
Cocos Bay, Manzanilla beach		HI	20720	4345	4.8				Sa	
UNITED KINGDOM										
Beaumaris Bay, Conway Estuary, Caernarvon	North Wales	I	4960	2802	1.8				Sa, M	
Birchington	Kent	S	0	0	0.0					
Donna Nook	Lincolnshire	E	0	0	0.0				Sa	
Eday	Orkney	X	0	0	0.0					
Hillswick, Urafirth, Shetland (Saint Magnus Bay)		E	0	0	0.0					
Holland Bay, Stronsay	Orkney	I	2356	3578	0.7					
Holmpton to Easington	East Riding Of Yorkshire	S	0	0	0.0					
Mounts Bay, Eastern Green beach, Penzance		HB	0	0	0.0	0.5	0.3	0.2	Sa	
The Wash, Haven River mouth, Boston, Norfolk		I	17745	26104	0.7					2
Whiteford Sands beach, Carmarthen Estuary (NE side of Whiteford Pt)	Wales	E	0	0	0.0					
URUGUAY										
Jaureguiberry		HB	9939	1225	4.9	0.6	0.11	0.3		

Table 1 (*concluded*).

COUNTRY / SITE NAME	DISTRICT	SITE TYPE	WIDTH (m)	INDENT (m)	W:I	SLOPE1 (Degrees)	SLOPE2 (Degrees)	SLOPE3 (Degrees)	SUBSTRATE	LARGE EVENTS
USA										
Avalon Beach State Park	FL	Lagoon	0	0	0.0					
Baldhead Island	NC	X	0	0	0.0					
Bayou Lafourche, West Of Pass Fourchon	Louisiana	E	0	0	0.0					
Bull Island	SC	X	0	0	0.0					
Cape Canaveral (near the lighthouse)	FL	X	0	0	0.0				Sa	
Cape Cod Bay	MA	Spit-bay	32380	36657	0.9	0.8	0.4	0.9		74
Cape Lookout		HB	154900	35222	4.4					
Cape Sable region, Everglades		S	0	0	0.0					2
Coquina beach (Bodie Island, N of ramp 2)	NC	E	0	0	0.0					
Corolla, Ocean Beach	NC	S	0	0	0.0					
Cow Cove, Block Island		B	1440	303	4.8					
Cumberland Island	SC	X	0	0	0.0					
Daytona Beach, Between South Daytona and New Smyrna Beaches	FL	S	0	0	0.0					
Flagler Beach (5 Miles South Of)	FL	S	0	0	0.0				Sa	
Florida Keys	FL	Key	0	0	0.0					11
Fort Myers Beach	FL	Lagoon	45624	13868	3.3					
Fort Pierce to Vero beach		Lagoon	0	0	0.0					
Highland Beach, Everglades	FL	S	86140	19175	4.5	0.06	0.02	0.03		
Hog Key, Everglades		X	0	0	0.0				M	
Jacksonville, N Of Little Talbot Is, Nassau Sound, Bird Is.	FL	E	0	0	0.0					
Kiawah Island		S	16938	2655	6.4	0.11	0.07	0.02		2
Lewis Bay, Hyannis, Barnstable		B	0	0	0.0					
Little Gasparil, Gum, S End Little Gasparilla Is	FL	Key	0	0	0.0					
Little St Simons Island, beach midway down island	SC	X	0	0	0.0					
Loggerhead Key, Dry Tortugas		Key	0	0	0.0					
Manasota Key & Gasparilla Island		Key	0	0	0.0					
Marco Island (Marco River/Factory Bay)	FL	X	0	0	0.0					
Mayport		E	0	0	0.0					
Melbourne, 11 Miles South Of	FL	X	0	0	0.0					
Naples	FL	X	0	0	0.0					2
Nantucket Island region		X	0	0	0.0					3
Pass-a-Grille beach, Pinellas county	FL	X	0	0	0.0					
Pavilion Key, West Coast Of Florida	FL	Key	0	0	0.0					
Ponte Vedra	FL	S	0	0	0.0					
Port Everglades National Park, NW Tip Of Sable Island	FL	X	0	0	0.0					
Pyramid Cove, San Clemente Island		HB	4518	1355	3.3	3.3	2.9	2.7	Sa, R	2
Richardson Creek, Georgia	GA	X	0	0	0.0					
Siesta Key	FL	S	0	0	0.0					
Simonton Cove, San Miguel Island		HB	4428	1271	3.5	1.2	0.4	0.3		
Siuslaw (Florence, 2.3Km S Of Jetty)	OR	Breakwater	0	0	0.0	0.4	0.8	1	Sa	
Squaw Island (near Kennedy Compound), Hyannis Port	MA	Breakwater	0	0	0.0	1.3	2.6			
St Augustine Beach	FL	S	0	0	0.0				Sa	
St Simons Island, South End Of		X	0	0	0.0					
Upper Captiva Island, Pine Island Sound, Lee	FL	E	0	0	0.0					
VENEZUELA										
Bahia Guamache, Margarita Island		HB	6009	2493	2.4				Sa	
ZANZIBAR										
Mtoni beach		HB	4584	1096	4.2				f.Sa, M	

Key: Type: B = bay of unspecified type; CI = bay with indented character and additional coastline or bathymetric complexity; E = estuary; HB = 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 = unknown (see Fig.1 for examples of bay types). W:I = Indentation ratio. Slope: 1 = nearshore; 2 = intermediate; 3 = offshore. Substrate: particle sizes, f = fine, m = medium, cs = coarse; Bo = boulder, M = mud, MS = mud and sand, Pb = pebble, R = rocky, S = sand, SSh = sand with shell fragments, St = stones (see Hamilton (1999) for information on this seabed characterisation scheme). Large events: number of live events with 10+ animals.

A representative total of 710 events resulted, including 74 events in Cape Cod Bay (USA) and 37 in Golden Bay (New Zealand). The data are described as representative because detailed records are typically only available for about 100 years at most, some areas do not have records, not all events are noted, and not all recorded events will have been discovered for this analysis. These factors are expected to be offset by the widespread geographical distribution of events (Fig. 2). Accurate descriptions of site types and characteristics are dependent on good positioning information. Geographic co-ordinates are often not included in the literature or databases, or are too broad to be useful. Positions for explicitly named or photographed locations such as beaches and bays were extracted from charts. Good locations could not always be found for sites described as being 'near to' some beach, population centre, or other feature. All 710 events were used for general statistical information on numbers and species in larger strandings, and for broader geographical distribution of events, but not all could be used for site specific analyses. Brabyn and McLean (1992) regarded each New Zealand herd stranding (2+ animals) as having a separate location, even if on the same beach. In the present paper, coastal features such as bays are regarded as one site only, whether one or many strandings occurred in them, resulting in 402 separate sites.

Description of sites

Where possible, site properties were characterised quantitatively by coastal indentation, seabed slopes, and

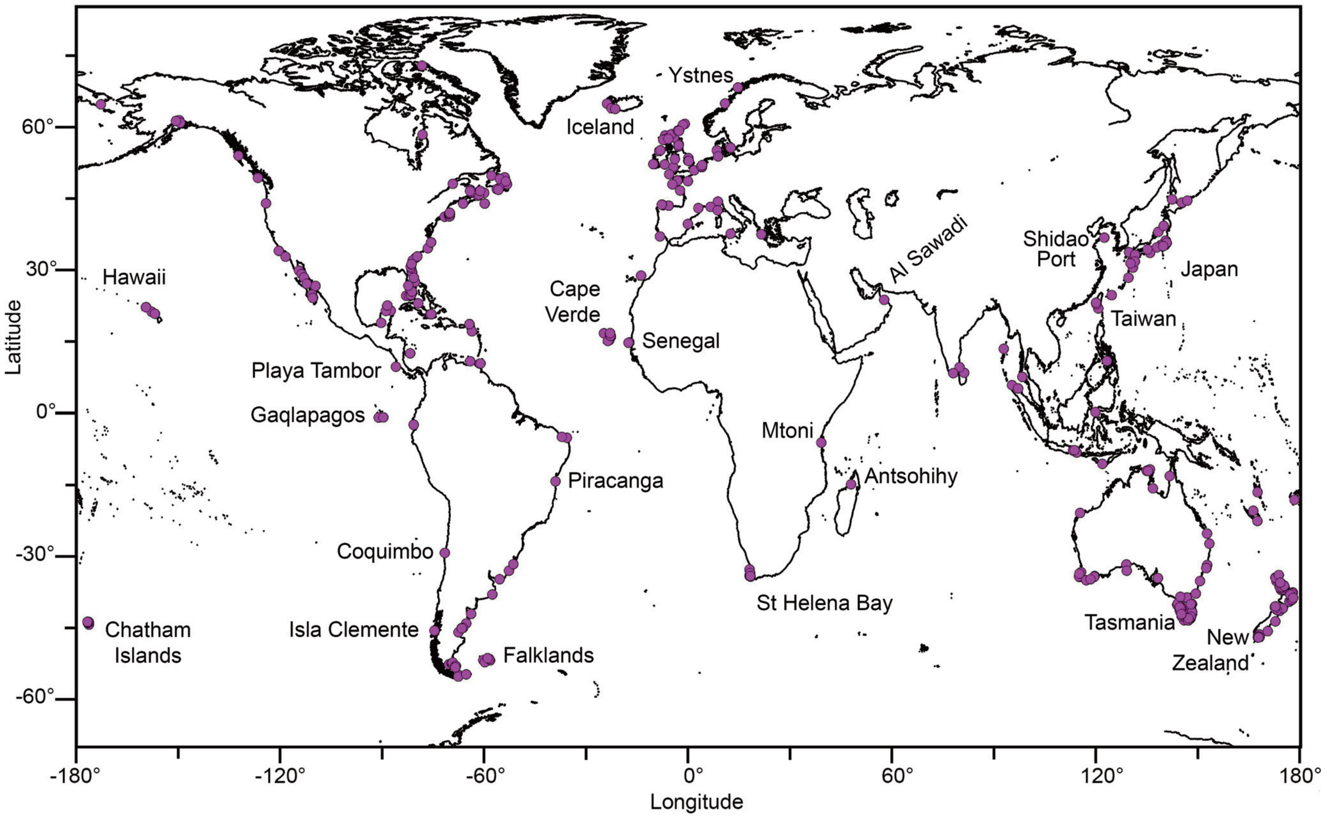


Fig. 2. Worldwide sites of larger strandings of odontocetes (toothed whales).

sediment grain size, following the approach of Hamilton and Lindsay (2014a). Planforms of coastal configurations were compiled as indications of the larger geomorphological environments of sites (for example bays, estuaries, lagoons), together with indications of complexity caused by reefs, islands, and convoluted coastlines. Some bays have a headland at both ends. Bay width (W) was measured from headland to headland when two were present, and from headland to beach end or to where the beach straightens for the single headland case (Fig. 1(b)). Bay indentation distance (I) was measured as the maximum value to shore perpendicular to the line specifying the bay width. Indentation ratio (W:I) is the ratio of bay width to bay indentation distance, and is a useful proxy for coastline curvature (Hamilton and Lindsay, 2014a).

Bays are separated into indented bays and headland-bays using planform and indentation. Headland-bays have indentation ratio greater than 2:1 and a characteristic log-spiral shape, and indented bays have ratio less than 2:1, although indented bays may have headland-bay character and vice versa (Fig. 1). The ratio of 2:1 was initially used by Hamilton and Lindsay (2014a) as an empirical value which separated Australian bays of a similar regular shape (subsequently identified as headland-bays), regardless of their sizes, from those of irregular shapes. It was found that coastal engineering studies had identified the value of 2 as the lower bound for indentation ratio approached by mature headland-bays (Silvester and Ho, 1972), giving the empirical findings a physical basis. Indented bays can have a variety of planforms, seabed slopes, and geomorphological origins such as wave formed, or drowned topography. Headland-bays are formed by the eroding effects of waves and swell on coastlines of relatively softer materials interspersed by harder materials which become headlands. The eroded material may range from block and boulder size to fine sands, depending on the state of maturity of the bay. Larger sizes are broken into smaller by continued attrition and abrasion. Finer sediments (silts and clays) are generally winnowed out by waves and currents. Headland-bays are often associated with a stream running along the bay side of the headland, which may supply additional sediments.

Bays were classed as follows (see Fig. 1): headland-bays with a gently curving half-heart planform (H); indented bays with a headland often not prominent or absent (I); headland bays with indented character (HI). Bay types H and I with additional complexity (C) caused by topographical or bathymetrical configuration are classed as HC and CI. Bay (B) is used for bays without a specific name or location. Other classes are estuary (E) (estuary, firth, fjord, forth, coastal lagoon), reef lagoon, relatively unindented or straight coasts, entrapment in ice, and unknown (X) for general locations specified for example as ‘St Andres Island’. The presence of breakwaters and groyne series are also noted. Spit-bays are also recognised as a particular indented bay type.

Seabed indicators on hydrographic charts were the primary source of sediment descriptions. These descriptions are made by charting agencies from visual and tactile examinations of fresh wet surficial samples. Hamilton (1999) has shown they are generally reliable and consistent assessments of non-cohesive sediments in particular with respect to the quantitative Udden-Wentworth sediment grainsize 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 (silts and clays) are collectively termed muds and particles with diameter greater than 2mm (termed gravel) range from granules to boulders.

Seabed slopes were measured for shore perpendicular transects for 105 sites for which quality information was available, nominally from shore to deeper than the usual wave base (30m depth). The slopes are measured perpendicular to shore along bay axes, not over low gradient areas or in enclosed areas such as estuaries. Digital charts were used for Australia, New Zealand (LINZ – Land Information New Zealand, *http://www.linz.govt.nz*), the USA, and parts of Japan and South America (Digital Nautical Charts from NGA Maritime Division). Elsewhere any available information was used. Seabed topography and coastal configuration can change markedly with time for some locations (river deltas, ports and harbours in particular), but older charts were seldom available.

RESULTS

Number of events by species

The 710 larger strandings are for long-finned pilot (*Globicephala melas*) (218), short-finned pilot (*Globicephala macrorhynchus*) (103), pilot whales of undetermined species (160), false killer whales (*Pseudorca crassidens*) (75), sperm whales (*Physeter macrocephalus*) (58), melon-headed whales (*Peponocephala electra*) (28), white whales (24), blackfish (these are unidentified odontocete species excluding dolphins and porpoises) (16), killer whales (*Orcinus orca*) (15), beaked whales (11) [Cuvier's (*Ziphius cavirostris*) (6), Baird's (*Berardius bairdii*) (1), Blainville's (*Mesoplodon densirostris*) (1), Gray's (*Mesoplodon grayi*) (3)], pygmy killer whales (*Feresa attenuata*) (3). Twelve long-finned pilot whale events of 200+ animals for the Falklands mentioned by Otley (2012) are not in these figures.

Numbers in a stranding

Maximum numbers in a stranding were for 'pilot' whales (1,000), false killer whales (835), long-finned pilot whales (500), melon-headed whales (265), short-finned pilot whales (200), white whales (186), sperm whales (72), pygmy killer whales (28), killer whales (25), Gray's beaked whale (28), Cuvier's beaked whale (15), Baird's beaked whales (10), Blainville's beaked whales (10). The figure of 835 for Mar del Plata, Argentina was well reported (Marelli, 1953). The figure of 1,000 pilot whales at Chatham Island is from the New Zealand Department of Conservation Tea Ara website (*http://TeAra.govt.nz*). Cape Cod Bay has historical drives of more than 1,400 pilot whales, but maximum in strandings of 500.

Areas with high numbers of strandings

Many events occur south of 30°S and north of 15–20°N (Fig. 2), coinciding with the known distributions of several odontocete species. Higher numbers of events are seen on the southern coast of Australia, particularly around Tasmania (Hamilton and Lindsay 2014a); the eastern coastlines of New Zealand (McCann, 1964; Brabyn and McLean, 1992); the southeastern coastline of South America (Goodall, 1989); and the far southwest of South Africa. In the northern hemisphere, the Ibaraki coast on eastern Honshu, Japan figures prominently, along with the British Isles, the east coast of North America (including the eastern interior shorelines of Cape Cod Bay; McFee, 1990; 1991), and the Gulf of California on the west coast. Islands such as Cape Verde (18 events), Chatham (26), Falklands (9), Galapagos (2), Hawaii (4) appear over represented compared to their size.

Regions of larger strandings by species

White whale strandings sometimes occur during lower low tides at Susitna River and Turnagain Arm in the muddy Cook Inlet, Alaska, with and without mortality (Fig. 3). These events are included as being similar to those associated with tides in locations such as Cape Cod Bay and elsewhere. Entrapments under ice with limited access to breathing holes ('savsats') occur for both white whale and narwhal (Porsild, 1918). At least 17 savsats are known for both species, with more than half in Disko Bay, Alaska, but they are not included in the database, as details are often lacking. Savsats sometimes involve hundreds of animals. A narwhal ice entrapment in Greenland in November 2008 yielded 629 animals (hauled out of 3 ice holes by Eskimo), with one white whale savsat of 260 animals in November 2015.

All six Cuvier's beaked whale events are in the northern hemisphere, three being in the Mediterranean (Fig. 3). New Zealand has three Gray's beaked whale events. A Baird's beaked whale event occurred at Isla San Jose, Mexico. An unconfirmed Blainville's event is recorded for the Canary Islands. No Australian beaked whale strandings of more than 6 animals appear in a 100-year record of 331 events (Hamilton and Lindsay, 2014b).

Blackfish events are widely spread (Fig. 3), indicating no particular bias to results except for New Zealand. False killer events are seen particularly around Japan, the British Isles, the Gulf of Mexico, and south of 30°S (Fig. 4). Melon-headed whales (*Peponocephala electra*) are a tropical pelagic species (Findlay *et al.,* 1992; Jefferson and Barros, 1997) and events lie between 40°N and 30°S, particularly for the Cape Verde Islands and eastern Japan, the latter geographically associated with the warm Kuroshio western boundary current (Fig. 5).

Pilot whale events occur particularly on the North American east coast, the British Isles, Japan, and south of 30°S (Figs 6 and 7). Most short-finned pilot events are in the northern hemisphere (Fig. 6). Short-finned and long-finned pilot strandings overlap to some extent on the eastern coast of North America from 35°N to 45°N, as noted by Abend and Smith (1999) for live sightings, and around the British Isles. Long finned pilot (Fig. 6) and killer whales (Fig. 4) have much the same geographical stranding patterns of north of 30°N and south of 30°S. The three pygmy killer strandings (Fig. 4) were on the southwest coast of Taiwan (Tzeng-wan river mouth and Ching-shan fishing port; Brownell *et al.,* 2009), and Xingda port. Sperm whale events are noted round the Gulf of California, the North Sea (Europe), eastern Japan (but not the Sea of Japan, and Nishimura [1965] notes an almost complete absence of sightings in this area), and south of 30°S (Fig. 5).

Site details

Site type was determined for 627 events. Three-quarters (76%) occurred in bays, with 14% in shallow topographically complex areas (estuarine environments

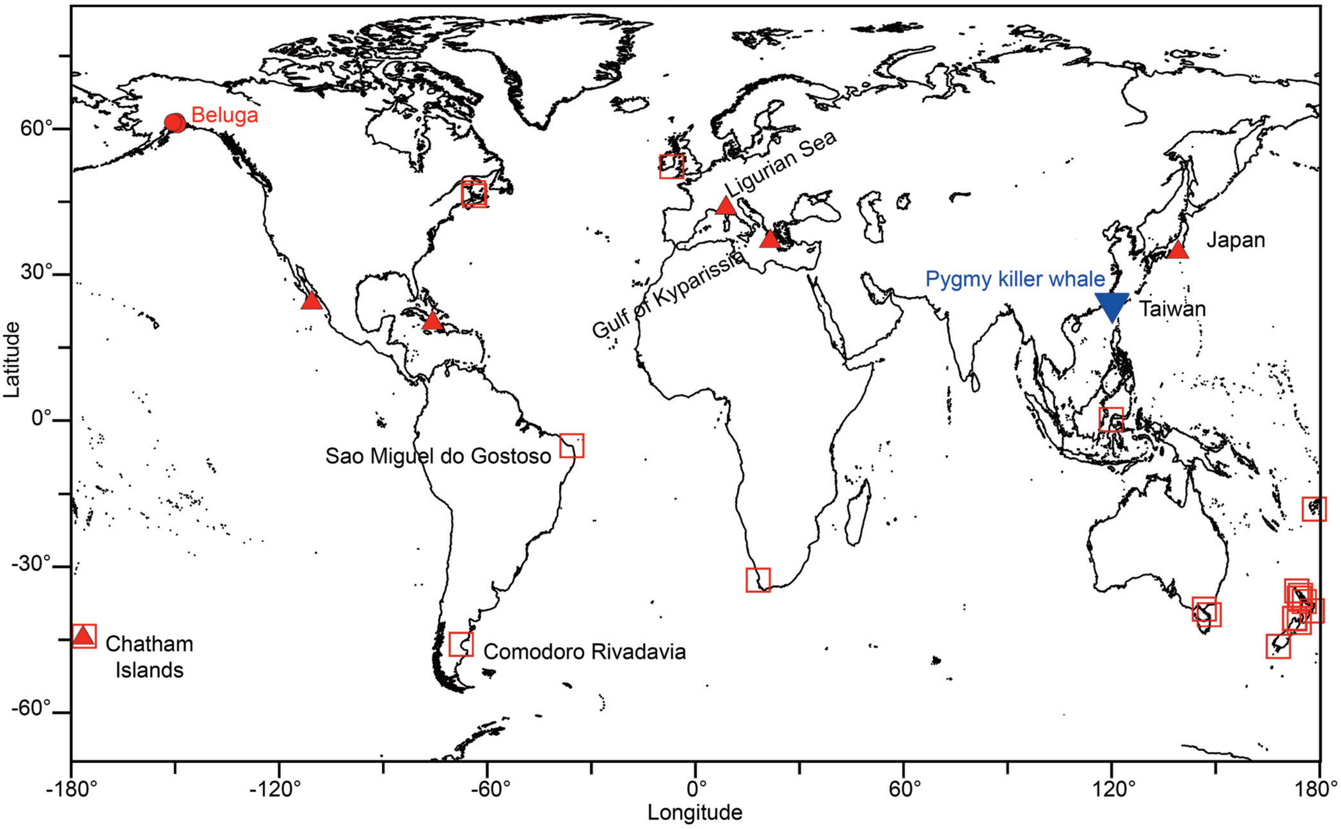


Fig. 3. Beaked (▲), Blackfish (unidentified odontocete species excluding dolphins and porpoises) (□), Pygmy Killer (▼),White whale (●) strandings.

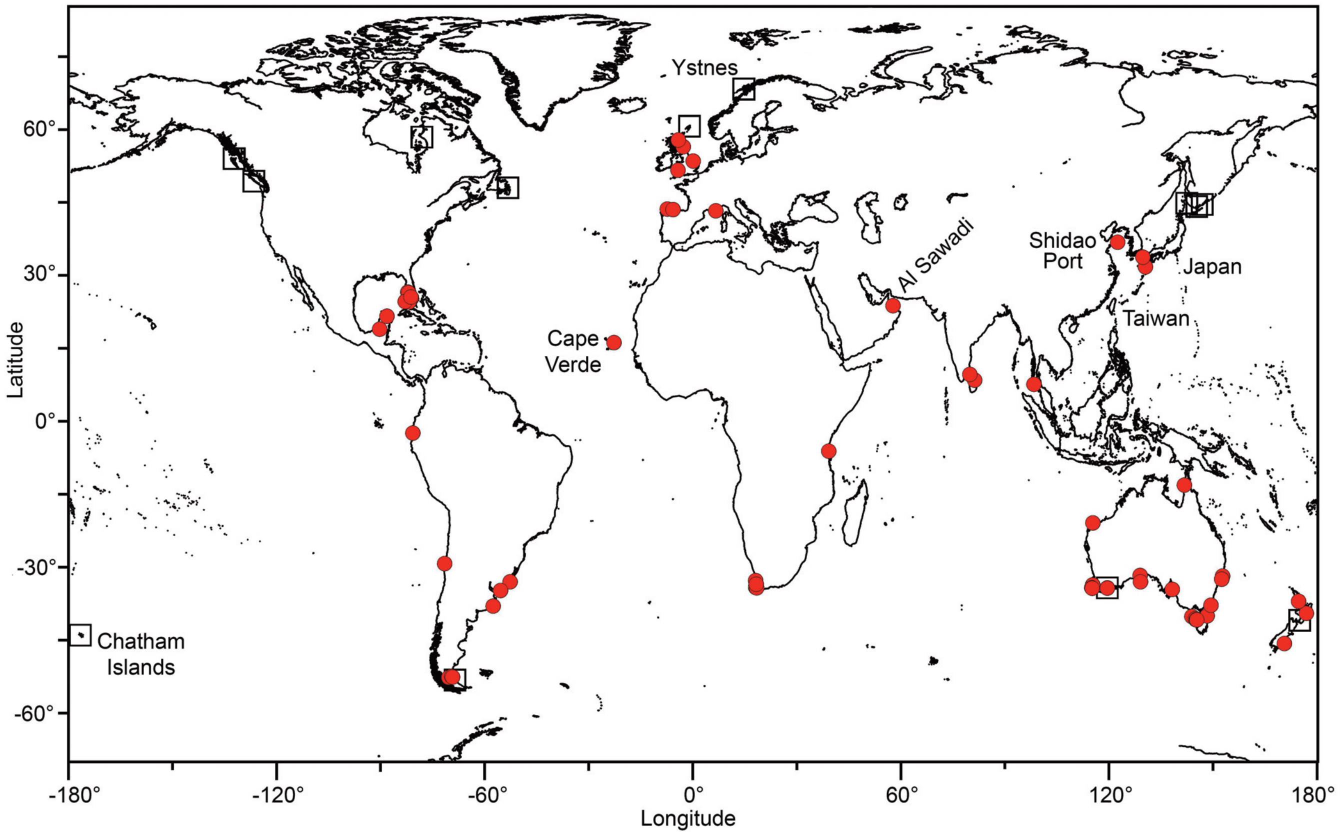


Fig. 4. False killer (●), Killer (□) whale strandings.

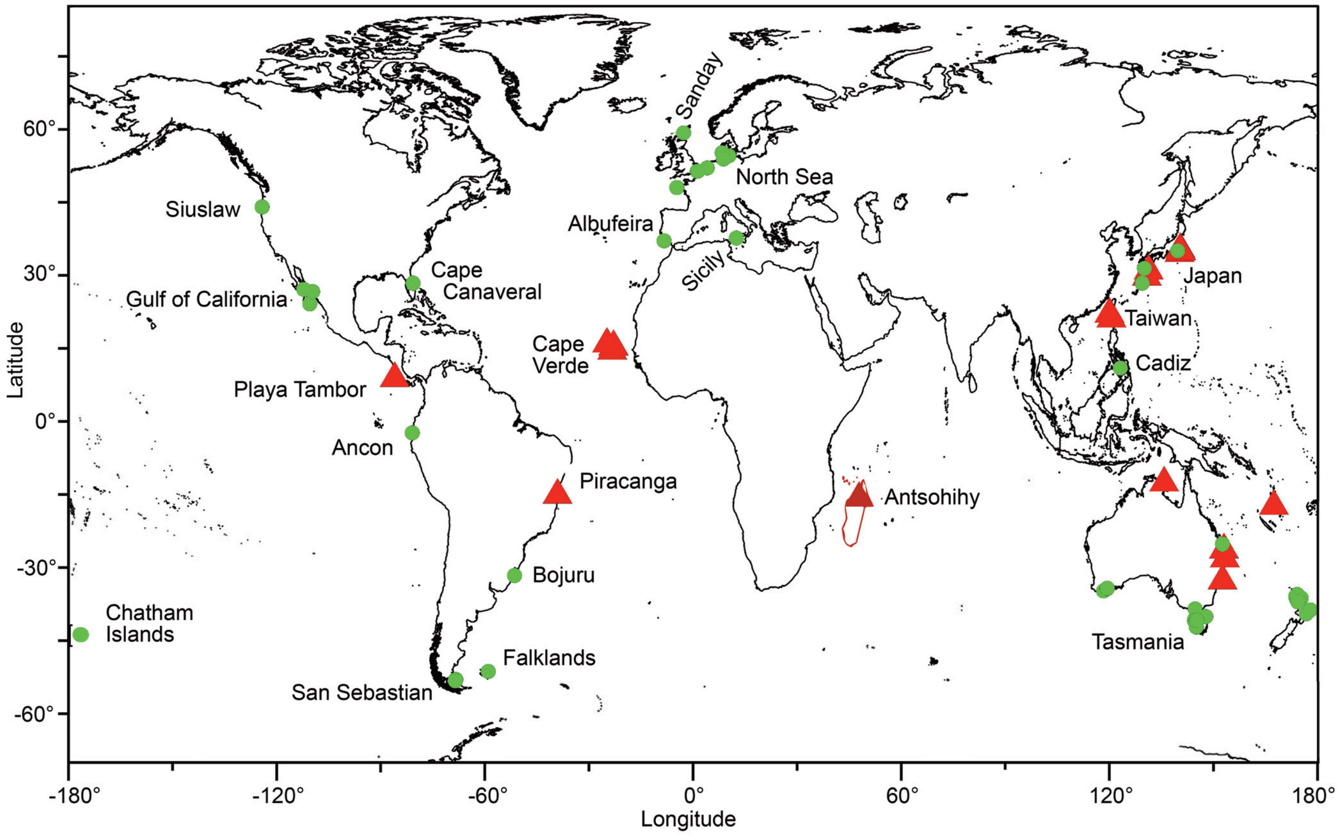


Fig. 5. Melon-headed whale strandings (▲) and sperm whale strandings (●).

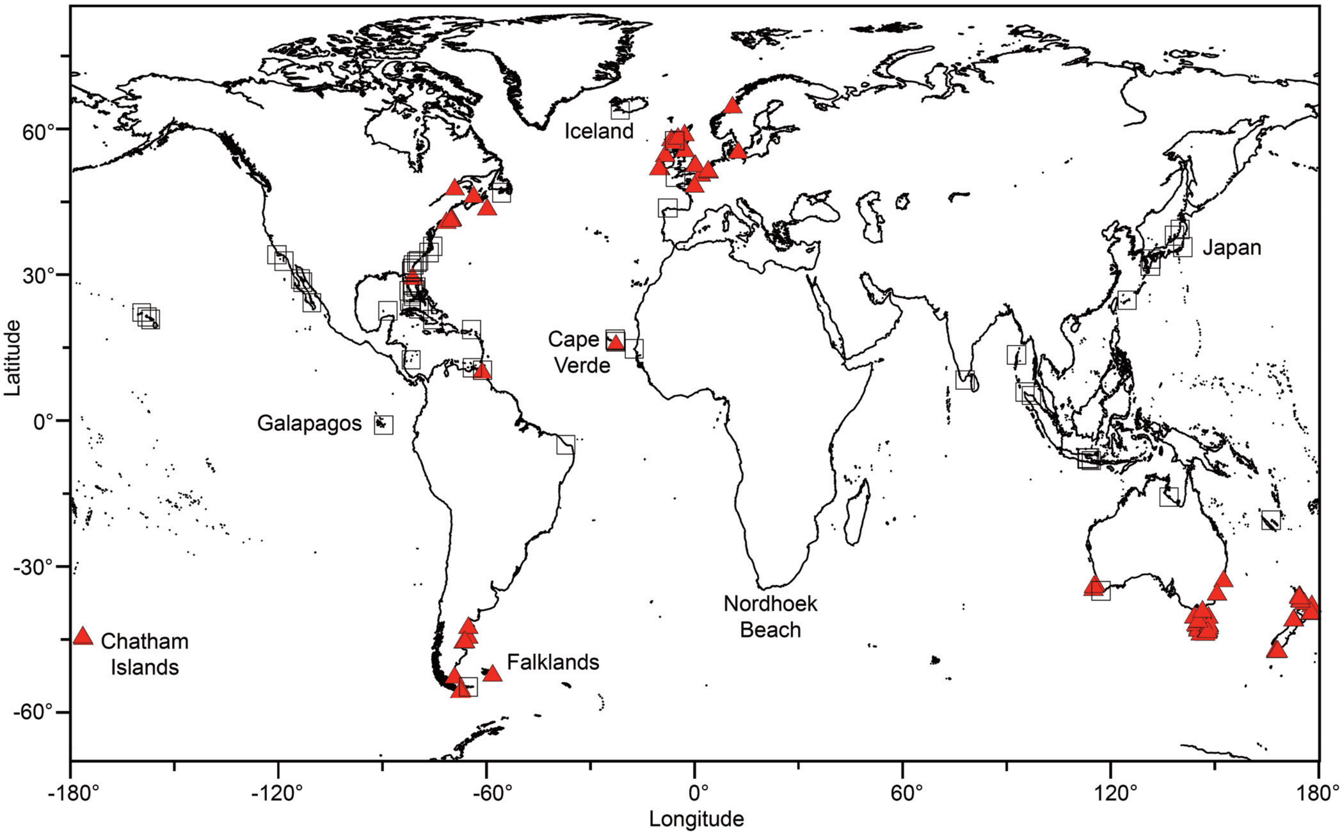


Fig. 6. Long-finned pilot (▲), Short-finned pilot (□) whale strandings.

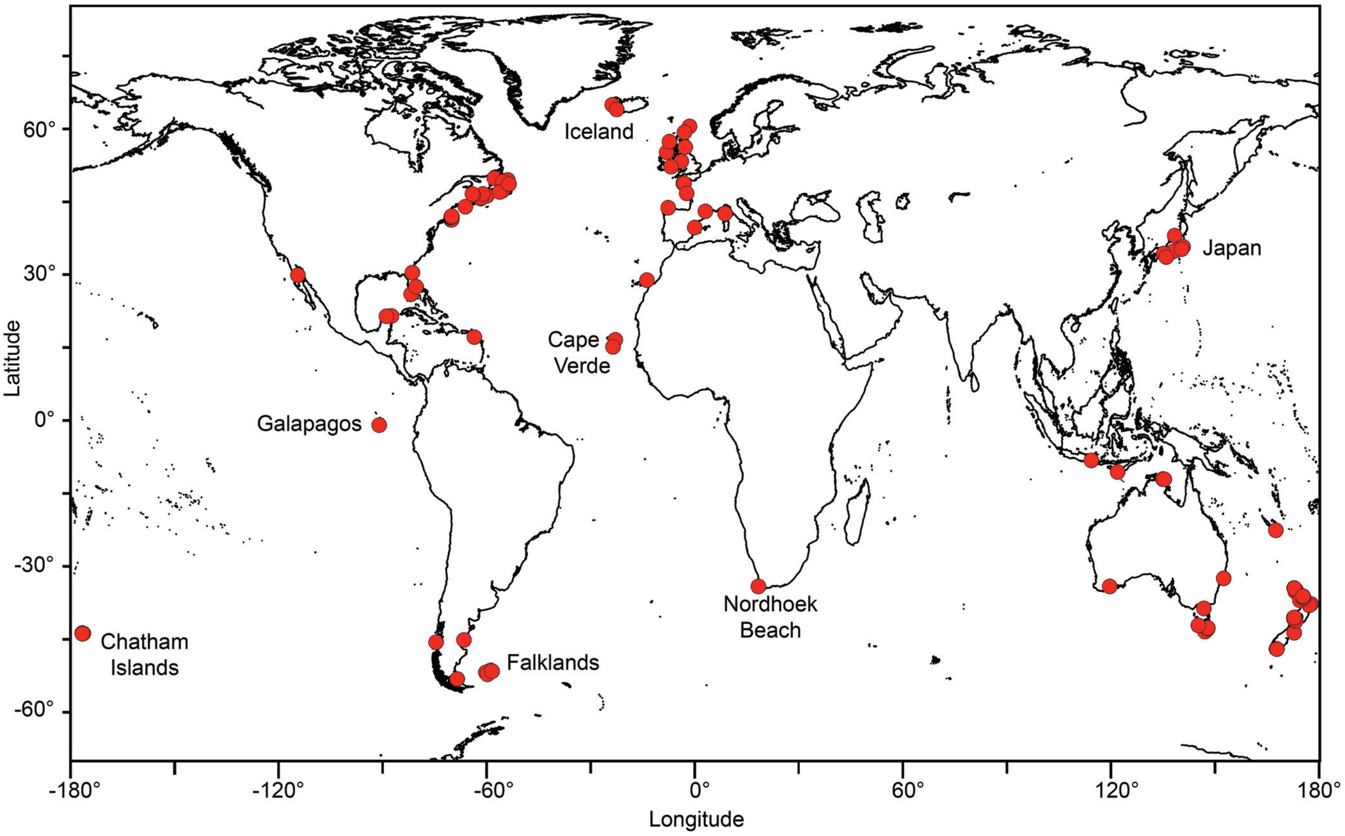


Fig. 7. Pilot whale strandings of undetermined species.

including firths, forths, fjords, straits, and keys, reef and coastal lagoons), 8% on relatively unindented coasts, with ice entrapment (of killer whales), breakwaters, and miscellaneous categories being 2%. For the 76% of bays, sites with headland-bay character have 42% of events, spit-bays 20% (even though there are only four of them), indented bays 9% and 5% are unspecified bay types. The shallow topographically complex areas include locations with restricted entry/egress, such as: (a) the long stretches of shore parallel shallow coastal lagoons of south-eastern USA, which are connected to the open ocean by occasional channels, (b) reef lagoons, (c) locally extensive shallow open ocean platforms with highly complex island and reef topography, channels and islands (Florida Keys, Okinawa Islands), and (d) estuaries, including firths, fjords, Magellan Strait, Denmark and Netherlands delta areas.

The 710 events occurred at 402 sites, 335 with one event only, and 67 (9%) with 2 to 74 events. Of the 67 sites with multiple events, 72% are bays, 12% are straight coasts, and 8% are in estuarine environments. These figures are within 4 to 6% of those in the previous paragraph for the 627 events with known site type, indicating an internal consistency of results and trends. Thirty-seven (37) sites have 2 events, eight sites have 3 events, five sites have 4, two sites have 5, four sites have 6, one site has 7, three sites have 8, Bream Bay and Florida Keys have 11, Petre Bay has 12, Hanson Bay has 14, Turnagain Arm has 20, Golden Bay has 37, and Cape Cod Bay has 74. Cape Cod Bay and Golden Bay (spit-bays) and Turnagain Arm (an estuary) have large tidal ranges and fine sediments.

Six events are in proximity to harbour breakwaters (Thorlakshofn and Rif, Iceland; Siuslaw, Oregon; Squaw Island, USA: An-ping and Ching-shan, Taiwan). Some sites have numerous groynes and groyne series (for example Mar del Plata, Argentina, and the Ibaraki coast, Japan). Also noted are river mouths with extensive shallow seawards sediment buildups (Bodri stream, Indonesia; Delsman, 1923); large bays with width over 30km, W:I < 2 and extensive interior shallows or estuaries (Cape Cod Bay, USA; Golden Bay, New Zealand; Perkins Bay, Australia; Tralee Bay, Ireland; Bahia San Sebastian, Argentina); and inland seas with shallow island platforms (Seto Sea, Japan).

DISCUSSION

The high numbers often observed in open ocean odontocete strandings are ascribed to their social nature and the formation of large pods of hundreds and even thousands of animals for some species. As noted by Hamilton and Lindsay (2014a) for Australia, odontocete species, species adult size, and bay size do not appear to be factors in worldwide larger stranding events. The species involved have adult sizes from 3m (melon-headed) to 18m (sperm whales). Bay sizes range from hundreds of m to 55km or more.

Species in larger mass strandings of odontocetes

Six species (false killer, long-fin pilot, melon-headed, short-fin pilot, sperm and white whales) contribute 96% of the mass strandings of 10+ animals, the remainder being killer whales, beaked whales, and pygmy killer whales. Some events for the latter three species appear to represent extreme cases or outliers. One of 15 killer whale events is at the head of a Norwegian fjord, and is attributed to chasing fish, and four are entrapments in ice. One of 11 Ziphiid events was associated with naval sonar activities (Frantzis, 2004).

Charging the beach

Eyewitnesses sometimes describe active mass strandings of an extreme nature. Robson and Van Bree (1971) describe sperm whales in a Gisborne, New Zealand event during a violent storm as 'charging the beach'. In a stranding at Duke Head beach, Flinders Bay, Western Australia, two large false killer whales broke away from a milling herd and 'sped ashore' (Leatherwood *et al.,* 1989). At The Grotto, Mamre, South Africa, false killer whales 'came ashore at a run, making determined efforts to strand themselves' (Leatherwood *et al.,* 1989). Birkby (1935) describes the false killer whales as 'rushing the shore', possibly in association with a 'furious southeaster'.

This behaviour implies the animals did not know what land was, or could not tell they were near land. In some cases, it is possible that surf zone noise may be misinterpreted as a continuation of open ocean. Further candidates to explain such behaviour are sonar termination or poor sonar transmission conditions, and simple confusion, particularly when storm conditions generate high levels of air and water borne sound, waves, wave and rain noise, suspended sediment, and bubbles. Suspended sediment may irritate whales and distract them. To partly discount the sonar termination hypothesis, Geraci (1978) stated that suspended particles offer no impediment to the transmission of underwater sound. Suspended sediments do attenuate sound through backscattering and viscous dissipation effects, but as a strong function of frequency and particle size. Attenuation is minimal at tens of kHz in usual circumstances, but sediment clouds are sometimes observed in side scan sonar imagery at hundreds of kHz. Resonant scattering by air bubbles in coastal waters (Dudok van Heel, 1962; Chambers and James, 2005) has potentially far greater effect on disrupting cetacean acoustic transmissions than suspended sediments.

Violent storms

Lacépède mentioned 17 sperm whales beached in 1723 in the mouth of the Elbe, Germany during a violent storm (van Beneden, 1888). New Zealand events at Gisborne (sperm whales) and Opoutama (long-finned pilot whales) occurred during violent storms (Robson and van Bree, 1971). Murata (2004) describes a stormy sea for a sperm whale stranding at Oura, Japan. An event near the Port Albert boat harbour entrance, Victoria, Australia was thought to occur when storms forced blackfish over a sandbar they could not recross (*The Age* newspaper, 1946). A Donna Nook, United Kingdom event has a similar report to Port Albert (Peacock *et al.,* 1936). Separate to the remarks in the previous section, these reports imply that whales sometimes founder on shores during storms in the same way as shipping, by simple misadventure.

Salients, Breakwaters, Groyne Series

Mazzucca *et al.* (1999) associated salients with strandings, rather than headlands, for three Hawaiian Island events. These are actually for odontocetes trapped in small sandy bays inside long fringing reefs with a constricted entry channel, and site complexity seems the important factor. However, other events perhaps do merit description as salients, such as Donna Nook (Fraser, 1936). Coastline configuration for a stranding at Tzeng-Wan river mouth, Taiwan also appears as a minor salient, but sediment buildup extends 4km seawards immediately north of the river mouth as a remnant subaqueous delta of less than 6 to 8m depth (Liu *et al.,* 2000). Delsman (1923) described an event at the mouth of the Bodri River, northern Java where sediment buildup extended seawards. The river mouth has changed considerably since, but previous configurations indicate an arrowhead delta projecting seawards from the river mouth. Three events in proximity to seawards extending breakwaters (Siuslaw, USA and An-Ping and Chin-Shan, Taiwan) have sediment buildups forming shore parallel ramps rising up to the breakwaters on both sides. Another event occurred in extensive shallow sediments west of the breakwater at Squaw Island (USA). The sediment ramps caused by the breakwaters may lead to the strandings, rather than the breakwaters themselves. The Ibaraki coast, Japan (8 events) is a fine sandy immature headland-bay of low curvature (W:I of 6.5) and nearshore slopes less than 1° which faces east into the Pacific Ocean. Complexity is introduced by occasional salients, streams, and shore perpendicular sandbars, plus several sets of T-shaped groynes (about 35 in total) of length 170 to 930m and 1km apart, and a series of 20 more of length 65m and 120m spacing. At Mar del Plata, Argentina 835 false killer whales stranded over 6km of coastline with W:I of 5.4. The coastline is fronted by an extended series of T-shaped groynes at 100 to 850m spacing, indicating site complexity as a factor.

Odontocetes and estuaries

Some recent apparently anomalous strandings in estuarine situations have been attributed to anthropogenic causes. An event in the Kyle of Durness, Scotland is believed to have been precipitated by panicked whales fleeing from underwater explosions (Brownlow *et al.,* 2015). An event at Antosohihy, Madasgascar is attributed to whales running from a multibeam sonar survey (Southall *et al.,* 2013). Estuaries in these circumstances form a particular type of topographic trap akin to deeply indented bays. Odontocetes also frequent estuaries in entirely natural circumstances, although perhaps not very often. There are records of tens of false killer whales being found swimming far into the Qiantung, Guanhe, and Yangtse (Chiangjiang) rivers in China (upstream distances of 30, 50, 220–300km respectively) (Leatherwood *et al.,* 1989). A killer whale was observed over 30km from the sea in the River Foyle at Londonderry, Ireland in November 1977 (*Daily Mail* Australia, 2016). In 1647 two cetaceans were observed near Cohoes Falls, Saratoga County, New York, over 225km from their presumed entry at New York (Sylvester, 1878). False killer whales stranded 65 and 120km into Magellan Strait, South America and 23km upstream in Dornoch Firth, Scotland. Eyewitness descriptions of a stranding of hundreds of pilot whales in Teal Inlet, Falkland Islands, 22km from the sea, imply a mass stampede of panicked animals (Hewlett, 1897), but the reason for the whales being there is unknown. For Norway, killer whales chasing fish stranded 12km from open water at Laupstad in Ostnesfjord, and pilot whales stranded in a strait north of Brossoya. In July 1852, 20+ short finned pilots stranded at Salt Lake, Calcutta, about 125km from the sea (Silas, 2010).

Sediments and seabed slopes

New Zealand has many gravel beaches but Brabyn and McLean (1992) found that about 80% of 41 New Zealand pilot whale herd strandings (2+ animals) generally occurred on sediments no coarser than sands and on beach slopes less than 3°. Hamilton and Lindsay (2014a) noted that one implies the other, since beach slope and sediment size increase together (Wiegel, 1965). Fine sands can have beach slopes less than 1°, and shingle beaches can reach slopes over 30° (Gilluly *et al.,* 1975). Similarly to New Zealand, none of 21 larger Tasmanian events occurred on gravel beaches, even though they make up more than one-sixth of the 1,596 Tasmanian beaches (Hamilton and Lindsay, 2014a). Fine sands were noted for many Australian sites (Hamilton and Lindsay, 2014a). The present analysis examines nearshore slopes with respect to Lowest Astronomical Tide, not beach slopes. They are less than 1° for 94 of 105 world sites, including 33 for New Zealand, and only two reach or exceed 3° (Pyramid Cove, USA, and Anini, Hawaii). Offshore slopes deeper than the wave base were typically less than 0.5°. Whether the sediment/slope observations for strandings is a physical phenomenon related to whale biology or other factors is unknown. It is common to all odontocete species with 10+ in a stranding regardless of species size.

Tides, shallow water and partial burial

Peacock *et al.* (1936) and Fraser (1936) associated ebbing tides with mass strandings. Fraser (1936) noted that the coast in several English events was characterised by a more or less extensive area of shoal exposed at low tide. Donna Nook, Lincolnshire for example had a wide sand and mud-flat extending seawards for about two miles, in which the struggling cetaceans had embedded themselves in silty sand. Recent photographs of events in Golden Bay (New Zealand), Calais (France) and elsewhere also show partial burial, and this can occur in mobile sediments by scour processes even if animals do not move if waves and currents are sufficiently strong to suspend sediment. In softer sediments, the weight of the animals may be sufficient to cause seabed deformation and initiate partial burial. Partially buried animals with restricted movement may be hampered from moving offshore as tides recede.

Falling tides are noted as involved in strandings for Cape Cod Bay (USA), Golden Bay (New Zealand), Bahia San Sebastian (Argentina), Magellan Strait (Chile), Penzance (England), the Kyle of Durness (Scotland), An-Ping (Taiwan), the Hooghly River (Salt Lake, India) and other locations. Some of these events were in confined areas, compounding the difficulty, and tides were not always the only cause of the strandings. At An-Ping the melon-headed whales were reported as trapped against the coast by the presence of several hundred offshore oyster cages (Wang *et al.,* 2001). The cages extend for 6km on both sides of An-Ping harbour. Cetaceans are believed to have entered the Kyle of Durness after being spooked by underwater explosions. The Hoogly river was in flood, and the cetaceans were 125km upstream when the water level fell.

Relation of strandings to coastal topography

In agreement with Dudok Van Heel (1962), Brabyn and McLean (1992) suggested that New Zealand herd strandings (2+ animals) did not happen at random locations. They described the majority of New Zealand stranding sites as 'gently sloping sandy beaches with an adjacent protruding section of coastline', where gently sloping meant less than 3°. Hamilton and Lindsay (2014a) showed that bays rather than beaches dominated larger Australian strandings (63 of 66 events and 33 of 36 sites), particularly mature headland-bays. The headland and downswell bay do not occur together by coincidence (Hamilton and Lindsay, 2014a), something not realised in previous stranding studies. Bays form the platforms for three-quarters of all the 627 generally well located world events, to which headland-bays contribute 42%. The protruding sections of coastlines for New Zealand also include spits. Bays associated with spits have very different character to other indented bays and headland-bays.

Spit-bays

Cape Cod Bay (USA) (74 events) and Golden Bay (New Zealand) (37 events) (Fig. 1a) have disproportionately high numbers of events compared to adjacent coastlines and other sites. They are large indented bays (15–30km width) partially enclosed by spits. An initial explanation for their high number of strandings presents no difficulty. The orientation and width of Cape Cod Bay place it directly in the path of any animals coming from the north parallel to the general trend of the coast. Whales in the bay seeking to move back to open water by tracking north along the east coast may move into the two south opening interior spit-bays (Provincetown and Wellfleet), and difficult to navigate mudflats, sand bars, shallows and low slopes of the eastern bay, where the strandings dominantly occur. They may come to difficulties there, or choose to rest in the sheltered, shallow area inside the spit. Tides at Wellfleet up to 4.7m and partial burial in silty sediments can then leave them stranded.

Similarly, Golden Bay has tides up to 4.5m, and 1km wide mudflats along 25–30km of its northern spit interior where the strandings occur. Strandings of 416 and 240 pilot whales occurred on the spit interior in February 2017 during a king tide. Bahia San Sebastian (Argentina) (5 events), originally a low relief valley formed by glaciers, is partially enclosed in the northeast by a 20km long attached south pointing gravel spit (Bujalesky, 2007). It has gravel shorelines in the south, but its five events are associated with mudflats in the northwest or with the spit. Goodall (1989) describes a 10.8m tide that recedes at walking pace over 10km (nominally a slope of 0.057°, matching the chart value of 0.063°), with the rapidly falling tide and low slopes leading to strandings.

The seawards sides of these bays are extended curving sand and gravel spits built up by waves and currents, not a headland of rocky material as for headland-bays. The sheltering effect of the spit extension modifies the depositional environment within the bay, allowing fine sediments (silts and clays ('muds') and fine sands) to accumulate on the landwards or inner side of the spit, including contributions from wave overtopping (Friedman *et al.,* 1992). A further characteristic is that large tides are caused by the constricting action of the spit on water flow. The result is that static factors (size, orientation, fine sediments, low slopes, and bathymetric and topographic complexity), couple with dynamic factors (large tides) to make spit-bays highly effective natural traps.

Perkins Bay (Australia), another notorious stranding site forms a related example. It has headland-bay structure in the east, extensive shallows, sandbars, islands, and channels in the west, and tidal range of 3m. The western side of Perkins Bay is not a spit, but is similarly constructed as a topographically and bathymetrically complex buildup of sand pushed eastwards into Bass Strait by currents and Southern Ocean swell.

Indented bays

Spit-bays are indented bays of a particular type. Other indented bays arise from drowned topography or irregular antecedent coastal shapes. These can have a variety of planforms, slopes, and sediments. Some larger indented bays may become stranding sites through size and interior bathymetric and coastline complexity, including estuaries, shallows, and interior bays. Cloudy Bay, Tasmania was cited as an example by Hamilton and Lindsay (2014a). The Wash, England (Fig. 1a) is a large indented rectangular bay (width 25km and W:I of 0.72) fed by several streams, with complex bathymetry, including extensive shallow saltmarsh, mudflats, sand bars, and channels, particularly in the south and west. Spring tidal range is 6.3m and neap is 3m.

Headland-bays

Headland-bays form the platform for 42% of 630 reasonably well located larger world events. Indented bays contribute 9%, spit-bays 20%, and bays of unknown type 5%. The ratio of 4.7:1 for headland-bays to indented bays (not including spit-bays) is somewhat puzzling, because many headland-bays have relatively simple planform and bathymetry, and seemingly have little reason to be stranding sites (Hamilton and Lindsay, 2014a). Indented bays would by their very nature be expected to be more difficult locations than headland-bays. There is no particular reason for odontocetes to strand in bays of relatively benign shape and bathymetry simply because they have a headland, especially as strandings generally occur towards the bay centre, not on the headland.

This points to factors other than coastline complexity, and Hamilton and Lindsay (2014a) advanced two possible reasons. One is purely geometrical. In their recognition and subsequent investigation of the role of headland-bays in strandings Hamilton and Lindsay (2014a) noted that mature Australian headland-bays shared a set of common properties apart from planform and indentation ratio, conditions occurring in mature headland-bays worldwide. They typically have fine sands of diameter less than 0.25mm, offshore slopes less than 0.5° (a depth change of 1m over 100m), and nearshore slopes of 1 to 2°. It is possible that odontocetes may not comprehend this gradual change in depth and may simply not realise they are heading into shallow water until it is too late, following which confusion and panic can occur. ‘The action of the animal was described as frantic’, eyewitness accounts for an event at Greens Point beach, Marrawah, Tasmania in Evans *et al.* (2002).

Another possibility is that acoustic propagation into shore over the low seabed slopes seen in headland-bays can be severely attenuated and distorted by multiple seabed and sea surface interactions, so that odontocetes using biosonar to navigate may infer the way ahead is open ocean when they are heading into shore. The attenuation of acoustic signals directed into a wedge is known as the sonar termination effect, and it was proposed by Dudok Van Heel (1962) as a possible cause of strandings. It has been noted that if sonar termination does occur then whales unexpectedly encountering a headland may turn landwards or seawards to avoid it, giving them a 50/50 chance of surviving the effect. Chambers and James (2005) modelled sonar termination as likely to occur at 0.5° but not at 5°, also noting that reduced wave noise in calm conditions may prevent whales from being alerted to the presence of the shore. Hamilton and Lindsay (2014a) noted this as especially likely in headland-bays, as their log-spiral planform acts to reduce wave action at the shore compared to other shapes (Silvester and Ho, 1972), as do their low beach and offshore slopes, which dissipate wave energy. Wave noise increases with beach slope, as breaker type changes from spilling to plunging.

Comparison of spit-bays and headland-bays

Headland-bays and spit-bays have different dynamic processes governing fine sediment deposition, and physically are very different environments. Headland-bays are wave and swell driven, and finer sediment in them is typically winnowed out by wave action and alongshore residual current, leaving fine sands and coarser sediments. In contrast, spit-bays accumulate finer sediments along the sheltered interior of the spit. Seabed slopes in the silt, clay, and sand flats of spit-bays can be much lower than the wave maintained values of 0.5 to 1° observed for fine sands in mature headland-bays, and the resulting bathymetry and topography much more complex. Spit-bays and headland-bays can therefore acquire quite different properties. Both can grow in size over time, but unconstrained headland-bays widen, and move towards a lower limit of 2 for indentation ratio, whereas spit-bays become more indented, and may eventually close. Spit-bays form a more difficult topographic and bathymetric hazard for odontocetes than headland-bays, these difficulties being compounded when occuring in conjunction with the high tidal ranges generated in spit-bays. Only 4 of 402 sites (1%) are spit-bays (Bahia San Sebastian, Cape Cod Bay, Golden Bay, and nominally Perkins Bay), but they own 20% of all 710 larger stranding events.

The passive influences of coastal topography and coastline orientation in spit-bays become especially hazardous to cetaceans through the dynamic assist of tides, storms, and by softer or mobile sediments not being able to support the weight of resting or stranded animals without deformation or scour. Strandings in these circumstances can be viewed as simple misadventure due to unfamiliarity not only with the coastal environment, but with the particularly unusual conditions in spit-bays. This also appears to be the case to some extent for headland-bays, but they do not generally have the muddy soft bathymetrically complex sediment deposits of spit-bays, or the obvious trap configuration of indented bays and estuaries with convoluted or funnel shaped coastlines. It also appears that tides are not necessarily a primary agent of strandings in headland-bays, as many of the Australian headland-bays with larger events are in micro-tidal regimes, not the macro-tidal environments of spit-bays.

Global scale stranding patterns

Ocean temperatures and currents

In the northern hemisphere, concentrations of events on the eastern coasts of North America and Japan (Fig. 2) are spatially correlated with the presence of warm polewards flowing biologically productive western boundary currents (the Gulf Stream and the Kuroshio). Extensions of the Gulf Stream to northwards of the British Isles and beyond lead to warmer seas than similar northern latitudes elsewhere, ameliorating the northern European climate, and hindering ice formation. This extends the northern range of marine mammals (see Christensen *et al.*, 1992, for remarks on Norwegian whale sightings and strandings), and larger stranding events are seen in Norway north of 65°N. In contrast the northern reaches of the eastwards flowing arm of the warm Kuroshio current east of Japan have a quasi-zonal flow restricted to south of 36–38°N (Hamilton, 2013), and winter ice forms around northern Japan. Several killer whale strandings on northern Hokkaido (44°N) are entrapment in ice near shore, rather than actual shore strandings. In the southern hemisphere Antarctic ice does not reach north to major landmasses.

Primary productivity

Widely separated oceanic islands such as Cape Verde (18 events), Chatham (26), Falklands (12+), Galapagos (2), Hawaii (4) have more larger stranding events than their sizes would indicate. Estimates of productivity (the amount of carbon per cubic metre of seawater) from satellite data show enhanced values about these islands, although to a much lesser extent around Hawaii (Fig. 8, from fig. 2 of Gregg *et al*., 2005). The Falklands and Chatham Islands lie in a generally more productive regime between 30 to 50°S associated with the Subtropical Front. Topographic (or island mass effect) upwelling stimulated by the island platforms further enhances local productivity and food supply. Local enhancement is also seen around the Galapagos, which additionally experience upwelling from the divergent equatorial current system flowing westwards along the equator (Fig. 8). It is inferred that locally enhanced food supply about the islands attracts higher numbers of odontocetes, leading to more strandings.

Much of the entire distribution of larger world strandings (Fig. 2) is also strongly correlated with regions of higher ocean productivity shown in Fig. 8, for example for the southern hemisphere south of 30°S. In particular, events in isolated locations such as Al Sawadi (Oman), Manapad (India), and Playa Tambor (Nicaragua) occur in conjunction with locally enhanced areas of productivity. It would perhaps be strange if a relationship of strandings with productivity did not exist, and the islands and isolated regions do point to such a relation. Many regions of higher productivity occur in upwelling areas near land, potentially explaining why odontocetes are in these areas, but not why they strand there. However, higher productivity regions along the western coasts of South America and South Island (New Zealand) have few to no strandings. This apparent anomaly is examined in the next section.

Continental scale coastal geomorphology

Notably few strandings compared to other areas are seen on the western coasts of South America, South Africa, Western Australia, and South Island (New Zealand), although productivity indicated in Figure 8 is high for all but Western Australia. Explanations for lack of strandings in some of these areas are routine. For example, the most westerly portion of Western Australia from 27 to 29°S is comprised of the Zuytdorp cliffs, and the 100m high Baxter and Bunda cliffs run unbroken for hundreds of kilometres in the smooth unindented southern coastline of Western Australia between latitudes 124°E to 132°20’E. These hard rocky cliffed coastlines are not favourable to stranding, and it is unlikely that strandings would be noticed even if they did occur.

The western coasts of South America, South Africa, and South Island have relatively smooth and steep coastlines running parallel to coastline trending rocky mountain chains or highlands (the Andes, the Southern Highlands, the Southern Alps), while the Drakensberg Highlands border the southeast coast of South Africa (Fig. 9). Few potential

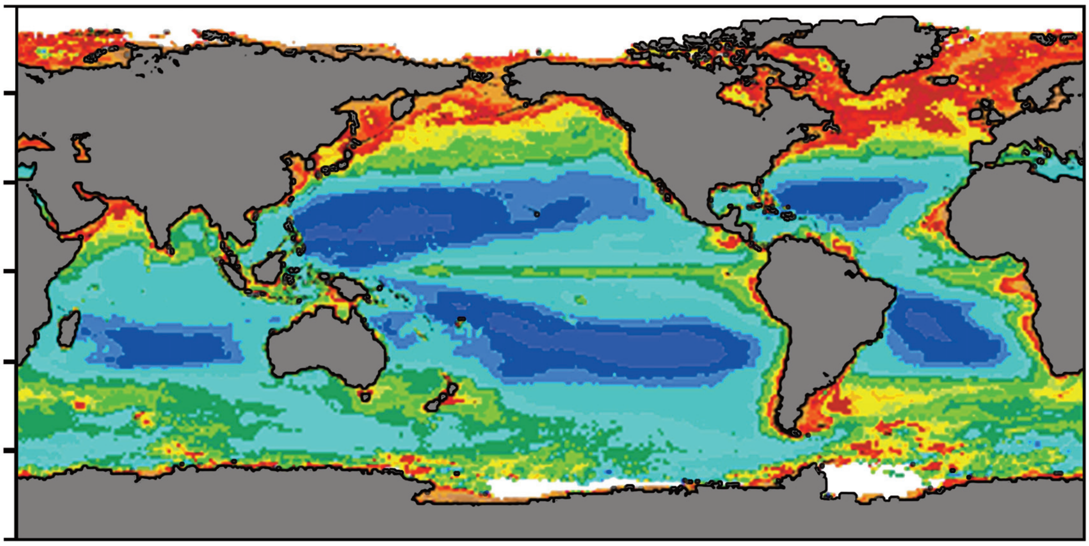


Fig. 8. Ocean primary productivity – SEAWIFS chlorophyll concentrations (mg m^{-3}) for 6-year annual best fit 1998 (this is the middle panel of fig. 2 of Gregg *et al.*, 2005).

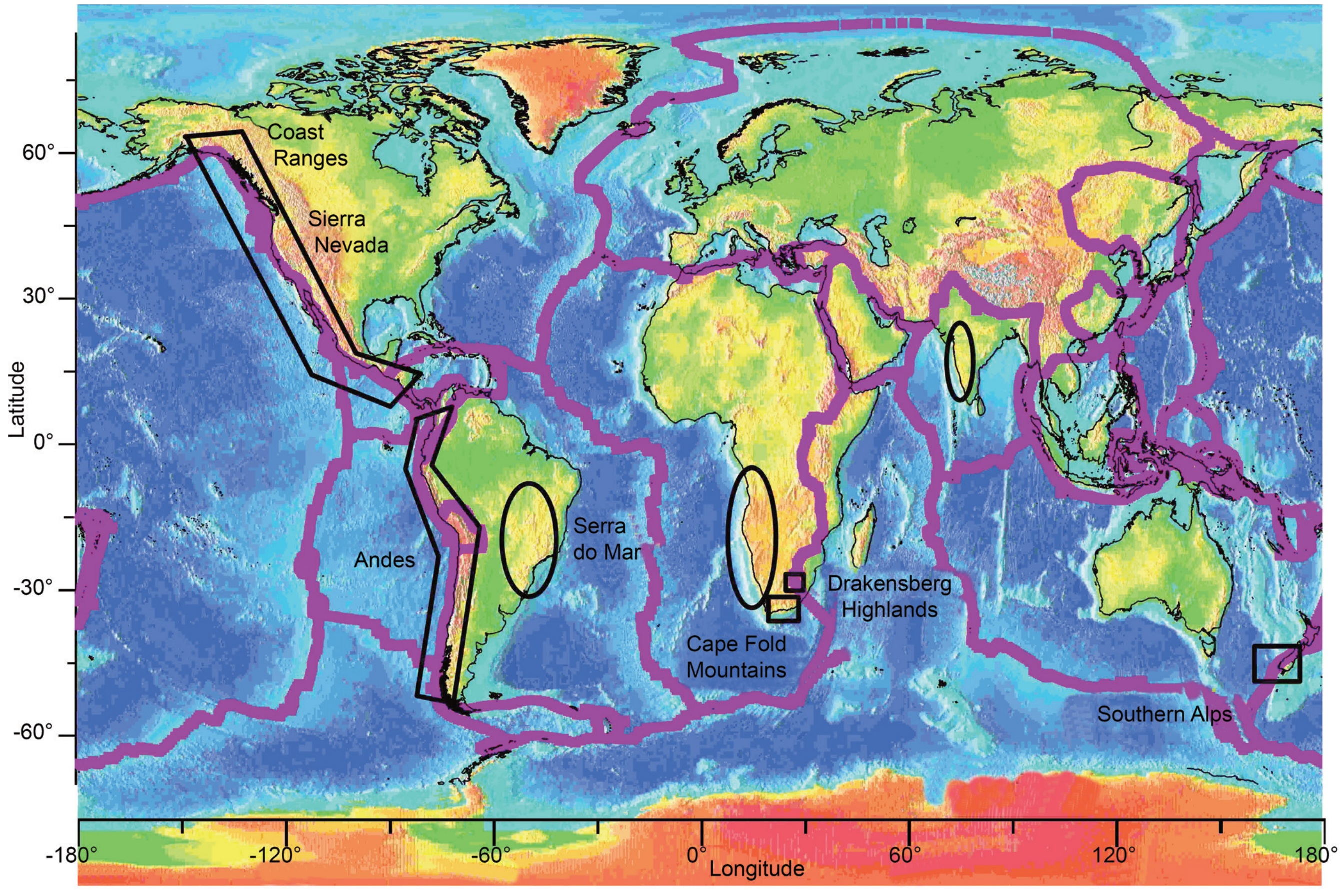


Fig. 9. Tectonic plate boundaries. Subduction of ocean tectonic plates under continental plates constructs mountain ranges such as the Andes of South America, and associated narrow continental shelves and steep shores. Comparison with Figs. 2 and 8 shows a general lack of larger stranding events along these steep shores, even in areas of enhanced primary productivity. Particular subduction zones are shown with polygons and rectangles. Ellipses show high ground near coasts. [Tectonic plate data and background topography from: *http://earthquake.usgs.gov*]

stranding sites such as mature headland-bays are seen in these areas. For example Harris *et al.* (2011) note that less than 2km of the 671km South African east coast is dissipative beach with respect to wave action (the type of low gradient beach found in mature headland-bays), whereas 19% (170km) of the 900km wave dominated southwest coast is dissipative sandy beach. This is apparently reflected in the number of sites in these areas with larger strandings. Morgan Bay hosts the only larger event on the African east coast south of 15°S, whereas there are six locations in the far southwest (False Bay, Long Beach, Melkboss Strand, Nordhoek Beach, St Helena Bay and Walkers Bay).

The spatial relationship of steeper smooth coasts adjacent to mountain chains is the result of plate tectonics. The mountain chains parallel to the western coastlines of South America and New Zealand are thrown up by the actions of tectonic plates subsiding under the continental landmasses, forming relatively new coasts which typically have narrow continental shelves and steep shores, with deep trenches close to shore (Gates and Lynn, 1990). Tectonic plate boundaries lie directly along the steeper western coastlines of South Island (New Zealand) and South America (Fig. 9). This situation would provide more time for wave and swell to sculpt potential stranding sites in the passive margins on these two landmasses than on their geologically newer steeper active western margins. This potentially explains the longstanding observations of McCann (1964) and Brabyn and McLean (1992) that herd strandings of two or more animals were not observed on the steeper west coast of South Island, New Zealand. In this respect it is noted that New Zealand has a longstanding well maintained stranding record so that the lack of recorded events on the west coast of South Island is unlikely explained by low observer effort.

Odontocete and baleen biosonar

Odontocetes regularly mass strand in large numbers, but with a very few exceptions baleens do not, even when forming large aggregates in feeding or in long migrations along world coastlines such as eastern and western Australia (Hamilton and Lindsay, 2014b). It is often said that baleens do not use biosonar, and there is some evidence for this (Beamish, 1978). This would mean they would not strand from susceptibility to the sonar termination effect. However, baleens make low frequency sounds (Stimpert *et al.*, 2007), and at least some baleens may receive sound with the same fatty sound reception mechanism as odontocetes (Yamato *et al.*, 2012). Low frequency sounds propagate further and more efficiently than high frequencies of the same energy, and it is possible that baleen sounds are more efficient at detecting the seabed or coastlines than the specialised high frequency odontocete sounds used to find and then localise small prey such as fish and squid (Dudok Van Heel, 1962). Further insights on odontocete mass strandings may well come from studies of baleen acoustics.

SUMMARY AND CONCLUSIONS

Stranding site properties, primary productivity and tectonic plates

Some investigators considered there were no convincing explanations linking site properties or coastal configuration to strandings. This is certainly not true for spit-bays, which generate both passive and active conditions (fine sediment flats of low slopes and complex bathymetry, high tidal ranges) conducive to stranding. Given that larger live strandings generally occur for nearshore slopes less than 3°, then it is not true for mature headland-bays either, in the sense that their mechanisms of formation and maintenance typically generate fine sands and nearshore slopes less than 1°. To discount the possible effect of coastal configuration and site properties on strandings, Sergeant (1982) regarded animals about to strand as being 'drift bottles' in a passive, moribund state, carried to the shoreline by currents. Eyewitness reports of strong swimming and milling behaviour prior to larger strandings in several countries do not support this view, particularly those described as 'charging the beach' mentioned earlier. Geraci (1978) saw no significance in strandings occurring on gently sloping beaches, arguing that no other physical configurations would be suitable for strandings, certainly not fjords, or sheer rock faces, or any other barrier, however small, 'In other words, whales do not strand where they cannot strand.' This statement makes a fair point, but provides no actual information. Where is it that they cannot strand? Odontocete strandings are of a random nature, and can be initiated by many factors, including simple misadventure, large tidal ranges, disorientation caused by storms, ingestion of poisonous algae, chasing prey, and attempt to escape from predators. This should arguably lead to strandings occurring on coastlines with a wide range of properties. However, the work of Dudok Van Heel (1962), Brabyn and McLean (1992), Hamilton and Lindsay (2014a) and the present paper shows that despite all other possible complicating agents, particular types of coastal locations with sets of properties (planform, sediments, seabed slopes) able to be specified quantitatively dominate larger live mass strandings worldwide. This allows some types of potential stranding sites to be identified by quantitative indicators.

The world geographical distribution of larger strandings is noticeably correlated with areas of locally higher primary productivity, potentially indicating why the odontocetes are near land. Pursuit of prey or search for calm conditions can then bring them to coastal areas, or they may simply approach coasts by chance. Once there for whatever reason, unfamiliarity with the inshore environment, particularly with shallows and low slopes, and dynamic factors such as tides and currents may confuse and confound them. Even the simple act of following the coast can bring disaster in spit-bays and features with trap or maze-like orientations. Sonar termination does not have to be invoked in these explanations, but forms a further possible cause, particularly for the relatively benign environments of many headland-bays. It is also possible that the effect of headland-bay configuration and properties in lowering surf zone noise in times of calms may prevent odontocetes from being alerted to the presence of land. Once in a panicked situation nearshore however, any wave noise might be taken as indicating open ocean, leading to strandings. In a similar mechanism, strandings might also occur as a result of surf zone noise during violent storms being taken as a continuation of open ocean.

There is a notable scarcity of strandings on some active continental margins, even in the presence of higher productivity, the western coastlines of South America and South Island, New Zealand being prime examples. Active margins have narrow continental shelves and relatively smooth and steeper swell resistant shores, caused by more geologically recent tectonic plate action. It is likely that swell action has not had time to construct as many coastal configurations and conditions associated with strandings on the active margins as on the older passive margins. This potential relation of strandings to large scale and long term earth and ocean processes is remarkable in its scale, and seemingly underscores the role that geomorphological mechanisms ultimately play in strandings.

Conclusions

It can be said that the 'where' of larger mass strandings of odontocetes is generally well known, and is even largely understood in a mechanical sense, even if the biological factors remain elusive. Odontocetes tend to strand on particular coastlines and in particular types of locations at global to local spatial scales. The beginnings of this view date back 55 years to the qualitative descriptions and insightful observations of Dudok van Heel (1962), and 25 years to the quantitative descriptions of New Zealand beach slopes and sediments of Brabyn and McLean (1992). These works were extended by recognition and explanation of the role of headland-bays in constructing stranding sites (Hamilton and Lindsay, 2014a). The present paper further defines the values of seabed slopes and sediment sizes associated with larger strandings, and explains the magnified role of spit-bays. It then proceeds to note presence and absence of larger mass strandings on some continental coastlines as the possible outcome of a chain of physical causes (plate tectonics, wave and swell action, locally enhanced regions of primary productivity near coasts with particular geomorphologies). However, while these largescale relations seem entirely plausible they are subject to the vagaries of very different rates of observer effort throughout the world and a range of other factors and must be regarded as working hypotheses.

ACKNOWLEDGEMENTS

I thank Chris May and Ben Berntsen for information and local knowledge on Falkland Islands strandings, and Alfredo le Bas for clarifying the location of the stranding at Jaureguiberry, Uruguay. The New Zealand Department of Conservation – Te Papa Atawhai is thanked for supplying some of the New Zealand records.

REFERENCES

Abend, A.G., Smith, T.D. 1999. Review of distribution of the long-finned pilot whale (*Globicephala melas*) in the North Atlantic and Mediterranean. US Department of Commerce, NOAA Technical Memorandum NMFS NE 117. 22pp.

Beamish, P. 1978. Evidence that a captive humpback whale (*Megaptera novaeangliae*) does not use sonar. *Deep-Sea Res.*: 25, 469–72.

Birkby, C. 1935. Two hundred killer whales hurl themselves ashore. *The Illustrated London News* 187 (5044), 1124–25. 21 December 1935. [Noted in Leatherwood *et al.,* 1989]

Brabyn, M.W. 1990. An analysis of New Zealand whale strandings. MSc Thesis in Zoology, University of Canterbury, New Zealand.

Brabyn, M.W. and McLean, I.G. 1992. Oceanography and coastal topography of herd-stranding sites for whales in New Zealand. *J. Mammal.* 73(3): 469–76.

Brownell, R.L., Yamada, T.K., Mead, J.G. and Allen, B.M. 2006. Mass strandings of melon-headed whales, *Peponocephala electra*: a worldwide review. Paper SC/58/SM8 presented to the IWC Scientific Committee, May 2006, St. Kitts and Nevis, West Indies (unpublished). 12pp. [Paper available from the Office of this Journal]

Brownell, R.L., Yao, C.J., Lee, C.S. and Wang, M.C. 2009. Worldwide review of pygmy killer whales, *Feresa attenuata*, mass strandings reveals Taiwan hot spot. Paper SC/61/SM1 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 20pp. [Paper available from the Office of this Journal]

Brownlow, A., Baily, J., Dagleish, M., Deaville, R., Foster, G., Jensen, S-K., Krupp, E., Law, R., Penrose, R., Perkins, M., Read, F. and Jepson, P.D. 2015. Investigation into the long-finned pilot whale mass stranding event, Kyle of Durness, 22nd July 2011. Report to Defra and Marine Scotland. 60pp.

Bujalesky, G.G. 2007. Coastal geomorphology and evolution of Tierra del Fuego (Southern Argentina). *Geologica Acta* 5(4): 337–362. [Available at: *http://www.geologica-acta.com*].

Chambers, S. and James, R. 2005. Sonar termination as a cause of mass cetacean stranding in Geographe Bay, south-western Australia. pp. 391–398. *In* T. McMinn (Ed.) *Proceedings, Australian Acoustical Society, Annual Conference 2005. Acoustics 2005: Acoustics in a Changing Environment, Busselton, Western Australia.* [Available at: *http://www.acoustics.asn.au/divisions/WA/2005-proceedings.php*: Australian Acoustical Society].

Christensen, I., Haug, T. and Øien, N. 1992. Seasonal distribution, exploitation and present abundance of stocks of large baleen whales (*Mysticeti*) and sperm whales (*Physeter macrocephalus*) in Norwegian and adjacent waters. *ICES J. Mar. Sci.* 49:341–55.

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

Daily Mail. 2016. Whale nicknamed 'Dopey Dick' after swimming up a river in Northern Ireland to find salmon 39 years ago is spotted off coast of Scotland. *Daily Mail* Newspaper article, 2 April 2016, Melbourne, Australia.

D'Amico, A., Gisiner, R., Ketten, D.R., Hammock, J.A., Johnson, C., Tyack, P.L. and Mead, J.G. 2009. Beaked whale strandings and naval exercises. *Aquat. Mamm. Sci.* 35(4), 452–72.

Delsman, H.C. 1923. Een stranding in straat Maduren. *De Tropische Natuur*. 12(3):33–9.

Dudok Van Heel, W.H. 1962. Sound and cetacea. *Neth. J. Sea. Res.* 1: 407–507.

Dudok Van Heel, W.H. 1966. Navigation in Cetacea. pp.597–606. In: Norris K.S. (Ed.), *Whales Dolphins and Porpoises*. University of California Press, Berkeley.

Evans, K., Morrice, M., Hindell, M. and Thiele, D. 2002. Three mass strandings of sperm whales (*Physeter macrocephalus*) in southern Australian waters. *Mar. Mammal Sci.* 18(3):622–43.

Ferreira, I.M. 2008. Growth and reproduction in false killer whales (*Pseudorca crassidens* Owens, 1846). MSc Thesis, University of Pretoria, USA.

Findlay, K.P., Best, P.B., Ross, G.J.B.and Cockcroft, V.G. 1992. The distribution of small odontocete cetaceans off the coasts of South Africa and Namibia. *Afr. J. Mar. Sci.* 12:237–70.

Frantzis, A. 2004. The first mass stranding that was associated with the use of active sonar (Kyparissiakos Gulf, Greece, 1996). pp.14–20. *In*: Proceedings of the workshop: 'Active Sonar and Cetaceans', 8 March 2003, Las Palmas, Gran Canaria. ECS newsletter 42 (special issue):

Fraser, F.C. 1936. Recent stranding of the false killer whale, *Pseudorca Crassidens*, with special reference to those found at Donna Nook, Lincolnshire. *Scott. Nat*. 220: 105–14.

Friedman, G.M., Sanders, J.E. and Kopaspa-Merkel, D.C. 1992. *Principles of Sedimentary Deposits*. McMillan, New York. 717pp.

Gaskin, D.E. 1968. The New Zealand Cetacea. Fisheries Research Bulletin No. 1. Fisheries Research Division, New Zealand Marine Department.

Gates, P.J. and Lynn, N.M. 1990. *Ships, Submarines and the Sea*. Brassey's Sea Power: Naval Vessels, Weapons Systems and Technology, Series. 2. Brassey's (UK) Ltd., London. 178pp.

Geraci, J.R. 1978. The enigma of marine mammal strandings. *Oceanus* 21(2): 38–47.

Gilluly, J., Waters, A.C. and Woodford, A.O. 1975. *Principles of Geology*. Fourth edition. W.H. Freeman and Company, San Francisco, USA. 527pp.

Goodall, R.N.P. 1989. The lost whales of Terra del Fuego. *Oceanus* 32(1): 89–95.

Gregg, W.W., Casey, N.W. and McClain, C.R. 2005. Recent trends in global ocean chlorophyll. Geophys. *Res. Lett.* 32(3): L03606.

Hamilton, L.J. 1999. Classification, grainsize relations, and sediment distributions inferred from visual sediment descriptions on RAN Hydrographic Office bathymetry charts of the northern Great Barrier Reef lagoon. *Aust. J. Earth Sci.* 46(4): 501–14.

Hamilton, L.J. 2013. Statistical clustering of drifting buoy trajectories around Japan and off Fukushima to identify Lagrangian circulation features. *Methods in Oceanography* 6: 16–32.

Hamilton, L.J. and Lindsay, K. 2014a. The relation of coastal geomorphology to larger mass strandings of odontocetes about Australia. *J. Cetacean Res. Manage.* 14(1): 176–84.

Hamilton, L.J. and Lindsay, K. 2014b. Beaked whale strandings on the coast of Australia in comparison to those of other cetaceans. *J. Cetacean Res. Manage.* 14(1): 1–14.

Harris, L., Nel, R. and Schoeman, D. 2011. Mapping beach morphodynamics remotely: A novel application tested on South African sandy shores. *Estuar. Coast. Shelf Sci.* 92: 78–89.

Hewlett, G. 1897. Stranding of whales at the Falkland Islands. *Launceston Examiner* 20 March 1897, p.11.

Jefferson, T.A. and Barros, N.B. 1997. *Peponocephala electra*. *Mamm. Species* 553: 1–6.

Leatherwood, S., McDonald, D., Baird, R.W. and Scott, M.D. 1989. The false killer whale, *Pseudorca crassidens* (Owen, 1846): a summary of information available through 1988. Oceans Unlimited Technical Report 89-001. 114pp.

Liu, J.T., Huang, J-S., Hsu, R.T. and Chyan, J-M. 2000. The coastal depositional system of a small mountainous river: a perspective from grainsize distributions. *Mar. Geol.* 165: 63–86.

Marelli, C.A. 1953. Documentos iconograficos sobre cetaceos de las costa Argentina. *Anales del Museo de Nahuel Huapi* 3:133–43.

Mazzuca, L., Atkinson, S., Keating, B. and Nitta, E. 1999. Cetacean mass strandings in the Hawaiian Archipelago, 1957–1998. *Aquat. Mamm.* 25(2): 105–14.

McCann, C. 1964. A coincidental distributional pattern of some of the larger marine animals. *Tuatara* 12(2) 119–24.

McFee, W.E. 1990. An analysis of mass strandings of the long-finned pilot whale, *Globicephala melas* on Cape Cod. MSc Thesis, Center for Vertebrate Studies, Northeastern University, Boston, Massachusetts. 96pp.

McFee, W.E. 1991. Common names applied to the long-finned pilot whale, *Globicephala melas*. *Can. Field Nat.* 105(4):564–66.

Murata, T. 2004. Detailed report on the mass stranding of sperm whales. Ship and Ocean Newsletter, Institute for Ocean Policy, Ship and Foundation. Selected Papers 4:12–13.

Mustika, P.L.K., Hutasoit, P., Madusari, C.C., Purnomo, F.S., Setiawan, A., Tjandra, K. and Prabowo, W.E. 2009. Whale strandings in Indonesia, including the first record of a humpback whale (*Megaptera novaeangliae*) in the Archipelago. *Raffles B. Zool.* 57(1):199–206.

Nishimura, S. 1965. The zoogeographical aspects of the Japan Sea. Part 1. Publications of the Seto Marine Biological Laboratory, Sirahama, *Departmental Bulletin* 13(1): 35–79.

Otley, H. 2012. The composition of the cetacean community in the Falkland (Malvinas) Islands, southwest South Atlantic Ocean. *Revista de Biología Marina y Oceanografía* 47(3)3: 537–51.

Peacock, A.D., Comrie, L. and Greenshields, F. 1936. The false killer whales stranded in the Tay estuary. *The Scottish Naturalist* 220: 93–104.

Porsild, M.P. 1918. On 'Savssats': A crowding of Arctic animals at holes in the sea ice. *Geogr. Rev.* 6(3):215–28.

Robson, F.D. and Van Bree, P.J.H. 1971. Some remarks on a mass stranding of sperm whales, *Physeter macrocephalus* Linnaeus, 1758, near Gisborne, New Zealand, on March 18, 1970. *Sonderdruck aus zeitschrift fur Sangetierkunde* 36(1): 55–60.

Sergeant, D.E. 1982. Mass strandings of toothed whales (odontoceti) as a population phenomenon. *Sci. Rep. Whales Res. Inst.* 34: 1–47.

Silas, E.G. 2010. Inaugural address. Workshop on Marine Mammal Stranding. held at CMFRI from 21–23 January 2010 under the auspices of CMFRI, NOAA, USA and Indo-US Science Forum, New Delhi Inaugural Function in Cochin, India.

Silvester, R. and Ho, S.-K. 1972. Use of crenulate shaped bays to stabilise coasts. *Coast. Eng.* 13: 1,347–65. [Available at: *http://journals.tdl.org/ICCE/article/viewFile/*, accessed 22 September 2012].

Southall, B.L., Braun, R., Gulland, F.M.D., Heard, A.D., Baird, R.W., Wilkin, S.M. and Rowles, T.K. 2006. Hawaiian melon-headed whale (*Peponocephala electra*) mass stranding event of 3–4 July 2004. NOAA Technical Memorandum NMFS-OPR-31. 73pp.

Southall, B.L., Rowles, T., Gulland, F., Baird, R.W. and Jepson, P.D. 2013. Final report of the Independent Scientific Review Panel investigating potential contributing factors to a 2008 mass stranding of melon-headed whales (*Peponocephala electra*) in Antsohihy, Madagascar. 75pp. [Available at: *https://iwc.int/2008-mass-stranding-in-madagascar*]

Stimpert, A.K., Wiley, D.N., Au, W.W.L., Johnson, M.P., and Arsenault, R. 2007. 'Megapclicks': acoustic click trains and buzzes used during nighttime foraging of humpback whales (*Megaptera novaeangliae*). *Biology Letters* 3(5): 467–4

Sylvester, N.B. 1878. *History of Saratoga County, New York.* Everts and Ensign, Philadelphia, Press of J.B. Lippincott and Company Philadelphia. 514pp.

The Age. 1946. Stranded on island. 140 whales off Port Albert. *The Age* newspaper 1 April 1946, Melbourne, Victoria.

Urban-Ramirez., J., Cardenas-Hinojosa, G., Gomez-Gallardo, A., Gonzalez-Peral, U., del Toro-Orozco, W. and Brownell, R.L. 2007. Mass stranding of Baird's beaked whales at San Jose Island, Gulf of California, Mexico. *Lat. Am. J. Aquat. Mamm.* 6(1):83–8.

Van Beneden, P.-J. 1888. Le Cachalot (*Physeter macrocephalus*). Mémoires couronnés et autres Mémoires publiés par l'Académie Royale de Belgique.

Vos, D.J. and Shelden, K.E.W. 2005. Unusual mortality in the depleted Cook Inlet beluga (*Delphinapterus Leucas*) population. *Northwest Nat.* 86:59–65.

Wang, J.Y., Yang, S-C. and Liao, H-C. 2001. Records of melon-headed whales, *Peponocephala electra* (Gray, 1846), from the waters of Taiwan. *Bull. Natl. Mus. Nat. Sci. Ser. A Zool.* 14:85–92.

Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments. *J. Geol*. 30: 377–92.

Wiegel, R.L. 1965. *Oceanographical Engineering*. Prentice-Hall. 531pp.

Yamato, M., Ketten, D., Arruda, J., Cramer, S. and Moore, K. 2012. The auditory anatomy of the minke whale (*Balaenoptera acutorostrata*): A potential fatty sound reception pathway in a baleen whale. *Anat. Rec.* 295: 991–8.

Sixteen years later: an updated evaluation of the impacts of chronic human interactions with bottlenose dolphins (*Tursiops truncatus truncatus*) at Panama City, Florida, USA

Jessica R. Powell[1], Abigail F. Machernis[2], Laura K. Engleby[1], Nicholas A. Farmer[1] and Trevor R. Spradlin[3]

Contact e-mail: jessica.powell@noaa.gov

ABSTRACT

Panama City, Florida is considered a notorious ‘hot spot’ in the southeastern United States for chronic illegal feeding and harassment of bottlenose dolphins. The nature and extent of these interactions was evaluated by Samuels and Bejder (2004); they concluded that food provisioning was the basis for human interactions with wild dolphins, and that these encounters were likely harmful to dolphins. A follow-up study was conducted in 2014 to reassess the current state of human interactions with wild dolphins. The number of conditioned dolphins ($n = 21$) tripled compared to the previous study. Both studies found conditioned dolphins engaged in human interaction events during approximately 75% of observable time points when vessels or swimmers were present. In this study, conditioned dolphins spent as much as 81% of their time begging or patrolling and significantly decreased their distance moved while doing so. Nested multinomial regression analysis revealed conditioned dolphins engaged in resting or foraging (i.e. natural) behaviour were extremely likely to switch to begging or patrolling (i.e. interaction) behaviours when vessels or swimmers were present. Numerous high risk situations were observed for both conditioned dolphins and humans during these interactions. The latest development in illegal feeding was documented: bait boats feeding dolphins to lure the animals into interactions with tour vessels and swimmers. Our observations indicate that the problem in Panama City has escalated: dolphins are being actively provisioned, often for long periods of time; the proportion of conditioned dolphins has increased; interacting dolphins and humans are both at increased risk for injury, illness, or death; and conditioned dolphin activity budgets and movement patterns continue to be negatively impacted by human behaviour. We recommend a more aggressive management strategy, such as targeted and sustained enforcement of existing regulations as well as additional restrictions that prohibit close approaches and in-water interactions for Panama City in order to curtail continued harassment of dolphins and reduce the risk of injury for both humans and dolphins.

KEYWORDS: BEHAVIOUR; BOTTLENOSE DOLPHIN; CONSERVATION; WHALE WATCHING

INTRODUCTION

Wildlife viewing in the marine environment has been growing at a rapid rate. Whale watching activities worldwide are currently estimated as a $2.1 billion USD industry and support approximately 13,000 jobs (O’Connor *et al.,* 2009) with capacity for future expansion (Cisneros-Montemayor and Sumaila, 2010). Commercial and private tours to view marine mammals range from land or vessel-based platforms observing animals to in-water swim-with activities that encourage close encounters and interactions with the animals. The impacts of tourism on bottlenose dolphins (*Tursiops* spp.) are well studied since the species is found year-round in close proximity to the shore and human populations. Dolphins are significantly affected by human interactions both at an individual and population level (Bejder *et al.,* 2006a; Bejder *et al*., 2006b; Lusseau *et al.,* 2006). Numerous studies examining the effects of viewing or swim-with tours have shown that vessels and swimmers disturb dolphins’ natural behaviour patterns, causing shifts in activity budgets, changes in group cohesion and group size, deviations in swim patterns, increased travelling behaviour, and reductions in natural foraging and resting behaviours (Allen and Read, 2001; Bejder *et al.,* 2006a; Bejder *et al.,* 2006b; Constantine *et al.,* 2004; Samuels and Bejder, 2004). These short-term behavioural changes can lead to long-term biological impacts for dolphin populations such as declines in reproductive health and permanent habitat displacement or abandonment (Bejder, 2005; Bejder *et al.,* 2006b; Lusseau, 2006; Lusseau *et al*., 2006; Parsons, 2012; Tyne *et al.,* 2014). The popularity and growth of marine mammal tourism continues despite a wealth of scientific literature documenting how marine mammals are negatively impacted by such interactions (O’Connor, 2009).

In addition, activities involving provisioning (i.e. feeding) the animals have emerged either with government approval (e.g. in Australia: Foroughirad and Mann, 2013; Mann *et al*., 2000; Mann and Kemps, 2003), in violation of laws prohibiting feeding (e.g. in the United States: Cunningham-Smith *et al*., 2006; Donaldson *et al*., 2010; 2012; Finn *et al*., 2008; NMFS, 1994; Samuels and Bejder, 2004), and has been defined as ‘ecologically intrusive’ by the International Whaling Commission (IWC) (Parsons *et al.,* 2006). In either scenario, feeding activities seek to facilitate reliable and close interactions between people and marine mammals in the wild. However, it has been well documented for more than 20 years that feeding wild dolphins can lead to a variety of high risk situations that place both dolphins and people in danger (Cunningham-Smith *et al.,* 2006; NMFS, 1994; Orams *et al.,* 2002; Samuels and Bejder, 2004). When dolphins learn to associate people with food, unnatural behaviours such as begging for handouts disrupt their natural foraging repertoire and become an abnormal and detrimental feeding strategy (NMFS, 1994; Powell and Wells, 2011). Conditioned dolphins approach boats more readily looking for handouts, thus increasing the animals’ risk for boat strike or gear entanglement (Bechdel *et al.,* 2009; Powell and

---

[1] *NOAA/ National Marine Fisheries Service, Southeast Regional Office, 263 13th Ave S, Saint Petersburg, FL 33701.*
[2] *Dolphin Ecology Project, 235 21st Ave SE, Saint Petersburg, FL 33705.*
[3] *NOAA/National Marine Fisheries Service, Office of Protected Resources, Silver Spring, MD 20910.*

Wells, 2011; Samuels and Bejder, 2004; Wells and Scott, 1997). Conditioned dolphins can also become targets for human acts of retaliation, often from fishers who become frustrated by dolphins begging, removing bait or catch from their lines or scavenging on undersized throw-backs (DOJ, 2006; 2007). Begging and other human-conditioned behaviours can be passed through a dolphin population via social learning, thus perpetuating and increasing the prevalence of the problem over time (Donoghue *et al.,* 2002; Wells, 2003; Whitehead *et al.,* 2004). Calves of provisioned mothers are at increased risk of compromised developmental and social learning skills, predation, and insufficient hunting experience due to neglect experienced while mothers are seeking handouts from humans (Foroughirad and Mann, 2013; Mann and Barnett, 1999; Mann and Kemps, 2003).

The Marine Mammal Commission (MMC) and the National Marine Fisheries Service (NMFS) have been concerned about the impacts of marine mammal tourism in the United States for several decades (i.e. Spradlin *et al.*, 1999)[4]. The Marine Mammal Protection Act (MMPA) and its implementing regulations prohibit the 'take'[5] and 'harassment'[6] of marine mammals. However, enforcement of those prohibitions has been challenging because of either real or perceived gaps in the scientific knowledge about the impacts of harassment, as well as varying interpretations about the legal definitions of those terms (e.g. Lewandowski, 2005). Feeding and attempting to feed a marine mammal in the wild is also included under the definition of 'take' and is prohibited under the MMPA (50 CFR 216.3). In 1998, the MMC funded a study (i.e. Samuels and Bejder, 1998) designed to systematically evaluate how chronic in-water interactions with humans affect the behaviour of free-ranging common bottlenose dolphins (*Tursiops truncatus truncatus*). From the results of Samuels and Bejder (1998), the MMC concluded that interacting with dolphins in the wild constitutes at least 'level B harassment', and recommended NMFS promulgate regulations to prohibit the activities (MMC letter to NMFS, 23 May 2000).

The problem in Panama City, Florida

Panama City, Florida has been a well-known 'hot spot' in the southeastern United States for chronic feeding and harassment of bottlenose dolphins for more than three decades. The study by Samuels and Bejder (1998; 2004), funded by the MMC, concluded that chronic levels of human interactions with wild dolphins near Panama City, Florida were likely harmful and increased animals' risk for injury, illness, or death. Currently, Panama City hosts approximately 25 dolphin viewing and swim-with vessel companies; most offering swim-with opportunities in contradiction to NMFS recommended but voluntary wildlife viewing guidelines and policies[7] and some feed the local dolphins to promote close interactions. Private recreational boaters also regularly feed and harass dolphins. Illegal feeding and conditioning of wild dolphins have been carried out for many years (Samuels and Bejder, 1998; 2004). Conditioned dolphins at Panama City are effectively trained to interact with people through 'variable reinforcement', in which reinforcement (i.e. illegal food handouts) is delivered only after an unpredictable number of behavioural responses (i.e. begging) (Zeiler, 1968). This results in a suite of maladaptive behaviours that are difficult to extinguish. Tour businesses anecdotally complained of increases in dolphin aggression towards swimmers (Orams *et al.,* 1996; Samuels and Gifford, 1997; Connor, 2000). There are safety risks for both swimmers and dolphins given the high numbers of engaged vessels (e.g. 20) maneuvring through and around dolphins and swimmers at any given time, sometimes in fast currents and narrow channels.

Since the Samuels and Bejder (1998; 2004) study, NMFS has invested significant resources in research, education and outreach[8], and enforcement at Panama City to address the problem. Outreach efforts have included public service announcements, brochures, signage, and educational letters distributed throughout the community (Vail, 2016), although the extent to which this approach is effective is unknown. In addition, NMFS commissioned human dimension surveys and focus groups to better design outreach and education projects (Duda *et al.,* 2013a; 2013b). Targeted, pulsed enforcement and the issuance of citations for violations of the MMPA feeding prohibition have also increased in the Panama City area. Despite these efforts, illegal feeding and harassment of wild dolphins continues on a larger and more surreptitious scale than in the past.

This study aimed to understand how human-dolphin interactions at Panama City have progressed specifically in the absence of viewing or swim-with regulations. This study replicates the methods of Samuels and Bejder (1998; 2004) and compares the current and past results to track how dolphin behaviour, the number of dolphins affected, and the potential impacts and risk to dolphins (and people) have changed over the past 16 years and recommends an improved management strategy. The goal of this study was to provide quantitative, longitudinal results to assist managers in designing, justifying, and implementing management strategies to protect populations of dolphins from commercial and recreational activities of concern.

METHODS

Samuels and Bejder (1998; 2004) focused effort around 'Interaction Beach' offshore of Shell Island and St. Andrew

---

[4] The National Marine Fisheries Service (NMFS) is charged with managing cetaceans in the United States by implementing the Marine Mammal Protection Act (MMPA). The Marine Mammal Commission (MMC) is an independent government agency charged by the MMPA to provide oversight and advise the National Marine Fisheries Service (NMFS).

[5] 'Take' as defined by the MMPA implementing regulations (50 CFR 216.3) means 'to harass, hunt, capture, collect, or kill, or attempt to harass, hunt, capture or kill any marine mammal. This includes, without limitation, any of the following: the collection of dead animals, or parts thereof; the restraint or detention of a marine mammal, no matter how temporary; tagging a marine mammal; the negligent or intentional operation of an aircraft or vessel; the doing of any other negligent or intentional act which results in disturbing or molesting a marine mammal; or feeding or attempting to feed a marine mammal in the wild'.

[6] Harassment is defined in the 1994 amendments to the MMPA (16 U.S.C. 1362) as any act of pursuit, torment, or annoyance that has the *potential to injure* a marine mammal or marine mammal stock in the wild (Level A harassment); or that has the *potential to disturb* a marine mammal or marine mammal stock in the wild by causing disruption of behavioural patterns, including, but not limited to, migration, breathing, nursing, breeding, feeding, or sheltering, but does not have the potential to injure a marine mammal or marine mammal stock in the wild (Level B harassment).

[7] NOAA Fisheries policy on human interactions with wild marine mammals and suite of viewing guidelines is available at *http://www.nmfs.noaa.gov/topic/marine-life-viewing-guidelines*

[8] Examples of education and outreach materials can be found at *http://sero.nmfs.noaa.gov/protected_resources/outreach_and_education/index.html.*

Fig. 1. The approximate perimeter of the study area near Panama City, Florida is shown in red and green. The original study area by Samuels and Bejder (1998; 2004) is outlined in red. Most human-interactions were documented on the beach side of Shell Island, known as 'Interaction Beach' and at the 'Bait Barge' located inside the northwest shore of the pass (highlighted by the star).

Bay near Panama City, Florida, USA (Fig. 1). The methodologies and survey design for this study mirrored those of Samuels and Bejder (1998; 2004) to the extent possible (Table 7). Between 15–27 June 2014, 78hrs 44min of on-water observations were conducted within 30 n.m.^{2} around 'Interaction Beach', St. Andrew Bay, Grand Lagoon (including the 'Bait Barge' located inside this area), East Bay, and West Bay (Fig. 1).

The analyses of Samuels and Bejder (1998; 2004) were repeated to facilitate longitudinal comparison and additional analyses were performed to more fully elucidate the progression of human-dolphin interactions in this area (Table 7).

Photo-identification and sightings

Photo-identification surveys were conducted throughout the study area (Fig. 1) using an unmarked 6.4m vessel with a 150hp 4-stroke engine. Although the vessel was unmarked, if asked by a tour business about our intentions, we identified ourselves and stated that we were studying the dolphins' behaviour. Tour businesses were not informed of our presence prior to the study.

The goals of photo-identification surveys were to determine the number of individual dolphins that engaged in human interactions and to locate prospective animals for focal follows. Surveys were expanded outside of areas studied by Samuels and Bejder (1998; 2004) to locate non-conditioned dolphins (i.e. animals that did not engage in human interactions) for focal follows and to document any new human interaction hot-spots. Survey effort was measured by recording the GPS location of the research vessel every 3mins when 'on effort', that is, actively searching for dolphins during surveys. Surveys were discontinued if the wind reached ≥ 4 on the Beaufort scale.

For each dolphin sighting, date, time, location, GPS coordinates, environmental parameters, number of dolphins, and behaviour of all dolphins were recorded (Tables 1 and 2). Whenever possible, all dolphins within the group were photographed. If a dolphin was seen engaging in human interactions (Table 2) during a sighting, the behaviour(s) and the corresponding photograph frame numbers were recorded. Photographs were analysed and identified in accordance with the standards defined in Urian *et al.* (1999) and Rosel *et al.* (2011) and assigned to a catalogue if of sufficient quality.

Samuels and Bejder (2004) defined 'conditioned' dolphins as those that were sighted accepting food and repeatedly exhibiting behaviours listed in Table 2. However, feeding was anticipated to be more clandestine than it was in the previous study based on increased enforcement presence and citations in recent years. Therefore, 'conditioned' dolphins were defined as those documented engaging in two or more

Table 1

Definitions of behaviours used for this study (adapted from Shane *et al.*, 1986).

Behaviour	Description
Mill	Non-directional movement; frequent changes in heading.
Forage	Characterised by efforts to capture prey, such as active diving, chasing fish, or pinwheeling.
Travel	Persistent, directional movement.
Rest	Involves slow movement as a tight group and in the absence of other identifiable activities.
Socialise	Includes all active interactions between dolphins, such as contact, chasing, rubbing, sexual interactions, etc.

Table 2

Dolphin behaviour event definitions indicative of chronic human interactions (adapted from Perrtree *et al*., 2014; Powell and Wells, 2011; and Samuels and Bejder, 2004).

Behaviour	Description
Remain close	Remain within touching distance of one or more humans that are in the water or in a vessel.
Head up	Approach with head out of water (either vertically or horizontally) to within 2m of vessel or human.
Beg	Approach with head out of water and open mouth to within 2m of vessel or human.
Lunge at vessel	Vertical lunge with open mouth and head and flippers out of water within 2m of a vessel.
Follow vessel	Rapid travel within 2m of the side or stern of a vessel that is moving at speed (but not riding the bow wave).
Accept food	Accept (or attempts to accept) food or non-food items from humans.
Patrol	Dolphin travels in repeated directions around fishing gear, vessel, or dock.

of the behaviours listed in Table 2 regardless of whether, or not, they were observed to accept food.

Focal follows

Methodology for focal follows was adapted from Samuels and Bejder (1998; 2004) with only minor adjustments to account for expanded dolphin behavioural repertoires, difficulty locating non-conditioned dolphins, and unsafe boating conditions due to waters crowded with vessels, personal watercrafts, and swimmers. During focal follows, 50m distance from the dolphin was maintained when possible; however, this distance was reduced when necessary to maintain a clear view of the focal animal. Dolphins were always approached at idle speed from the side and slightly behind. Given the presence and behaviour of the research vessel was a constant variable and minimally invasive, we presumed that observed dolphin behavioural responses were a result of other variables such as tour vessels or swimmers; however, the research vessel may potentially have been a confounding variable.

A conditioned focal dolphin was selected if it was observed engaging in at least two human interaction behaviours (Table 2) during the initial sighting and ideally, had distinctive dorsal fin markings. Non-conditioned dolphins were selected if the animal and no others in the group displayed behaviours indicative of human interactions during the initial sighting. In only one instance, did an originally selected non-conditioned animal begin to display human interaction behaviours shortly after beginning a follow. That animal was re-categorised as a conditioned focal dolphin. Focal follows were conducted throughout the study area, although the majority were concentrated near ‘Interaction Beach’ to maintain consistency with Samuels and Bejder’s (1998; 2004) methodology (Fig. 2).

Standard behavioural sampling techniques were applied (Altmann, 1974). Nearly all data were collected via 3min point samples including: GPS location, group size, number of subgroups, group cohesion, presence/absence of dolphin behaviour events indicative of human interaction (Table 2), number of vessels within 10m and 50m (not including the research vessel), number of swimmers within 10m and 50m, and any notable comments. Focal dolphin activity as well as the overall group activity were recorded as the most predominant activity observed over the 3min interval (Tables 1 and 2). All human-dolphin interactions were documented that presented potential risk to either humans or dolphins during each point sample (Table 3). Samuels and Bejder (1998; 2004) collected point samples at 1min intervals when focal dolphins were in close proximity to human activity. However, a 3min interval was maintained when focal dolphins were in close proximity to humans due to the difficulties of safely manoeuvring the research vessel amongst the large number of vessels and swimmers present while also monitoring the focal animal.

Statistical analyses

Replication of Samuels and Bejder methodologies

Behavioural data from focal follows were compiled and summarised according to conditioned or non-conditioned status (Samuels and Bejder, 1998; 2004). The percent time during a follow that a focal dolphin was within 10m or 50m of a swimmer or vessel, the percent time the focal dolphin engaged in human interaction events, the percent time the focal dolphin was fed or attempted to be fed, and the percent time the focal dolphin or interacting human was at risk were all quantified.

Supplementary analysis: Markov chains

First-order discrete-time Markov chains were used to build transition matrices of proceeding to succeeding behaviour

Table 3

Human-dolphin interactions that present risk of injury, illness, or death (adapted from Samuels and Bejder, 2004).

Interaction risk code	Type of interaction	Sources of risk
D1	Human and dolphin make physical contact (or within touching distance).	Human may inadvertently touch vulnerable body parts of dolphin; human may be aggressive and injure dolphin; human attempts to ride dolphin; potential for disease transmission.
D2	Dolphin is in close proximity to vessels.	Dolphin may be injured by propeller, hit by moving vessel, crushed or trapped between two vessels, or injured by an object that falls or is dropped form a vessel.
D3	Dolphin is in close proximity to deployed fishing gear.	Dolphin may be entangled, hooked, or ingest fishing gear; dolphin may learn to steal fish from fishers; dolphin may be injured by retaliatory action by fisher.
D4	Human feeds dolphin.	Dolphin may ingest tainted fish or inappropriate food; young dolphins may not learn appropriate foraging skills; dolphin less vigilant and prone to predation; conspecific aggression.
D5	Human offers object to dolphin.	Dolphin may ingest object and sustain internal injuries.
H1	Human and dolphin make physical contact (or within touching distance).	Dolphin may inadvertently touch vulnerable body parts of human; dolphin may be aggressive and injure human; potential for disease transmission.

states. Separate chains were constructed for the presence and absence of human stimuli (i.e. vessels or swimmers) within 10m and 50m. Both conditioned and non-conditioned dolphins were included in this analysis. The use of Markov chains is well described in the literature and is typically used to quantify disturbance impacts to marine mammals from anthropogenic sources (e.g. Dans *et al.,* 2008; Lusseau, 2003; Lusseau, 2004; Meissner *et al.,* 2015; Peters *et al*., 2013; Stockin *et al.,* 2008). These chains quantify the dependence of a behaviour on the preceding ones and provide probabilities of transition from one behaviour to another (Lusseau, 2003). This method allows for a direct comparison to other marine mammal behavioural studies.

Data were compiled into two-way contingency tables as described in Lusseau (2003) using *Proc Freq* in SAS v9.3 (SAS Institute, Inc., Cary, NC). Intra-specific socialising was never observed and resting only observed once as the dominant activity state over a 3min period; therefore, these behaviours were excluded from the analysis. Begging and patrolling behaviour states were combined into an 'Interaction' behaviour category because the sample size for begging was small ($n = 13$). Begging was not often witnessed as a dominant behavioural state over a 3min interval but was typically an event that occurred while the dolphin was patrolling near vessels or swimmers. The transition probabilities were calculated for all Markov chains as:

$$p_{i,j} = \frac{a_{i,j}}{\sum_{j=1}^{4} a_{i,j}}, \sum_{j=1}^{4} p_{i,j} = 1$$

where $p_{i,j}$ is the transition probability from preceding behaviour i to succeeding behaviour j and $a_{i,j}$ is the number of observed transitions from behaviour i to behaviour j. Transition probabilities were compared using an exact test for Pearson chi-square for proportions (Pearson, 1900).

Following the Perron-Frobenius Theorom and ergodic theorem (Caswell, 2001), the dominant left eigenvector of the dominant eigenvalue for each transitional matrix corresponds to a stationary behavioural state distribution (Lusseau, 2003). Eigenanalyses were conducted using the library *popdemo* (Stott *et al.,* 2012) in R (R Core Team, 2013). Stationary behavioural states (i.e. activity budgets) between presence and absence of human stimuli at 10m and 50m, respectively, were compared using a z-test for proportions (Zar, 1996).

Supplementary analysis: multinomial logistic regression

To evaluate the likelihood and significance of specific behavioural transitions in the presence or absence of a human stimulus, odds ratios were generated from a multinomial logistic regression with a cumulative logit link using *Proc Genmod* in SAS v9.3. Unlike the Markov chain approach, this modelling approach controlled for the effects of individual variability by using focal dolphin as an aggregating (i.e. repeated measures) variable. Specifically, group activity, focal activity, change in number of dolphins, increase in number of dolphins, change in number of subgroups, increase in number of subgroups, change in cohesion, and increase in cohesion were examined as responses to the presence or absence of a human stimulus.

For this analysis, focal activities were aggregated into three categories: interaction (begging and patrolling), natural (foraging and one period of resting), and transitional (travelling and milling). Aggregation into three categories greatly simplified interpretation of the response profiles from the multinomial logistic regression analysis. Travelling was considered a transitional state because conditioned dolphins moved between vessels or swimmers and successively engaged in human interaction events. The behaviour of moving between vessels was often documented as travel rather than patrol since it was not possible to distinguish when the focal dolphin was deliberately travelling while opportunistically happening upon a vessel/swimmer to interact with, versus deliberately patrolling for provisions. This is similar to Samuels and Bejder's (1998; 2004) findings in which all recorded travel by conditioned dolphins was from vessel to vessel. Milling was combined with travelling because it was infrequently observed and other studies have suggested it may be a transitional state (Constantine *et al.,* 2004; Peters *et al.,* 2013).

Any missed point samples in which the focal animal was temporarily out of sight were excluded from the analysis. Regression models incorporated single time step lagged response variables as covariates to control for autocorrelation inherent in time series data. Three human stimuli covariates were evaluated at each distance: presence of a human stimulus in the current time step, presence of a human stimulus in the previous time step, and persistence of a human stimulus from the previous to the current time step. Separate regressions were performed for human stimuli at 10m and 50m to examine the differential impacts of proximity of human stimuli upon dolphin behaviour.

Supplementary analyses: ranging patterns and space use

Spatial data were projected in ARC GIS 10.1 (ESRI, Redlands, CA) to create a map of all observed human interaction events (Table 2) from focal follows and sightings. To determine whether conditioned and non-conditioned dolphins exhibit differences in ranging patterns, both linear distance moved per 3min point sample and overall space use were examined. General linear modeling (GLM) in SPSS v17.0 (IBM Corp., Armonk, NY) was used to test for differences in distance moved. GLMs controlled for the random effects of the focal individual and interaction behaviour while evaluating differences in the marginal means of distance moved per minute of observation by conditioned versus non-conditioned focal dolphins. To test for differences in space use, minimum convex polygons (MCPs) were developed for each focal dolphin using Geospatial Modeling Environment (Beyer, 2012). After the shoreline was clipped out of each MCP using existing county maps and satellite imagery, MCP areas were computed in a NAD UTM83 Zone 17N projection. Minimum convex polygon sizes for conditioned and non-conditioned dolphins were compared in Microsoft Excel (Microsoft Corp., Redmond, WA) using a two-sample t-test assuming unequal variances. To ensure that track duration did not have an impact upon the estimated MCP, mean MCP sizes for conditioned and non-conditioned dolphins were estimated to include and exclude tracks of less than 1hr duration.

RESULTS

Photo-identification and sightings

A total of 56 sightings of bottlenose dolphins were recorded; of these, 28 (50%) included a dolphin engaging in a behaviour event indicative of chronic human interaction (Fig. 2). A minimum of 57 individual, identifiable dolphins were sighted; of these, 21 (36.8%) were identified as conditioned. Photo-identification data from the original study was not available for comparison of fins.

Fourteen of the 21 conditioned dolphins (66.7%) were sighted near 'Interaction Beach'; of these, five (23.8%) were seen there on multiple days (Fig. 2). Seven of the 21 conditioned dolphins (33.3%) were sighted at the 'Bait Barge' near the northwest shore of the pass; of these, four (19.0%) were seen there on multiple days (Fig. 2). One conditioned dolphin (4.8%) was sighted at both 'Interaction Beach' and the 'Bait Barge'. Ten of the 21 conditioned dolphins (47.6%) were documented to 'accept food' from a person; five conditioned dolphins were fed at 'Interaction Beach', four were fed at the 'Bait Barge' (on three different days), and one was fed in the channel of St. Andrew's Pass.

Focal follows: evaluating impacts of human stimuli on dolphin behaviour

During this study, focal follows were conducted for 11 individual dolphins and a male pair, for a total of 12 follows. Six conditioned dolphins were followed for a total of 9hrs 39mins and seven non-conditioned dolphins (including the male pair) were followed for a total of 8hrs 48mins. Focal follows ranged from 48mins to 2hrs 25mins. Conditioned focal dolphins followed included one juvenile/sub-adult and five adults (including one female with a calf). Non-conditioned focal dolphins included two juveniles, one sub-adult/adult, and four adults (including two females with calves and a male pair).

Replication of Samuels and Bejder methodologies

On average, conditioned focal dolphins (n = 6) were observed engaging in chronic human interaction events in 52.85% (range: 5.25–100%) of point samples observed. On average, conditioned dolphins were within 50m of a vessel or swimmer in 56.48% (range: 10.53–75%) of observed point samples, and within 10m in 45.08% (range: 10.53–70.91%) of observed point samples. Furthermore, when a vessel or swimmer was within 50m or 10m of a conditioned focal dolphin, the focal animal engaged in chronic human interaction events during 73.39% (range: 0–100%) and 80.46% (0–100%) of observations, respectively. One conditioned dolphin was fed while being followed. This particular conditioned dolphin was fed (or attempts were made to feed) during 65.45% observed point samples. Non-conditioned dolphins were observed within 50m and 10m of a vessel or a swimmer on average during 4.55% (range: 0–17.24%) and 1.14% (range: 0–4.88%) of observed point samples, respectively.

During a follow, conditioned dolphins were at risk of injury, illness, or death as a result of human-interactions (Table 3) during an average 45.60% (range: 0–74.55%) of observations (or at least 9.2 times per 1hr) whereas non-conditioned dolphins were at risk during an average of 1.7%

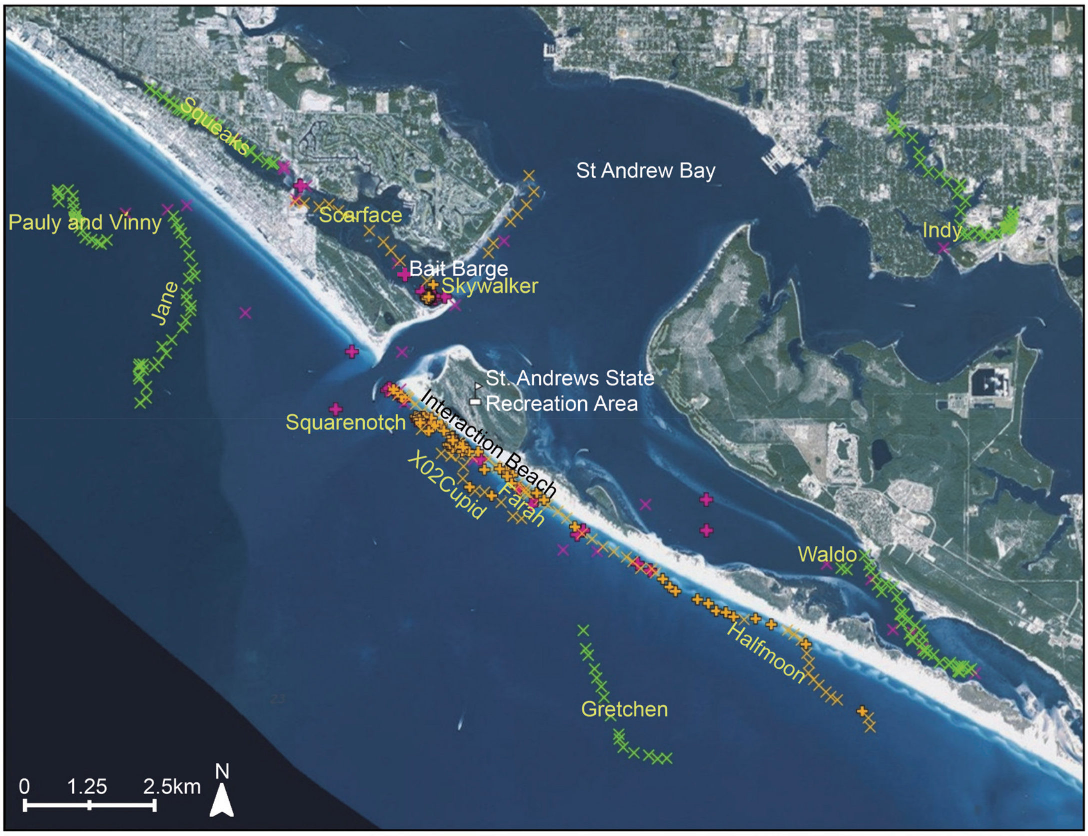


Fig. 2. Sightings (pink) and focal follow point samples for conditioned (orange) and non-conditioned (green) dolphins, highlighting locations of recorded human-dolphin interactions (crosses) in waters near Panama City, Florida. Human-dolphin interactions are clustered around 'Interaction Beach' and the 'Bait Barge' due to food provisioning of dolphins in these areas.

(range: 0–10.34%) of observations (or at least one time per 3.21hrs). Humans interacting with conditioned dolphins were at risk of injury (Table 3) during 18.13% (range: 0–32.73%) of observations or at least 3.75 times per 1hr. No direct injury for either humans or dolphins was observed as a result of an interaction, however, this was difficult to confirm given the number of vessels and swimmers in the water with an animal at one time.

Supplementary analysis: Markov chains

The use of first-order Markov chains revealed considerable differences in dolphin activity budgets in the presence versus in the absence of human stimuli (i.e. vessel or swimmer) at both 50m and 10m (Table 4, Fig. 3). In the absence of a human stimulus, dolphins spent significantly more time travelling and foraging. When a human stimulus was present, dolphins spent significantly more time interacting (i.e. begging or patrolling) with swimmers or vessels. When a human stimulus was within 50m, dolphins spent 64% of their time interacting with swimmers or vessels; with a human stimulus present within 10m, dolphins spent 81% of their time interacting with swimmers or vessels. There were no significant differences detected for the time spent milling with or without a human stimulus present.

Table 4

Detailed activity budgets (a); and corresponding Z and p values calculated based on first order Markov chain analyses (b). Milling was the only behaviour found not to be significantly different when in the presence or absence of a human stimulus at either 50 or 10m.

(a)		Activity budget			
Distance	Human stimulus	Forage	Interaction	Mill	Travel
50m	No	15%	4%	11%	70%
	Yes	3%	64%	7%	26%
10m	No	14%	4%	11%	71%
	Yes	3%	81%	4%	12%

(b)			Forage		Interaction		Mill		Travel	
Distance	Human stimulus	N	Z	p	Z	p	Z	p	Z	p
50m	No	210	2.97	< 0.0001	–11.84	< 0.0001	1.04	0.30	7.40	< 0.0001
	Yes	103								
10m	No	235	2.59	< 0.0001	–14.00	< 0.0001	1.86	0.06	9.09	< 0.0001
	Yes	78								

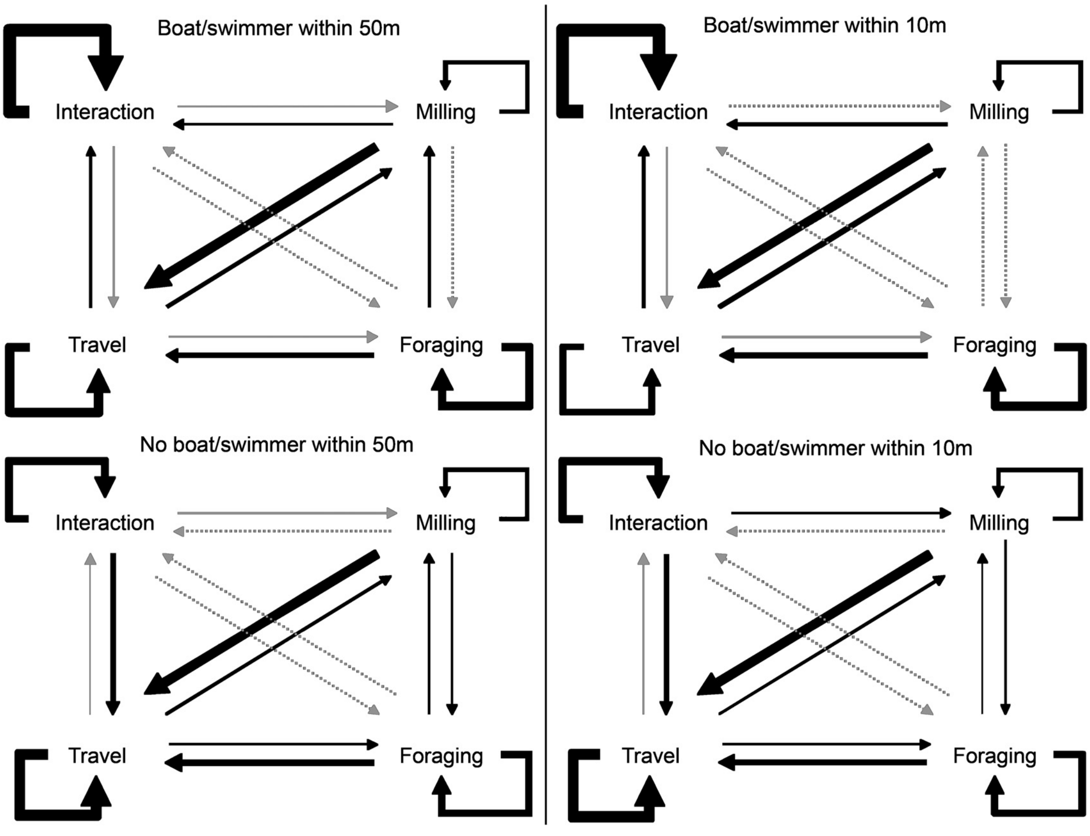


Fig. 3. Behavioural transitions by focal animals in four observed scenarios (1. Vessel/swimmer within 50m; 2. No vessel/swimmer within 50m; 3. Vessel/swimmer within 10m; 4. No vessel/swimmer within 10m). Thickness of arrows corresponds to transitional probabilities from first-order Markov chains (Table 4) with insignificant results denoted by grey dashed lines.

Table 5

Likelihood ratio model fit summary statistics for Type 3 analysis for multinomial regression analysis of human stimulus impacts on dolphin behaviour in waters near Panama City, Florida. Significant human stimulus effects in **bold**. Subscripts denote lagged variables.

Response	Human stimulus	Parameter	DF	Chi-square	Pr > ChiSq
Change in group activity	50m	Individual	9	45.87	< 0.0001
		Group activity$_{-1}$	2	71.45	< 0.0001
		Human stimulus	1	3.24	0.072
	10m	Individual	9	43.22	< 0.0001
		Group activity$_{-1}$	2	9.36	0.0093
		Human stimulus	1	2.07	0.15
Change in focal activity	50m	Individual	10	46.41	< 0.0001
		Focal activity$_{-1}$	2	20.64	< 0.0001
		Human stimulus	**1**	**6.68**	**0.0098**
	10m	Individual	10	47.49	< 0.0001
		Focal activity$_{-1}$	2	18.69	< 0.0001
		Human stimulus	**1**	**17.8**	**< 0.0001**
Change in no. dolphins	50m	Individual	10	38.27	< 0.0001
		Number of dolphins$_{-1}$	1	0.11	0.7351
		Human stimulus	1	3.25	0.0714
	10m	Individual	10	52.45	< 0.0001
		Number of dolphins$_{-1}$	1	0.11	0.7351
		Human stimulus	**1**	**11.98**	**0.0005**
Increase in no. dolphins	50m	Individual		No significant results	
		Number of dolphins$_{-1}$			
		Human stimulus			
	10m	Individual	10	53.71	< 0.0001
		Number of dolphins$_{-1}$	1	0.05	0.8207
		Human stimulus	1	0.33	0.5645
Change in no. subgroups	50m	Individual	10	41.1	< 0.0001
		Number of groups$_{-1}$	1	38.86	< 0.0001
		Human stimulus	1	1.55	0.2126
	10m	Individual		No significant results	
		Number of groups$_{-1}$			
		Human stimulus			
Increase in no. subgroups	50m	Individual	10	39.64	< 0.0001
		Number of groups$_{-1}$	1	9.04	0.0026
		Human stimulus	1	1.15	0.2845
	10m	Individual	10	38.15	< 0.0001
		Number of groups$_{-1}$	1	10.25	0.0014
		Human stimulus	1	0.02	0.9003
Change in cohesion	50m	Individual	8	25.72	0.0012
		Cohesion$_{-1}$	1	16.97	< 0.0001
		Human stimulus	1	0.78	0.3783
	10m	Individual	8	21.98	0.005
		Cohesion$_{-1}$	1	16.92	< 0.0001
		Human stimulus	1	0.18	0.6744
Increase in cohesion	50m	Individual	8	11.39	0.1808
		Cohesion$_{-1}$	1	17.57	< 0.0001
		Human stimulus	1	0.01	0.9152
	10m	Individual	8	11.56	0.1717
		Cohesion$_{-1}$	1	17.96	< 0.0001
		Human stimulus	1	0.89	0.3459

Supplementary analysis: multinomial logistic regression

Odds ratio (OR) contrast estimation within the nested multinomial regression framework revealed significant trends in how dolphins react to the presence/absence of human stimuli (Table 6, Fig. 4). When a human stimulus was within 50m, odds of switching from resting or foraging to interaction behaviour substantially increased ($\mathrm{OR}_{natural \rightarrow interaction}$: 12.31); when a human stimulus was within 10m, these odds more than doubled ($\mathrm{OR}_{natural \rightarrow interaction}$: 32.17). Similarly, odds of remaining engaged in interaction behaviour when there was a human stimulus within 50m were high ($\mathrm{OR}_{interaction \rightarrow interaction}$: 3.62); when there was a human stimulus within 10m, these odds nearly tripled ($\mathrm{OR}_{interaction \rightarrow interaction}$: 9.24). When a human stimulus was present within 10 or 50m, odds of dolphins remaining in a travel/milling behaviour or transitioning to a foraging or resting behaviour were extremely low. In the absence of a human stimulus within 10 or 50m, dolphins were likely to remain in or switch to a travel/milling behaviour.

The logistic regression analysis indicated dolphins sometimes transitioned to interaction behaviour when a

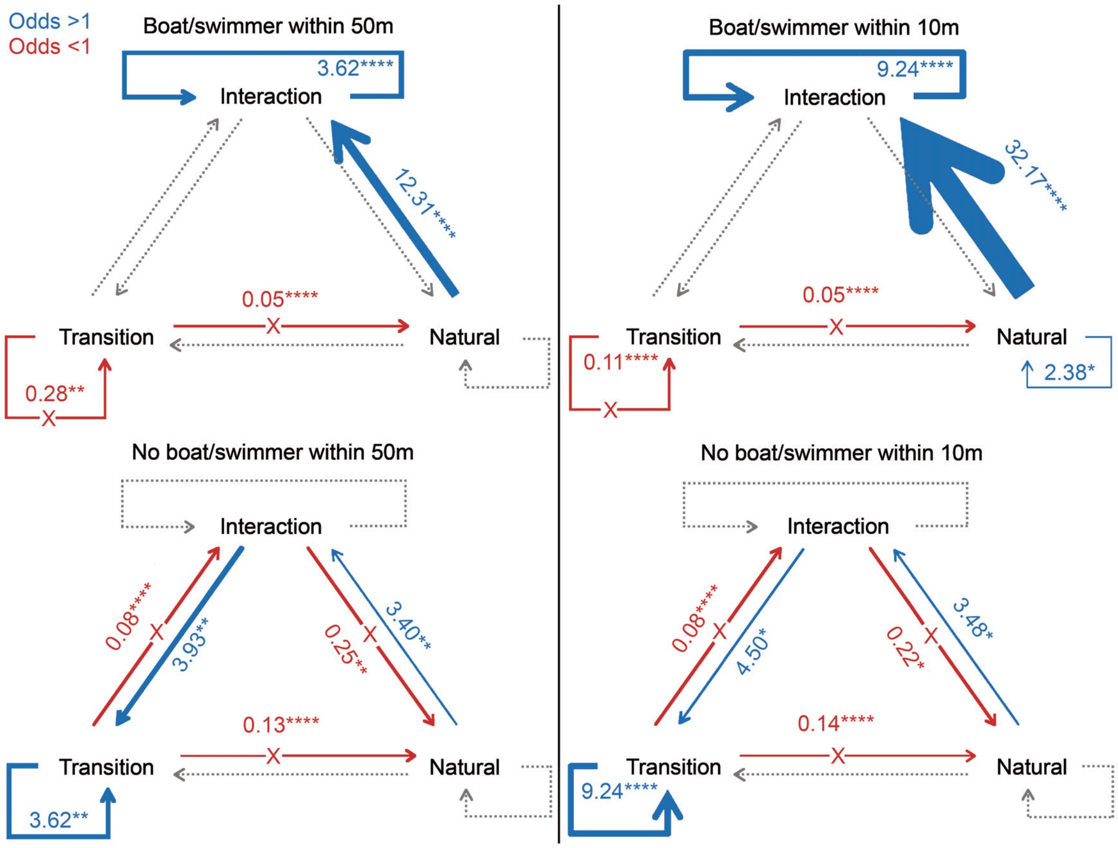


Fig. 4. Odds of specific behaviour transitions by focal animals in four observed scenarios (1. Vessel/swimmer within 50m; 2. No vessel/swimmer within 50m; 3. Vessel/swimmer within 10m; 4. No vessel/swimmer within 10m). Focal activity was aggregated into three categories: interaction (begging and patrolling), natural (resting and foraging), or transitional (travelling and milling). Thickness of arrows corresponds to transitional probabilities from nested multinomial logistic regression analysis (Table 6) with insignificant results denoted by grey dashed lines. Blue lines denote trends with odds greater than one (i.e. more likely to happen); red lines with ‘X’ denote trends with odds less than one (i.e. less likely to happen).

Table 6

Odds ratio statistics from contrast estimation for significant multinomial logistic regression model fits for the impacts of human stimuli (i.e. vessels or swimmers) upon dolphin behaviour in waters near Panama City, Florida. Significant contrasts in **bold**. The range following the ‘mean’ represents the 95% confidence limits.

Response	Human stimulus	10m			50m		
		Mean	χ^2	Pr > χ^2	Mean	χ^2	Pr > χ^2
Change in focal activity							
Travel→Travel	No	9.24 (3.19–26.81)	16.78	**< 0.0001**	3.62 (1.37–9.59)	6.69	**0.01**
Natural→Natural		3.08 (1.00–9.51)	3.84	0.05	2.74 (0.98–7.66)	3.67	0.06
Interaction→Interaction		0.32 (0.11–1.00)	3.84	0.05	0.37 (0.13–1.02)	3.67	0.06
Interaction→Natural		0.22 (0.06–0.78)	5.56	**0.02**	0.25 (0.07–0.87)	4.75	**0.03**
Interaction→Travel		4.50 (1.29–15.71)	5.56	**0.02**	3.93 (1.15–13.44)	4.75	**0.03**
Natural→Interaction		3.48 (1.56–7.78)	9.24	**0.00**	3.40 (1.53–7.58)	9.00	**0.00**
Natural→Travel		2.18 (0.59–8.09)	1.36	0.24	2.52 (0.71–9.02)	2.03	0.15
Travel→Interaction		0.08 (0.02–0.29)	15.02	**0.00**	0.08 (0.02–0.27)	16.06	**< 0.0001**
Travel→Natural		0.14 (0.06–0.33)	19.73	**< 0.0001**	0.13 (0.06–0.32)	20.41	**< 0.0001**
Travel→Travel	Yes	0.11 (0.04–0.31)	16.78	**< 0.0001**	0.28 (0.10–0.73)	6.69	**0.01**
Natural→Natural		2.38 (1.11–5.12)	4.94	**0.03**	1.55 (0.73–3.27)	1.32	0.25
Interaction→Interaction		9.24 (3.19–26.81)	16.78	**< 0.0001**	3.62 (1.37–9.59)	6.69	**0.01**
Interaction→Natural		0.53 (0.13–2.08)	0.83	0.36	0.39 (0.10–1.56)	1.76	0.18
Interaction→Travel		1.89 (0.48–7.43)	0.83	0.36	2.53 (0.64–9.99)	1.76	0.18
Natural→Interaction		32.17 (8.73–118.55)	27.21	**< 0.0001**	12.31 (3.74–40.51)	17.07	**< 0.0001**
Natural→Travel		0.24 (0.04–1.32)	2.71	0.10	0.70 (0.13–3.64)	0.18	0.67
Travel→Interaction		0.25 (0.04–1.57)	2.18	0.14	0.21 (0.04–1.18)	3.14	0.08
Travel→Natural		0.05 (0.01–0.20)	17.13	**< 0.0001**	0.05 (0.01–0.21)	16.85	**< 0.0001**
Change in no. dolphins							
	Yes	0.11 (0.03–0.42)	10.82	**0.00**			

human stimulus was absent (Table 6, Fig. 4); this result is explained by differences in sampling methodologies – focal dolphin behaviour was recorded as the dominant state over a 3min period, whereas vessel and swimmer counts were recorded as point samples. Therefore, at times, the dominant behaviour over the 3min interval was a form of interaction behaviour, but a human stimulus was not recorded for the point sample because it had just moved beyond a 10 to 50m radius of the dolphin.

Supplementary analyses: ranging patterns and space use

When movements were considered in aggregate, there were no significant differences of movement between conditioned and non-conditioned focal dolphins; however, significant differences were apparent when distance moved was compared between times focal dolphins were interacting with a vessel or swimmer versus times they were not. Mean distance moved per minute of observation was 56 ± 1m for dolphins not interacting; interacting dolphins moved significantly less (16 ± 5m less, $F_{1,333} = 12.8$, $p < 0.001$) per minute of observation. The overall space use of conditioned and non-conditioned focal dolphins, as measured by MCPs, was not significantly different ($p > 0.05$).

DISCUSSION

In the original study near Panama City, Samuels and Bejder (1998; 2004) documented 7 of 89 (8%) dolphins encountered as conditioned. In 2014, 21 of 57 (37%) dolphins encountered were conditioned. The number of conditioned dolphins identified in this study is likely underestimated. Due to the crowding and collision risk from vessels and swimmers surrounding groups of conditioned dolphins, it was sometimes difficult to monitor and acquire photographs of all individual group members during a sighting. In order to adjust for this constraint, surveys along 'Interaction Beach' were sometimes timed just prior to the arrival of tour vessels so that photo-identification data could be collected more completely, however, this was not always possible. Furthermore, there were a number of dolphins that were observed engaging in human interaction events but could not be individually identified due to lack of distinguishing dorsal fin markings.

Despite the expanded study area and increased field time compared to the previous study, only 57 distinct conditioned and non-conditioned dolphins were identified, versus the 89 individuals identified by Samuels and Bejder (1998; 2004) in 1998 (Table 7). The number of identifications documented here are not representative of the entire St. Andrew Bay stock population, but rather a sub-set of the population. However, the reduction in identifications between the two studies warrants further exploration. Numerous studies have documented declines in the abundance of dolphin populations exposed to intensive tourism pressure as a result of diminished reproductive health or permanent habitat displacement or abandonment (Bejder, 2005; Bejder *et al.,* 2006b; Lusseau, 2006; Lusseau *et al.*, 2006; Tyne *et al.,* 2014). Additionally, an increase in the number of dolphin deaths in this area was documented between 1999 and 2006. The Panhandle region of Florida experienced three bottlenose dolphin Unusual Mortality Events (1999–2000, 2004 and 2005–2006), which had an unknown impact on the population of resident dolphins (Balmer *et al.,* 2008; Schwacke *et al.,* 2010). The observations of focal dolphin 'X02', examined and freeze-branded during NMFS' 2005 bottlenose dolphin health assessment project in nearby St. Joseph Bay (43km to the east), demonstrates some dolphins move between and utilise different habitat areas along the Florida Panhandle. Baseline population data will be important in helping to understand the status of this population and the impacts of human interactions.

Impacts of human stimuli on dolphin behaviour

When a human stimulus was present within 50m, conditioned focal dolphins engaged in human interactions

Table 7

Comparison of results between this project (2014) and Samuels and Bejder (1998; 2004) specifically related to human-dolphin interactions near Panama City, Florida.

	2014 study	Samuels and Bejder (1998; 2004)
Study length	12 days (15-27 June 2014)	5 days (4-9 August 1998)
Study area	30 n.miles^2	24 n.miles^2
Field methods	Photo-identification, focal follows	Photo-identification, focal follows
Statistical analysis	Descriptive statistics, Markov chains, multinomial logistic regression, spatial analysis	Descriptive statistics
Conditioned dolphins identified	21/57 (37%)	7/89 (8%)
Hot spot locations	Interaction Beach and Bait Barge	Interaction Beach
Non-conditioned dolphins focal follows:		
No. of follows	6 (8h, 48min.)	5 (5h, 28min.)
Age/sex class	1 juvenile,1 adult/sub-adult; 4 adults (2 females with calves and male pair)	Single dolphin (unknown sex/age); mixed groups
Conditioned dolphins focal follows:		
No. of follows	6 (9h, 39min.)	4 (6h, 32min.)
Age/sex class	1 juvenile/sub-adult; 5 adults (including 1 female with calf)	1 juvenile; 1 adult
Time engaged in chronic human interactions	73% of 3min. samples	77% of 1 min. samples
Risk	Dolphins: 9.2x/hr; humans: 3.75x/hr	e.g. HiMidLo-5x/hr; humans-2x/hr
Ranging patterns	No sig. diff. overall from non-conditioned; sig. less movement when begging/patrolling	<1 n.mile of Interaction Beach; travel less than non-conditioned
Activity budgets	Atypical behavior: 64-81% of time begging/ patrolling; no social; 1 period of resting	e.g. HiMidLo-atypical behavior (2 incidents of social; 1 incident of forage)

events during 73% of observation points (Table 7), similar to the 77% interaction rate documented by Samuels and Bejder (1998; 2004). The well-established ability of dolphins to learn by observation (i.e. social learning) likely contributed to the increase in number of individual dolphins that engage in human interaction behaviours over time (Cunningham-Smith *et al*., 2006; Donoghue *et al.,* 2002; Wells, 2003; Whitehead *et al.,* 2004). Also, dolphins in Panama City are now routinely fed in at least two locations: 'Interaction Beach' and the 'Bait Barge' versus the one location ('Interaction Beach') as described in Samuels and Bejder (1998; 2004) (see Fig. 2). In general, this highlights how unnatural foraging strategies, including begging, may increase in frequency given high rates of reinforcement by humans.

Activity budgets, a standard measure of animals' behavioural states, are particularly useful in understanding how energy expenditure or acquisition is impacted by human activities (Christiansen *et al.,* 2014; Lusseau *et al.,* 2009; Williams *et al.,* 2006). Samuels and Bejder (1998; 2004) profiled the behaviour of a specific juvenile animal 'HiMidLo' to show that the activity budget of a conditioned dolphin is not representative of unconditioned dolphin behaviour (Table 7). For example, the conditioned dolphin, 'HiMidLo', was followed over three days for a total of 5hrs and 53mins and was only observed socialising with other dolphins twice and foraging naturally once (Samuels and Bejder, 1998; 2004). In the 2014 study, the activity budgets of focal conditioned dolphins were also atypical when a human stimulus was present within 10 or 50m (Table 7). In these circumstances, conditioned focal dolphins spent the majority of their time (stimulus within 50m: 64%, stimulus within 10m: 81%) begging or patrolling near vessels and people, which meant less time was devoted to natural behaviours such as resting, foraging, and socialising. Additionally, there were extremely high statistical odds that dolphins engaged in natural behaviour would switch to an interaction behaviour when a human stimulus was present.

In the absence of a human stimulus within 50m, focal dolphin activity budgets (conditioned and non-conditioned combined) were somewhat comparable to activity budgets for other dolphins on Florida's West coast, especially in terms of time spent travelling, foraging, and milling (Waples, 1995). However, in Panama City, major differences included no social behaviour and only a single sample of resting behaviour. The lack of observed intra-specific social behaviour in the presence of high boat traffic has also been documented for other cetacean species (Constantine, 2001; Dans *et al.,* 2008; Lundquist *et al.,* 2008; Williams *et al.,* 2006). It is also possible that conditioned dolphins are re-allocating their energy to begging or patrolling to seek provisions, thus decreasing the amount of time interacting with conspecifics. Considering that the development of play is crucial for animal social skills, less interaction with conspecifics particularly for conditioned juveniles or calves could result in developmental delays or associated problems (Foroughirad and Mann, 2013; Mann and Barnett, 1999; Mann and Kemps, 2003; Samuels and Bejder, 2004). Resting is one of the most easily disturbed natural behaviours; the lack of observed resting behaviour was consistent with numerous studies, which documented declines in bottlenose dolphin resting behaviour in the presence of vessels (Arcangeli *et al*., 2009; Constantine *et al.,* 2003; Constantine *et al.,* 2004; Lusseau, 2003; Yazdi, 2007).

Once a conditioned dolphin began to engage in an interaction behaviour state, the animal tended to continue to do so. If the stimulus was removed, the dolphin would often switch to travel behaviour, but travel behaviour was often terminated when the animal arrived at another vessel or swimmer, highlighting the likelihood that the animal was travelling in search of provisions. Overall, the conditioned dolphin activity budgets found here are somewhat similar to other dolphin disturbance studies, with one key difference. Most of the literature supports that dolphins spend less time foraging and resting and more time milling and travelling in the presence of vessels and swimmers (Arcangeli *et al.,* 2009; Lusseau, 2004; Lundquist *et al.,* 2012; Meissner *et al.,* 2015; Montero-Cordero and Lobo, 2010; Steckenreuter *et al.,* 2012; Stockin *et al.,* 2008). In these cited studies, responses are likely disturbance responses from non-conditioned dolphins and attributed to animals' efforts to avoid human stimuli. However, in this study, dolphins increased their time travelling and decreased time milling because they were conditioned and actively sought out additional provisioning opportunities from vessels/swimmers, rather than avoiding the stimuli.

Samuels and Bejder (1998; 2004) found dramatically different ranging patterns between conditioned and non-conditioned dolphins (Table 7). Conditioned dolphins stayed within < 1 n. mile^2 area around 'Interaction Beach' and the adjacent pass, whereas, non-conditioned dolphins travelled distances of several nautical miles (Samuels and Bejder, 1998; 2004). In this 2014 study, conditioned animals were mainly observed around 'Interaction Beach', the adjacent pass, and inside the bay near the 'Bait Barge'. Conditioned dolphins moved significantly less only when engaged in interaction behaviours. Distance traveled and space use by conditioned dolphins when not interacting was likely comparable to non-conditioned animals because conditioned dolphins travelled from one vessel/swimmer to another in search of food. In addition, in a few instances, conditioned dolphins moved to deeper water away from the beach at times when the number of vessels and swimmers peaked during an interaction. The swim-with tour vessels would typically not follow the dolphins into the deeper water presumably due to the decline in water clarity. This type of vertical and horizontal avoidance strategy exhibited by conditioned animals is frequently utilised by non-conditioned bottlenose dolphins potentially as a way to avoid tourism pressure (Latusek, 2002; Lemon *et al.,* 2006; Lusseau, 2004; Lusseau, 2006).

Food provisioning

As described 16 years earlier in Samuels and Bejder (1998), illegal food provisioning still facilitates swim-with activities with dolphins in Panama City. Ten dolphins were documented being provisioned during this study. In one case, a focal animal, 'X02', and two other dolphins in his group were fed repeatedly by the captain of a bait boat (a vessel that fishes for and then holds live bait fish to sell to recreational fishers) anchored off 'Interaction Beach' for nearly two hours (Fig. 5). The captain would throw handfuls of bait at the dolphins and then cast his net on top of or near the bait while the dolphins scavenged under the guise that to protect his nets, he had to feed the dolphins. The captain also began radio communication as soon as the dolphins arrived, and dolphin tour vessels arrived on site within 15 minutes of the call. The bait boat captain was then observed throwing handfuls of bait into the middle of the group of swimmers, attracting the scavenging dolphins close enough for swimmers to closely approach and touch the animals (Fig. 5). X02 and his companions displayed aggressive behaviours such as bubble-blowing and tail-slapping directed at swimmers during these interactions.

The 'Bait Barge' has emerged as a new provisioning location. The 'Bait Barge' is an anchored barge where fishermen can purchase live bait fish. Dolphins were observed being fed there on four different dates. At the 'Bait Barge', an attendant was observed using a boat hook to slap the water, essentially training a dolphin through variable food reinforcement to station near the barge where swimmers were dropped off by commercial vessels to swim and interact with the animal (Fig. 6). This technique is very similar to how marine mammal trainers work with dolphins at zoos/aquariums (Ramirez, 1999). An individual on the commercial vessel then passed a small object with a dip net to the barge attendant after the swimmers were finished with the interaction. Based on the size of the object and the nature of interaction, this 'object' may have been monetary compensation; however, this could not be confirmed.

In multiple incidences, dolphins displayed aggressive behaviour (i.e. tail-slapping, bubble-blowing, chuffing) when swimmers entered the water near dolphins (Orams *et al.,* 1996; Samuels and Gifford, 1997; Connor, 2000). Dolphins were also aggressive when they anticipated a boater may have a food provision on board, but were not fed. In one instance, '90050' reached its head over the vessel's gunwale in an attempt to bite the data clipboard out of the hand of a field assistant, apparently perceiving it as food. Food provisioning and animal aggression causing injuries to humans have been documented in a variety of other species including baboons (Kamal *et al*., 1997; Wrangham, 1974), macaques (Aggimarangsee, 1993; Fa, 1992), chimpanzees (Goodall, 1986), bears (Gunther, 1992), and larger fishes

Fig. 5. The captain of the bait boat reaches for more bait to feed the begging bottlenose dolphins to keep the animals nearby as a tour boat puts swimmers in the water. The photo was taken on 21 June 2014 at 'Interaction Beach', Panama City, Florida.

Fig. 6. An attendant at the 'Bait Barge' in Panama City, Florida uses a boat hook to slap the water to attract a bottlenose dolphin towards swimmers that were dropped off by tour vessels to swim and interact with the animal. This dolphin was provisioned during this incident. The photo was taken on 23 June 2014.

(Perrine, 1989). NMFS Southeast Regional Office has recorded 18 cases of dolphins biting people in the Southeastern United States since 1997; these injuries typically occurred while the person was feeding, swimming, or harassing a dolphin. Furthermore, intra-species aggression is also a consequence of provisioning by humans, which tends to increase when animals are aggregated more densely as a result of human provisioning (Orams, 2002) or when adult males are present (Orams *et al.*, 1996).

Provisioning wild dolphins may have other unanticipated consequences. Once dolphins learn to associate humans with food through provisioning, the animals may be more likely to engage in more risky behaviours such as depredating or scavenging from fishermen (Powell, 2010). In Panama City, two conditioned dolphins previously observed begging, were also sighted patrolling and attempting to depredate from recreational fishermen off 'Interaction Beach'. Interacting with recreational fishermen presents increased risks of injury or death for conditioned dolphins due to acts of retaliation by fishers or entanglement and ingestion in fishing gear (Adimey *et al.*, 2014; DOJ 2006, 2007; Read, 2008; Stolen *et al.*, 2013; Wells *et al.*, 2008).

CONCLUSION

This study confirms that the problem in Panama City has escalated over the last 16 years: dolphins are actively provisioned; the proportion of conditioned dolphins has increased substantially; conditioned dolphin activity budgets, behaviours, and movement patterns continue to be impacted by human interactions; and the risk of injury or mortality for both dolphins and humans from their interactions occurs multiple times per hour. NMFS has attempted to address the harassment to and illegal provisioning of dolphins in this area with outreach and educational campaigns, as well as intermittent law enforcement, including undercover operations. Unfortunately, it appears that the tour operators have adapted surreptitious provisioning methods over time to hide from enforcement efforts. Dolphin provisioning in Panama City by local tour businesses has progressed from: (1) tour operators provisioning dolphins directly from vessels; (2) tour operators disguising feeding by provisioning animals underwater; (3) tour operators throwing a metal bucket (sometimes containing fish) over the side of the vessel when dolphins were near; to (4) tour operators capitalising on local bait fishermen and barge operators who feed dolphins under the guise that they are throwing back unwanted fish or feeding the animals to keep them from damaging their gear (Samuels and Bejder, 1998; 2004).

A more aggressive management strategy is recommended for Panama City to reduce and eliminate high risk human-dolphin interactions. Given that long-term, high profile outreach/education and pulsed enforcement efforts have proven unsuccessful, we suggest a targeted and sustained enforcement campaign based on the existing regulations at 50 CFR 216 that prohibit feeding and other forms of 'take' and 'harassment'. Additional regulations should also be developed as soon as possible to clearly restrict close approaches and in-water interactions. All efforts will require a consistent enforcement effort for effectiveness. Lessons learned from immediate enforcement efforts will better inform the development of potential future proposed rulemakings.

In addition, long-term and consistent monitoring studies throughout the year would be ideal to evaluate seasonal and long-term population-level impacts resulting from human interactions. Minimally, we recommend repeating this study in the off-season months when tourism pressure subsides so that both conditioned and non-conditioned dolphin behaviour can be re-examined and compared with the summer tourism peak to allow for a more complete understanding of how human interactions affect dolphin behaviour. Human dimension studies on the motivation and incentives for both businesses and tourists to engage in close interactions with wild dolphins may also provide insight on social expectations (e.g. Filby *et al.,* 2015) and could help guide management actions to maximise safe and enjoyable wild dolphin viewing opportunities.

ACKNOWLEDGEMENTS

We thank Kristen Spzak and Sam Beck for their assistance in the field, Maddie Evans for photo-id assistance, and Brian Balmer for providing information on focal animal, 'X02', and other suspected dorsal fin matches between the Panama City and St. Joseph Bay catalogs. We also thank Lars Bejder and Stacey Horstman for providing advice and assistance. We appreciate the reviews of this manuscript provided by David Laist and Dee Allen (Marine Mammal Commission) and Randall Wells (Sarasota Dolphin Research Program). This research was funded by MMC contract MMC14-193, and conducted under the NMFS Office of Protected Resources Permit No.14450-0

Dedication: This study is dedicated to Dr Amy Samuels (1950–2008) who conducted the original research on human-dolphin interactions in Panama City, Florida in 1998. Amy was a rigorous scientist, passionate conservation biologist, and great mentor who pioneered the application of quantitative behavioural research methods in the marine mammal science field. She devoted her life to collecting detailed behavioural observations of animals that provided important new insights into the social behaviour of both cetaceans and primates. Amy worked on several research projects to assess human impacts on dolphins, both in the wild and at public display facilities, and the data she collected enabled government agencies around the world to make informed management decisions to protect the health and welfare of both animals and the public. In replicating her ground-breaking research project in Panama City, we humbly aspired to honour Amy's life work and legacy, and hopefully have provided additional new information that will inform future management efforts to further protect dolphin and human safety.

REFERENCES

Adimey, N.M., Hudak, C.A., Powell, J.R., Bassos-Hull, K., Foley, A., Farmer, N.A., White, L. and Minch, K. 2014. Fishery gear interactions from stranded bottlenose dolphins, Florida manatees, and sea turtles in Florida, USA. *Mar. Pollut. Bull.* 81:103–15.

Aggimarangsee, N. 1993. Survey for semi-tame colonies of macaques in Thailand. *Nat. Hist. Bull. Siam Soc.* 40:103–166.

Allen, M.C. and Read, A. J. 2000. Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. *Mar. Mamm. Sci.* 16:815–24.

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behav.* 49:227–267.

Arcangeli, A., Crosti, R., del Leviatano, A. and Rome, I. 2009. The short-term impact of dolphin-watching on the behaviour of bottlenose dolphins (*Tursiops truncatus*) in Western Australia. *J. Mar. Anim. Ecol.* 2:3–9.

Balmer, B.C., Wells, R.S., Nowacek, S.M., Nowacek, D.P., Schwacke, L.H., McLellan, W.A., Scharf, F.S., Rowles, T.K., Hansen, L.J., Spradlin, T.R. and Pabst, D.A. 2008. Seasonal abundance and distribution patterns of common bottlenose dolphins (*Tursiops truncatus*) near St. Joseph Bay, Florida, USA. *J. Cetacean Res. Manage.* 10(2):157–67.

Bechdel, S.E., Mazzoil, M.S., Murdoch, M.E., Howells, E.M., Reif, J.S., McCulloch, S.D., Schaefer, A.M. and Bossart, G.D. 2009. Prevalence and impacts of motorized vessels on bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida. *Aquat. Mamm.* 35:367–77.

Bejder, L. 2005. Linking short and long-term effects of nature-based tourism on cetaceans. PhD Thesis, Dalhousie University. 158pp.

Bejder, L., Samuels, A., Whitehead, H. and Gales, N. 2006a. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Anim. Behav.* 72:1149–58.

Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M., Watson-Capps, J., Flaherty, C. and Krutzen, M. 2006b. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conserv. Biol.* 20:1791–8.

Beyer, H.L. 2012. Geospatial Modelling Environment (Version 0.6.0.0). [Available at: *http://www.spatialecology.com/gme*]

Byrd, B.L., Hohn, A.A., Lovewell, G.N., Altman, K.M., Barco, S.G., Friedlaender, A., Harms, C.A., McLellan, W.A., Moore, K.T., Rosel, P.E. and Thayer, V.G. 2014. Strandings illustrate marine mammal biodiversity and human impacts off the coast of North Carolina, USA. *Fish. Bull.* 112:1–23.

Caswell, H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. 2nd edition. Sinauer Associates Inc., Sunderland, MA.

Cisneros-Montemayor, A.M. and Sumaila, U.R. 2010. A global estimate of benefits from ecosystem-based marine recreation: potential impacts and implications for management. *J. Bioecon.* 12(3):245–68.

Christiansen, F., Rasmussen, M.H. and Lusseau, D. 2014. Inferring energy expenditure from respiration rates in minke whales to measure the effects of whale watching boat interactions. *J. Exp. Mar. Biol. Ecol.* 459:96–104.

Connor, R.C., Wells, R.S, Mann, J. and Read, A.J. 2000a. The bottlenose dolphin: social relationships in a fission-fusion society. pp. 91–126. *In*: J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead (Eds). *Cetacean Societies: Field Studies of Dolphins and Whales*. The University of Chicago Press, Chicago. 448pp.

Constantine, R. 2001. Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term swim-with-dolphin tourism. *Mar. Mamm. Sci.* 17:689–702.

Constantine, R., Brunton, D.H. and Baker, C.S. 2003. Effects of tourism on behavioural ecology of bottlenose dolphins of northeastern New Zealand. Department of Conservation Science Internal Series 153. Department of Conservation, Wellington, New Zealand. 26pp.

Constantine, R., Brunton, D.H. and Dennis, T. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biol. Conserv.* 117:299–307.

Cunningham-Smith, P., Colbert, D.E., Wells, R.S. and Speakman, T. 2006. Evaluation of human interactions with a provisioned wild bottlenose dolphin (*Tursiops truncatus*) near Sarasota Bay, Florida, and efforts to curtail the interactions. *Aquat. Mamm.* 32:346–56.

Department of Justice. 2006. *Florida Charter Boat Captain Pleads Guilty to Shooting at Dolphins*. DOJ Press Release issued on 8 August 2006.

Department of Justice. 2007. *Shooting of Dolphin Leads to Federal Charges*. DOJ Press Release issued on 19 January 2007.

Dans, S.L., Crespo, E.A., Pedraza, S.N., Degrati, M. and Garaffo, G.V. 2008. Dusky dolphin and tourist interaction: effect on diurnal feeding behaviour. *Mar. Ecol. Prog. Ser.* 369:287–96.

Donaldson, R., Finn, H. and Calver, M. 2010. Illegal feeding increases risk of boat-strike and entanglement in bottlenose dolphins in Perth, Western Australia. *Pac. Conserv. Biol.* 16:157–61.

Donaldson, R., Finn, H., Bejder, L., Lusseau, D., Calver, M., Gompper, M. and Williams, R. 2012. The social side of human-wildlife interaction: wildlife can learn harmful behaviours from each other. *Anim. Conserv.* 15:427–35.

Donoghue, M., Reeves, R.R. and Stone, G. 2002. Report on the workshop on interactions between cetaceans and longline fisheries held in Apia, Samoa, November 2002. New England Aquatic Forum Series Report 03-1. 44pp.

Duda, M.D., Beppler, T. and Horstman, S.C. 2013a. Attitudes toward illegal feeding and harassment of wild dolphins in Panama City. *Hum. Dimens. Wildl.* 18:236–8.

Duda, M.D., Jones, M., Beppler, T., Bissell, S.J., Criscione, A., Doherty, P., Duda, M., Hughes, G., Ritchie, A., Schilli, C.L., Winegord, T., and Lanier, A. 2013b. Attitudes toward the protection of wild dolphins and dolphin-human interactions. Focus group report. Conducted for the National Marine Fisheries Service by Responsive Management, Harrisonburg, VA. 79pp.

Fa, J.E. 1992. Visitor directed aggression among the Gibraltar macaques. *Zoo Biol.* 11:42–52.

Filby, N.E., Stockin, K.A. and Scarpaci, C. 2015. Social science as a vehicle to improve dolphin-swim tour operator compliance? *Mar. Policy* 51:40–7.

Finn, H., Donaldson, R. and Calver, M. 2008. Feeding flipper: a case study of a human dolphin interaction. *Pacific Conserv. Biol.* 14:215–25.

Foroughirad, V. and Mann, J. 2013. Long-term impacts of fish provisioning on the behaviour and survival of wild bottlenose dolphins. *Biol. Conserv.* 160:242–9.

Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behaviour*. Harvard University Press, Cambridge, MA.

Gunther, K. 1992. Changing problems in bear management: Yellowstone National Park twenty years after the dumps. Proceedings of the Ninth Annual International Conference on Bear Research and Management, Missoula, MT, February 1992 (unpublished). [Available from: *http://www.bearbiology.org*]

Kamal, K.B., Boug, A. and Brain, P.F. 1997. Effects of food provisioning on the behaviour of commensal Hamadryas, baboons *Papio hamadryas*, at Al Hada Mountain in western Saudi Arabia. *Zool. Middle East* 14:11–22.

Latusek, J.N. 2002. Impact of boat traffic on bottlenose dolphins in Core Creek, NC, with a case study of dolphin-watch activities and consumer perspectives. MS Thesis. Duke University, Durham, North Carolina.

Lemon, M., Lynch, T.P., Cato, D.H. and Harcourt, R.G. 2006. Response of travelling bottlenose dolphins (*Tursiops aduncus*) to experimental approaches by a powerboat in Jervis Bay, New South Wales, Australia. *Biol. Conserv.* 127:363–72.

Lewandowski, J.K. 2005. Assessing public input on further regulatory measures by the National Marine Fisheries Service to address harassment of wild marine mammals from interactive viewing activities. MS Thesis, George Mason University, Fairfax, Virginia. 124pp.

Lundquist, D., Sironi, M., Würsig, B. and Rowntree, V. 2008. Behavioural responses of southern right whales to simulated swim-with-whale tourism at Peninsula Valdes, Argentina. Paper SC/60/WW4 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 15pp. [Paper available from the Office of this Journal].

Lundquist, D., Gemmell, N.J. and Würsig, B. 2012. Behavioural responses of dusky dolphin groups (*Lagenorhynchus obscurus*) to tour vessels off Kaikoura, New Zealand. *PLoS ONE* 7: e41969.

Lusseau, D. 2003. Effects of tour boats on the behaviour of bottlenose dolphins: using Markov chains to model anthropogenic impacts. *Conserv. Biol.* 17:1785–193.

Lusseau, D. 2004. The hidden cost of tourism: detecting long-term effects of tourism using behavioural information. *Ecol. Soc.* 9:2.

Lusseau, D. 2006. The short-term behavioural reactions of bottlenose dolphins to interactions with boats in Doubtful Sound, New Zealand. *Mar. Mamm. Sci.* 22:802–818.

Lusseau, D., Slooten, L. and Currey, R. J. 2006. Unsustainable dolphin-watching tourism in Fiordland, New Zealand. *Tour. Mar. Envir.* 3:173–178.

Lusseau, D., Bain, D. E., Williams, R. and Smith, J.C. 2009. Vessel traffic disrupts the foraging behaviour of southern resident killer whales *Orcinus orca*. *Endanger. Species Res.* 6:211–21.

Mann, J. and Barnett, H. 1999. Lethal tiger shark (*Galeocerdo cuvier*) attack on bottlenose dolphin (*Tursiops* sp.) calf: defense and reactions by the mother. *Mar. Mamm. Sci.* 15:568–75.

Mann, J., Connor, R.C., Barre, L.M. and Heithaus, M.R. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behav. Ecol.* 11:210–19.

Mann, J. and Kemps, C. 2003. The effects of provisioning on maternal care in wild bottlenose dolphins, Shark Bay, Australia. *In*: N. Gales, M. Hindell and R. Kirkwood (Eds.) *Marine Mammals and Humans: Towards a Sustainable Balance*. CSIRO Publishing. 480pp.

Meissner, A.M., Christiansen, F., Martinez, E., Pawley, M.D., Orams, M.B. and Stockin, K.A. 2015. Behavioural effects of tourism on oceanic common dolphins, *Delphinus* sp., in New Zealand: the effects of Markov analysis variations and current tour operator compliance with regulations. *PLoS ONE,* 10: e0116962

Montero-Cordero, A. and Lobo, J. 2010. Effect of tourist vessels on the behaviour of the pantropical spotted dolphin, *Stenella attenuata*, in Drake Bay and Caño Island, Costa Rica. *J. Cetacean Res. Manage.* 11(3):285–91.

National Marine Fisheries Service. 1994. *Report to Congress on Results of Feeding Wild Dolphins: 1989–1994*. National Marine Fisheries Service, Office of Protected Resources. 23pp.

National Oceanic and Atmospheric Administration Fisheries. 2014a. Dolphin harassment continues in Florida panhandle, tour boat operator fined. [Available at: *http://www.nmfs.noaa.gov/ole/slider_stories/2014/19_081914_panama_ city_dolphin_ harassment.html*. Accessed: 8 Nov 2016].

National Oceanic and Atmospheric Administration Fisheries. 2014b. Dolphin harassment leads to penalties for fisherman and tour boat captains. [Available at: *http://www.nmfs.noaa.gov/ole/slider_stories/2014/12_031214_dolphin _harassment.html*. Accessed: 8 Nov 2016].

O'Connor, S., Campbell, R., Cortez, H. and Knowles, T. 2009. Whale watching worldwide: tourism numbers, expenditures and economic benefits. A special report from the International Fund for Animal Welfare, Yarmouth, MA. 295pp.

Orams, M.B. 1996. A conceptual model of tourist–wildlife interaction: The case for education as a management strategy. *Aust. Geogr.* 27(1):39–51.

Orams, M.B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tour. Manag.,* 23:281–293.

Orams, M.B., Hill, G.J.E. and Baglioni, A.J. 1996. 'Pushy' behaviour in a wild dolphin feeding program at Tangalooma, Australia. *Mar. Mamm. Sci.* 12(1):107–17.

Parsons, E.C.M. 2012. The negative impacts of whale watching. *J. Mar. Biol.* 2012, Article ID 807294. 9pp. [doi:10.1155/2012/807294].

Parsons, E.C.M., Fortuna, C.M., Ritter, F., Rose, N.A., Simmonds, M.P., Weinrich, M., Williams, R. and Panigada S. 2006. Glossary of whalewatching terms. *J. of Cetacean Res. Manage.* 8 (Suppl.):249–51

Pearson, K. 1900. On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. *Phil. Mag. Ser. 5* 50(302):157–75. [doi:10.1080/14786440009463897].

Peltier, H., Dabin, W., Daniel, P., Van Canneyt, O., Dorémus, G., Huon, M. and Ridoux, V. 2012. The significance of stranding data as indicators of cetacean populations at sea: modelling the drift of cetacean carcasses. *Ecol. Indic.* 18:278–90.

Perrine, D. 1989. Reef fish feeding; amusement or nuisance? *Sea Frontiers* 35(5):272–9.

Perrtree, R.M., Kovacs, C.J., and Cox, T.M. 2014. Standardization and application of metrics to quantify human-interaction behaviours by the bottlenose dolphin (*Tursiops* spp.). *Mar. Mamm. Sci.* 30(4):1320–34.

Peters, K.J., Parra, G.J., Skuza, P.P. and Möller, L.M. 2013. First insights into the effects of swim-with-dolphin tourism on the behaviour, response, and group structure of southern Australian bottlenose dolphins. *Mar. Mamm. Sci.* 29: E484–E497.

Powell, J.R. 2009. Depredation and angler interactions involving bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. MS thesis, University of South Florida.

Powell, J. R. and Wells, R. S. 2011. Recreational fishing depredation and associated behaviours involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Mar. Mamm. Sci.* 27:111–29.

R Core Team. 2013. *R*: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available at: *http://www.R-project.org/*].

Ramirez, K. 1999. How we train (a simplified version). pp.12–16. *In: Animal Training: Successful Animal Management Through Positive Reinforcement*. Shedd Aquarium, Chicago, IL. 578pp.

Read, A.J. 2008. The looming crisis: Interactions between marine mammals and fisheries. *J. Mammal.* 89(3):541–8.

Rosel, P.E., Mullin, K.D., Garrison, L., Schwacke, L., Adams, J., Balmer, B., Conn, P., Conroy, M.J., Eguchi, T., Gorgone, A., Hohn, A., Mazzoil, M., Schwartz, C., Sinclair, C., Speakman, T., Urian, K., Vollmer, N., Wade, P., Wells, R. and Zolman, E. 2011. Photo-identification capture-mark-recapture techniques for estimating abundance of bay, sound and estuary populations of bottlenose dolphins along the US East Coast and Gulf of Mexico: A workshop report. NOAA Technical Memorandum NMFS-SEFSC–621. 30pp.

Samuels, A. and Bejder, L. 1998. A pilot study of habitual interaction between humans and wild bottlenose dolphins near Panama City Beach, FL. Report to the Marine Mammal Commission, Silver Spring, TS370089. 19pp.

Samuels, A, Bejder, L. and Heinrich, S. 2000. A review of the literature pertaining to swimming with wild dolphins. Report to the Marine Mammal Commission, Silver Spring, MD, T74463123. 57pp.

Samuels, A., Bejder, L., Constantine, R. and Heinrich, S. 2003. Swimming with wild cetaceans in the Southern Hemisphere. pp.277–303. *In*: N. Gales, M. Hindell and R. Kirkwood (Eds.) *Marine Mammals: Fisheries, Tourism and Management Issues*. CSIRO Publishing, Collingwood. 466pp.

Samuels, A. and Bejder, L. 2004. Chronic interaction between humans and free-ranging bottlenose dolphins near Panama City Beach, Florida. *J. Cetacean Res. Manage.* 6(1):69–77.

Samuels, A. and Gifford, T. 1997. A quantitative assessment of dominance relations among bottlenose dolphins. Mar. Mamm. Sci. 13:70–99.

Schwacke L.H., Twiner, M.J., De Guise, S., Balmer, B.C., Wells, R.S., Townsend, F.I., Rotstein, D.C., Varela, R.A., Hansen, L.J., Zolman, E.S., Spradlin, T.R., Levin, M., Leibrecht, H., Wang, Z. and Rowles, T.K. 2010. Eosinophilia and biotoxin exposure in bottlenose dolphins (*Tursiops truncatus*) from a coastal area impacted by repeated mortality events. *Environ. Res.* 110(6):548–55.

Shane, S.H., Wells, R.S. and Würsig, B. 2006. Ecology, behaviour and social organization of the bottlenose dolphin: a review. *Mar. Mamm. Sci.* 2(1):34–63.

Spradlin, T.R., Drevenak, J.K., Terbush, A.D. and Nitta, E.T. 1999. Interactions between the public and wild dolphins in the United States: biological concerns and the Marine Mammal Protection Act. Presented to the 13th Biennial Conference on the Biology of Marine Mammals, 28 November – 3 December 1999, Maui, Hawaii, USA.

Steckenreuter, A., Moller, L. and Harcourt, R. 2012. How does Australia's largest dolphin-watching industry affect the behaviour of a small and resident population of Indo-Pacific bottlenose dolphins? *J. Environ. Manag.* 97:14–21.

Stockin, K.A., Lusseau, D., Binedell, V., Wiseman, N. and Orams, M.B. 2008. Tourism affects the behavioural budget of the common dolphin *Delphinus* sp. in the Hauraki Gulf, New Zealand. *Mar. Ecol. Prog. Ser.* 355:287–95.

Stolen, M., Noke-Durden, W., Mazza, T., Barros, N. and St. Leger, J. 2013. Effects of fishing gear on bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon system, Florida. *Mar. Mamm. Sci.* 29 (2):356–64.

Stott, I., Hodgson, D.J. and Townley, S. 2012. Popdemo: an *R* package for population demography using projection matrix analysis. *Methods in Ecology and Evolution* 3:797–802. [doi: 10.1111/j.2041-210X.2012.00222.x].

Tyne, J.A., Pollock, K.H., Johnston, D.W. and Bejder, L. 2014. Abundance and survival rates of the Hawai'i Island associated spinner dolphin (*Stenella longirostris*) stock. *PLoS ONE.* 9:e86132.

Urian, K.W., Hohn, A.A. and Hansen, L.J. 1999. Status of the photo-identification catalog of coastal bottlenose dolphins of the western North Atlantic: Report of a workshop of catalog contributors. NOAA Tech Memo NMFS-SERFSC-425. 24pp.

Vail, C. 2016. An overview of increasing incidents of bottlenose dolphin harassment in the Gulf of Mexico and possible solutions. *Frontiers in Marine Science* 3: 1–7. [doi: 10.3389/fmars.2016.00110].

Waples, D.M. 1995. Activity budgets of free-ranging bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. MS thesis. University of California Santa Cruz.

Waring, G.T., Josephson, E., Maze-Foley, K. and Rosel, P.E (Eds.). 2016. US Atlantic and Gulf of Mexico marine mammal stock assessments – 2015. NOAA Tech Memo NMFS NE 238. 501pp.

Wells, R.S. and Scott, M.D. 1997. Seasonal incidence of boat strikes on bottlenose dolphins near Sarasota, Florida. *Mar. Mamm. Sci.* 13:475–80.

Wells, R.S. 2003. Dolphin social complexity: Lessons from long-term study and life history. pp.32–56. *In:* F.B.M. de Waal and P.L. Tyack (Eds) *Animal Social Complexity: Intelligence, Culture, and Individualized Societies*. Harvard University Press, Cambridge, MA.

Wells, R.S., Allen, J.B., Hofmann, S., Bassos-Hull, K, Fauquier, D.A., Barros, N.B., DeLynn, R.E., Sutton, G, Socha, V. and Scott, M.D. 2008. Consequences of injuries on survival and reproduction of common bottlenose dolphins (*Tursiops truncatus*) along the west coast of Florida. *Mar. Mamm. Sci.* 24(4):774–94.

Wells, R.S., Allen, J.B., Lovewell, G., Gorzelany, J., Delynn, R.E., Fauquier, D.A. and Barros, N.B. 2015. Carcass-recovery rates for resident bottlenose dolphins in Sarasota Bay, Florida. *Mar. Mamm. Sci.* 31(1):355–68.

Whitehead, H.L., Rendell, L., Osborne, R.W. and Würsig, B. 2004. Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biol. Conserv.* 120:427–37.

Williams, R., Lusseau, D. and Hammond, P.S. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biol. Conserv.* 133:301–11.

Wrangham, R.W. 1974. Artificial feeding of chimpanzees and baboons in their natural habitat. *Anim. Behav.* 22:83–93.

Yazdi, P. 2007. Impact of tour boats on the behaviour and energetics of bottlenose dolphins (*Tursiops truncatus*) off Choros Island, Chile. Paper SC/59/WW20 presented to the IWC Scientific Committee, May 2007, Anchorage, USA (unpublished). 9pp. [Paper available from the Office of this Journal].

Zar, J.H. 1996. *Biostatistical Analysis,* 3rd Edition. Prentice-Hall, Inc., New Jersey. 662pp.

Zeiler, M.D. 1968. Fixed and variable schedules of response-independent reinforcement. *J. Exp. Anal. Behav.* 11:405–14.

Patterns of predator-prey dynamics between gray whales (*Eschrichtius robustus*) and mysid species in Clayoquot Sound

R. BURNHAM AND D. DUFFUS

Whale Research Lab, Department of Geography, University of Victoria, PO 3060 STN CSC, Victoria, BC V8W 3P5, Canada

Contact e-mail: burnhamr@uvic.ca

ABSTRACT

The patterns of foraging intensity of gray whales (*Eschrichtius robustus*) over a 17-year period (1997–2013) in Clayoquot Sound, Vancouver Island are examined. In this area, epibenthic mysid species are gray whales' primary prey. The analysis indicates a top-down modification on habitat quality by this apex predator. Intense foraging in one or two summer season contributes to reduced prey resources available in the following summer. Years of heavy predation pressure were followed by at least one year of reduced foraging, probably allowing a reprieve in which the mysids could repopulate. Over the time span several patterns were noted including: boom-bust cycles; extended periods of reduced foraging; an overall declining trend of foraging whales using Clayoquot Sound, followed by a significant prey recovery in 2010. Life history patterns of mysids are discussed in the context of their ability to recover from predation, and how this recovery during a reprieve may buffer the intensity of foraging from the previous year. The continuing ability of mysids to recover from repeated and persistent removal will determine the use of Clayoquot Sound as a gray whale foraging area in the future.

KEYWORDS: PREDATION; FOOD/PREY; FEEDING GROUNDS; PACIFIC OCEAN; SURVEY-VESSEL; TRENDS; NORTHERN HEMISPHERE

INTRODUCTION

Predation shapes community structure by exerting top-down pressure. When positioned at the apex of an interaction web, cetaceans are both consumers, and in some cases habitat architects (Highsmith *et al.*, 2006; Oliver and Slattery, 1985). Whale distribution is, however, determined by prey location and abundance, which in turn, is under the influence of bottom-up forces of plankton blooms or benthic primary production. Therefore, the life history of both the predatory whales and their zooplankton prey shape the strength of their interaction, consequently creating the spatial dynamics of whale populations and foraging patterns over time.

Temporal patterns of use by gray whales (*Eschrichtius robustus*, Lilljeborg, 1861) of a foraging site in Clayoquot Sound (49°14'36"N, 126°6'10"W and 49°18'51"N, 126°14'30"W) on the west coast of Vancouver Island, British Columbia, Canada were examined (see Fig. 1). Whales have been noted in the area for over 40 years (Hatler and Darling, 1974). Almost 200 individual whales have foraged in Clayoquot Sound since 1997, with many of these (48.52 %) returning for multiple summers (2–12 years, Whale Lab, unpublished photo-id data, pers. obs.). Deep unproductive waters that are devoid of prey border the study area, creating a spatially discrete site that is separated from other foraging sites by at least 25km. There is no evidence to suggest that population mixing between mysid swarms is hindered within Clayoquot Sound, however comparisons between prey populations in the study area and of those sampled in foraging areas 40km further north found them to be genetically distinct (Short, 2005).

This study focused on gray whale foraging patterns in Clayoquot Sound following a prey switch from benthic to epibenthic resources. Having apparently driven local amphipod (*Peracardia, Amphipoda*) reserves into major decline by about 1997 (Duffus, 1996: Burnham and Duffus, 2016), foraging has since targeted swarming mysid species (*Peracardia, Mysida*; Duffus, 1996; Dunham and Duffus, 2001; 2002). Previous work (Feyrer and Duffus, 2014) has shown strong positive correlation between gray whale feeding behaviour and mysid prey density in Clayoquot Sound.

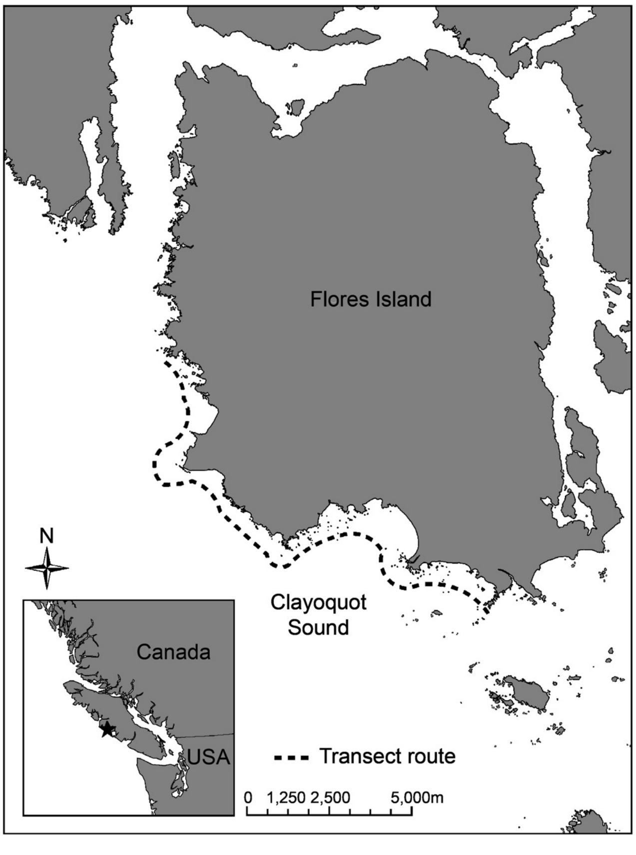


Fig. 1. The study area, Clayoquot Sound. The study area survey route is indicated by the dotted line, approximately following the 10m isobath.

The whale data are considered in light of the patterns of growth and reproduction of mysids. It is expected that cool water temperatures and lower general productivity of the winter months result in lower mysid reproduction. Thus, despite refuge from their major predator over winter, most mysid reproduction is initiated following productivity increases; thus the late summer brood in September becomes a cache/foundation for the following years' prey stock.

METHODS

Approach

The objective of the study was to assess the relationship between gray whale foraging activity and prey abundance over time. The approach taken was to: (1) quantify within-season patterns of whale foraging intensity for each summer in the 17-year span of data collection; and (2) examine whether the magnitude of one seasons' foraging affected the next, in order to determine any between-season patterns in predation. In particular, the number of whales in the late season was compared to those in the early part of the following summer.

The tested hypothesis is that the number of whales foraging in a given year impacts the available prey resources in the next year(s). The expectation is that in years of high foraging intensity (i.e. where prey removal exceeds population growth), prey populations will be depressed the following year. The influence of the number of foraging whales at the end of one season (i.e. in autumn) on the number of individual whales recorded at the beginning of the next foraging season (i.e. summer) was examined on the expectation that heavy autumn foraging would depress mysid reproduction and thus abundance in the following spring, thereby depressing whale foraging effort (whales would move elsewhere) in the subsequent season or seasons.

Field methods

Whale data

Whale data were obtained from boat-based census surveys, each covering approximately 20km^2 of the nearshore of the long-term study area, on the southwest coast of Flores Island. Although the surveys were conducted predominantly over mysid habitat, the study area also encompassed known locales for amphipods, crab larvae (*Pachycheles* and *Petrolisthes* spp.) and other occasional prey species.

The transect survey followed the 10m isobath (see Fig. 1) and the route, aimed at maximising the possibility of locating foraging whales, was developed by intense observation and surveying between 1994 and 1997. A survey was conducted at least twice a week between 24 May and 8 September for the years 1997 to 2013. Differences in the timing and number of surveys in each season (see Table 1 and Results) were due to weather conditions.

Vessel speed remained constant at 13km h^{-1} to avoid double counting, with a minimum of four observers constantly scanning 360° for whales. Surveys were aborted if visibility became reduced or if sea state exceeded Beaufort 3.

Only foraging whales were recorded on transect surveys; foraging was determined by observations of behaviour including dive location, length and distance travelled (Malcolm and Duffus, 2000; Feyrer and Duffus, 2014). Prey habitat locations have previously been well defined through sampling, sonar surveys and modelling (Laskin *et al.*, 2010).

Mysid data

To complement the whale data, 12 prey sampling stations were randomly selected within known mysid habitat strata and sampled monthly during the winter and every second week in the summer over a three-year period (2010–12). Samples were taken by towing a 'bongo' style plankton net with two 30cm openings and a 500µm mesh. The net was deployed, allowing it to sink to the rocky substrate, dragged laterally for at least 30 seconds at an average speed of 4kmh^{-1}, and then pulled straight to the surface. This was repeated three times at each of the stations and the samples pooled to make temporal comparisons. Mysids were preserved in 70% ethanol, enumerated, measured (body length rostrum to telson tip), sexed and identified according to Kathman *et al.* (1986). Gravid females were identified by the presence of a brood pouch with young.

Analysis

Within-season patterns of whale foraging were analysed by the skew and kurtosis of the distribution of the 'whale foraging days' recorded from each survey through the summer (Sokal and Rohlf, 2012). In addition to these metrics, the maximum single survey number of foraging animals and its timing were used to identify the temporal peak of prey demand. The peak date acts as the 'centre point' of the distribution of whale foraging effort, with patterns described relative to this seasonal maximum. Skew is the degree of symmetry around this peak date, whereas kurtosis quantifies the degree to which the distribution is peaked or flattened compared to a normal distribution (Sokal and Rohlf, 2012). They are calculated as:

$$skew = \frac{\sum (x-\bar{x})^3}{(n-1)s^3}$$

$$kurtosis = \frac{\sum (x-\bar{x})^4}{(n-1)s^4}$$

where: $\bar{x}$ is the sample mean; N the number of data points, and s the sample standard deviation.

For analysis of inter-annual patterns, the mean number of foraging whales surveyed per year was compared to the mean over the 17-year period. Years were classified as relatively high or low based upon whale numbers and thus foraging pressure based on this 17-year average. A regression analysis was used to establish the dependence of the number of whales supported by the prey stock in the late spring/early summer of each season to that of the latter stages of the previous season. In all cases, whale presence was used as a proxy for mysid stock size. This assertion is supported by mysid density measurements made in 1996 and 1997 with plankton nets, flow meters and four consecutive years of intense quantitative sonar surveying from 2004 to 2008, establishing a high correlation between whales and mysid biomass (Dunham and Duffus, 2001; Feyrer and Duffus, 2014).

RESULTS

The results from the boat surveys are summarised by year in Table 1 and Figure 2. Between 1997 and 2013, 580 surveys were conducted (annual average, 34.1, range 15–59). The mean number of whale foraging days per year ranged from just under 1 (in 2007 when surveys occurred on 47 days) to as high as 18.3 (in 2013 when surveys occurred on 23 days) whilst the overall mean was just under 7 whales/survey; the peak date for foraging whales being present ranged from 6 June to 26 August (Table 1, Fig. 2). The maximum number of whales seen on a single survey was 38 individuals (2013, Fig. 2).

Comparison of mean numbers of foraging whales

Table 1 shows that on four occasions, years with a mean number of foraging whales that exceeding the global mean over the period, therefore relatively high foraging pressure (1998, 2002, 2004, 2006), were followed by at least one year with a mean below the global average value. There were two very high years consecutively in 2010 (16.4) and 2011 (11.3) followed by one low year. There were two sets of three consecutive years with low foraging effort. The 1999–2001 set followed high (9.58) foraging in 1998 while the 2007–09 set following a set of descending high-low pairs between 2002 and 2006. The highest foraging effort in the series occurred in 2013 i.e. the final year.

Temporal distribution of foraging within years

For all years, except 2007, 2010 and 2011, the temporal distribution of foraging whales displayed a positive skew i.e. site utilisation was greater before the peak date. This skew

Table 1

Summary of transect survey data 1997–2013.

Year	Number of surveys	Sighting period	Mean (SD)	Peak date	Skew	Kurtosis
1997	55	29/06–04/09	6.22 (3.13)	19/08	0.209	–0.387
1998	59	06/06–03/09	9.58 (5.32)	08/08	0.888	–0.825
1999	30	03/06–26/08	3.30 (1.66)	04/08	0.543	–0.661
2000	18	02/06–12/08	3.39 (2.38)	12/07	0.489	0.534
2001	46	25/05–12/09	2.37 (1.59)	13/08	0.696	2.13
2002	42	24/05–05/09	10.74 (7.80)	07/07	0.861	–0.153
2003	30	27/05–07/09	5.10 (2.74)	26/07	0.658	–0.901
2004	26	24/05–12/09	10.65 (8.36)	16/07	0.773	–0.632
2005	26	31/05–07/09	2.23 (1.19)	09/07	0.583	–0.549
2006	32	25/05–08/09	7.13 (5.80)	31/07	1.10	–1.209
2007	47	24/05–08/09	0.936 (1.14)	27/06	–0.168	2.78
2008	15	01/06–04/09	3.33 (2.75)	02/08	0.364	0.611
2009	32	27/05–06/09	3.81 (3.60)	05/08	0.677	0.191
2010	30	26/05–09/09	16.4 (6.54)	26/08	–0.0459	–0.848
2011	36	25/05–06/09	11.3 (6.20)	07/08	–0.821	–0.988
2012	33	25/05–02/09	4.73 (3.08)	06/06	0.266	0.916
2013	23	25/05–01/09	18.3 (8.02)	05/08	0.488	1.34
Overall	580	24/05–06/09	6.96 (4.19)	–	–	–

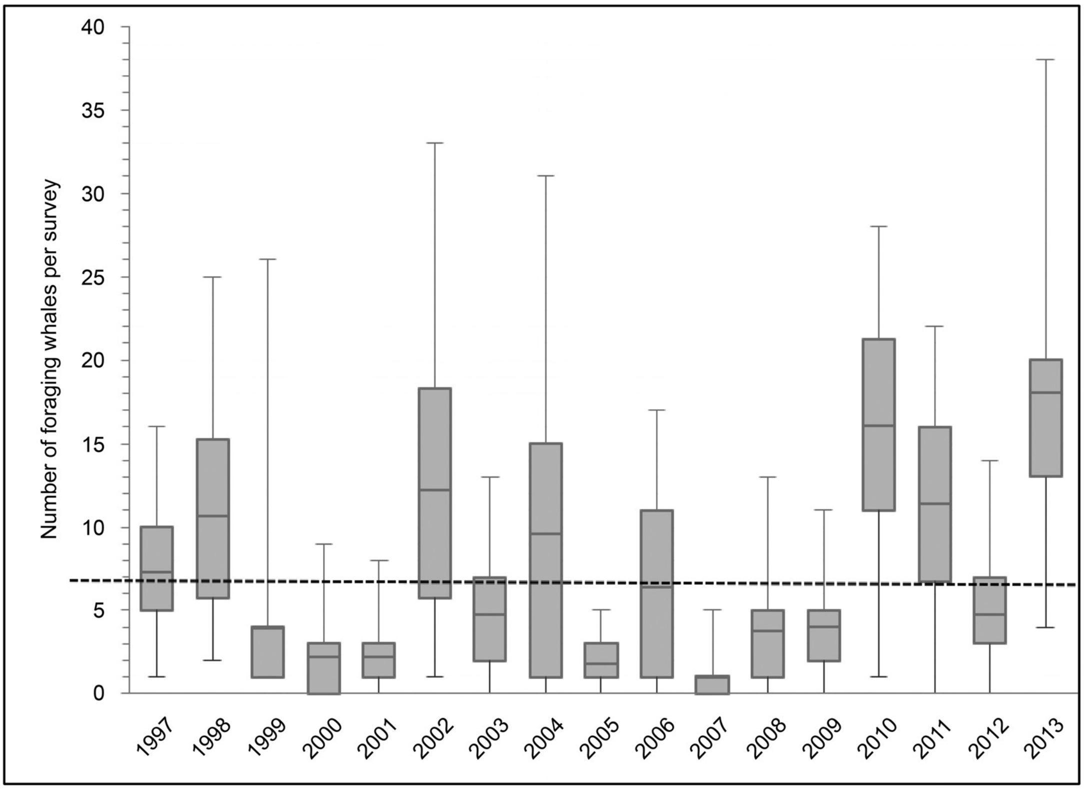


Fig. 2. Boxplot to indicate foraging intensity in the study site, calculated by the number of foraging whales sighted per transect survey. The dashed line is the overall average for all years, and allows for comparison between years.

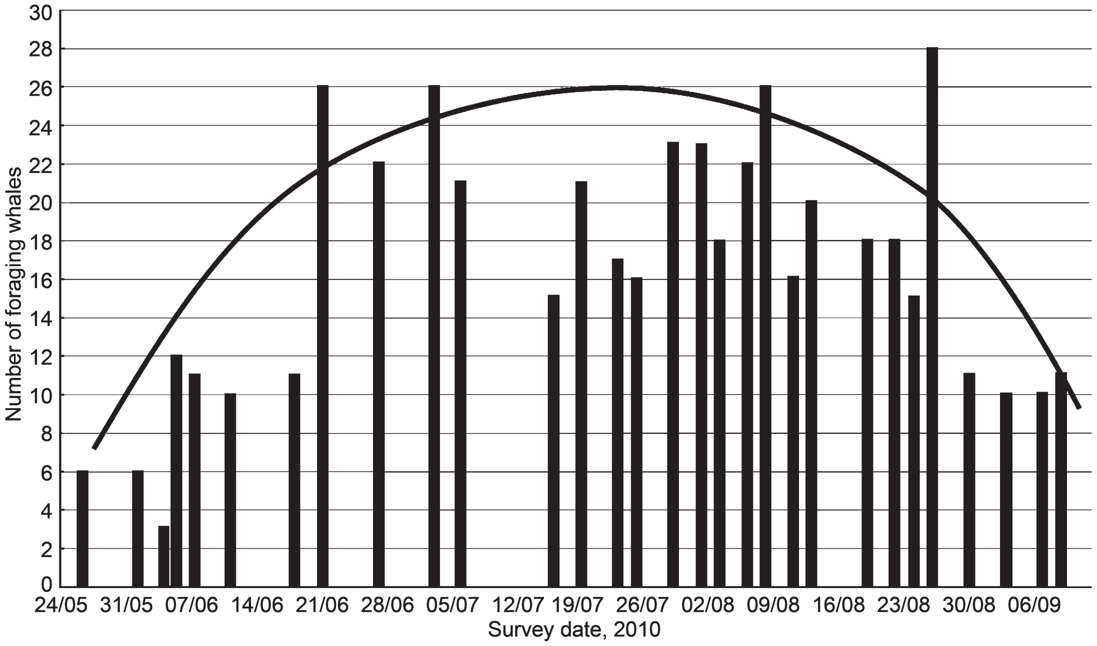


Fig. 3. Survey data of foraging whales from 2010, showing a negative skew and platykurtic distribution. Curve added to highlight skew to the left of the peak date.

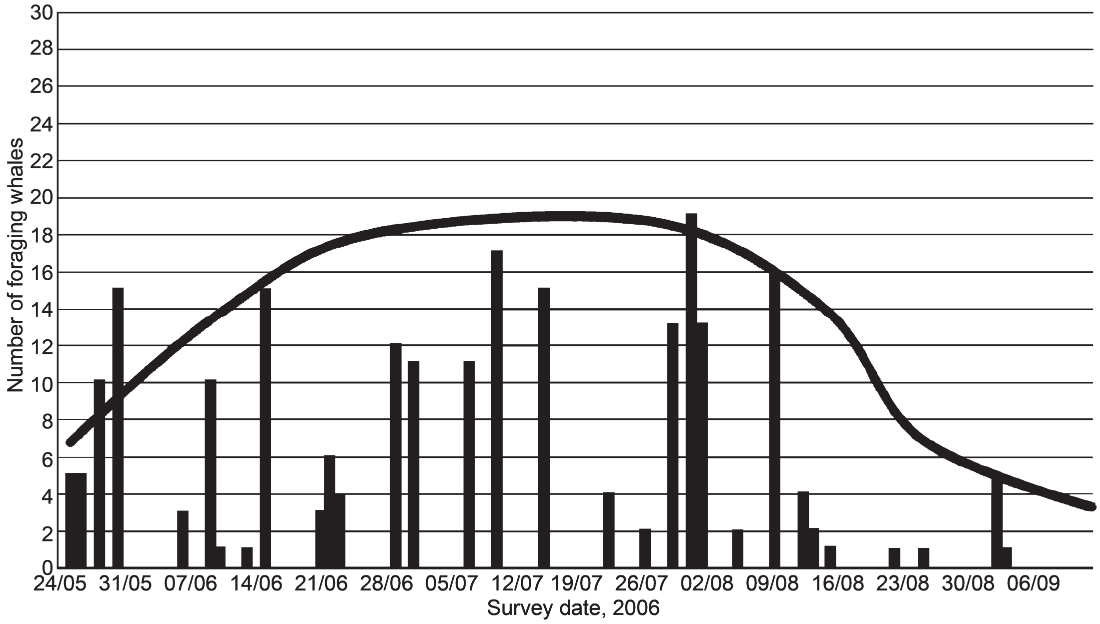


Fig. 4. Survey data of foraging whales from 2006, showing positive skew and platykurtic distribution. Curve added to highlight these features.

was particularly high in 1998, 2002 and 2006 (see Fig. 4) where the presence of foraging whales was predominantly pre-peak and rapidly dropped to almost complete site abandonment in some cases. For the other three years, more foraging whales were observed after the peak date. The relatively early peak date in late June, shaped the negative skew for 2007, despite whale numbers being low throughout the summer (see Fig. 5). For 2010 and 2011, the negative skew (much lower in 2010) was consistent with foraging continuing into the late season, peaking in August for both years (see Fig. 3).

For most (11 out of 17) years, summer distributions were platykurtic (Table 1). The distributions show a flat data spread and more consistent numbers of foraging whales over a longer time span (e.g. see Figs 3 and 4 for 2006 and 2010). This is contrasted to years where the whale presence is strongly focused around the peak date, e.g. 2009 (see Fig. 6).

Comparison of numbers of foraging whales in subsequent seasons

A regression analysis was performed on the mean number of whales foraging in the last two weeks of the season, (26 August–8 September) and then a similar period at the beginning of the subsequent season (24 May–6 June). The prediction was that intense foraging in the late season would depress early season prey stocks the following year and *vice versa*. The relationship was insignificant ($f = 0.376$, $p = 0.55$, $r^2 = 0.047$) and did not support the hypothetical expectation of dependence. Some of the confounding variables that may obscure such a relationship are discussed below.

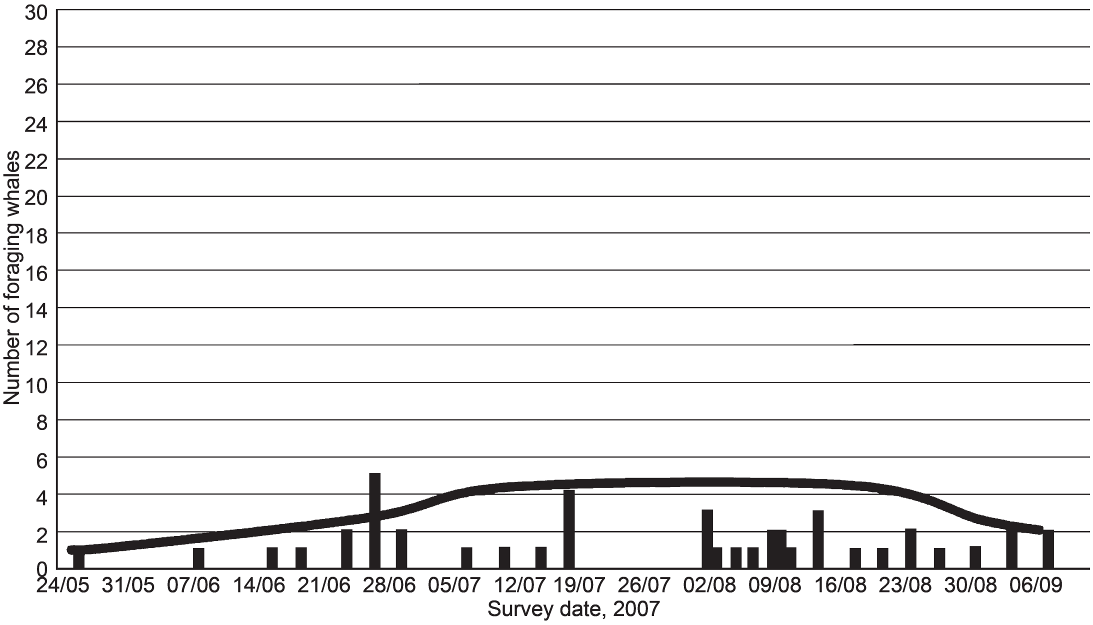


Fig. 5. Survey data of foraging whales from 2007, showing a negative skew and leptokurtic distribution. Curve added to highlight both skew and consistent distribution of whale observations.

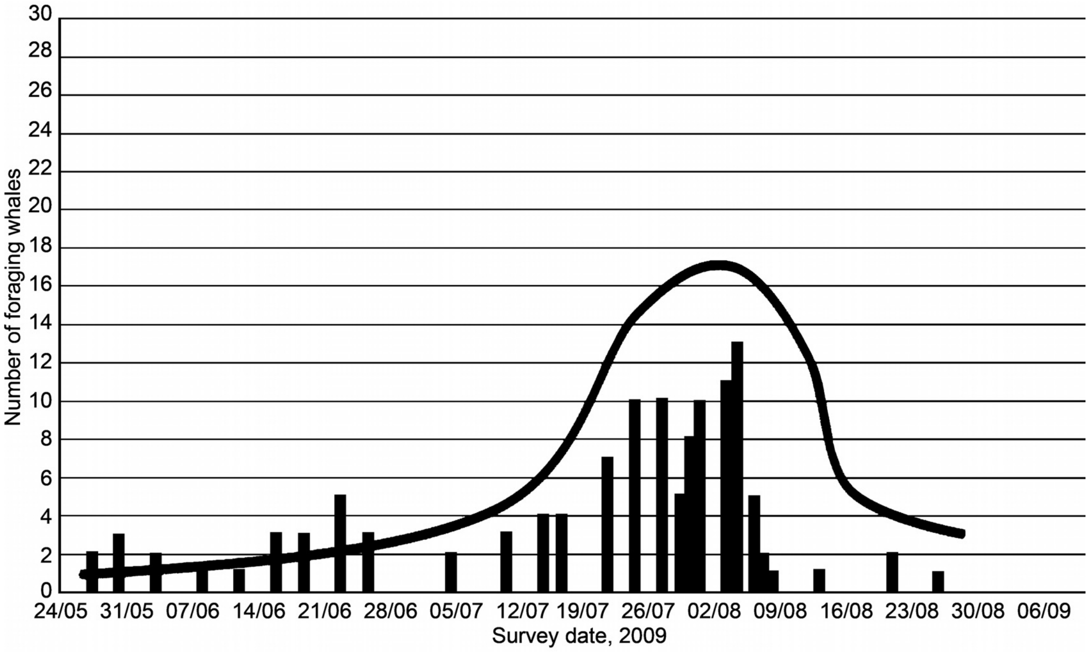


Fig. 6. Survey data of foraging whales from 2009, showing positive skew and leptokurtic distribution. Curve added to show how the data peaks around the peak data and just left of the peak.

Growth and reproduction of mysids

The growth and reproductive patterns of the four dominant mysid species (*Holmesimysis sculpta,* Tattersall, 1933; *Neomysis rayii,* Murdoch, 1885; *Telacanthomysis columbiae,* Tattersall, 1933; and *Columbiaemysis ignota*, Holmquist, 1892) were examined using the data collected from 2010–12. The mean length of individual mysids by 1mm size classes and the range of sizes were calculated (Figs 6–9). The length-frequency data were used to identify broods and growth, with the proportion of gravid females by species also quantified seasonally (Fig. 10). Mysid samples have gravid females in all seasons for the most numerically dominant species, but with distinct reproductive pulses. Brood production for many of the species present depends on warmer waters and increased productivity with juvenile release at the end of May, mid-June to early July and in late August to early September, with a fourth found for *H. sculpta* in November (Burnham, 2015). Average brood size for the species considered here is 50 (Feyrer, 2010a), with sexual maturity achieved in approximately 60 days (Mauchline, 1980; Wittman, 1984; Stelle, 2001; Mulkins *et al.,* 2002). Overwinter reproduction in *H. sculpta* represents a period where population recruitment, growth and maturation with removals from predators much reduced (Burnham, 2016).

DISCUSSION

The ability of gray whales to severely reduce benthic ampeliscid amphipod prey has been documented (Coyle

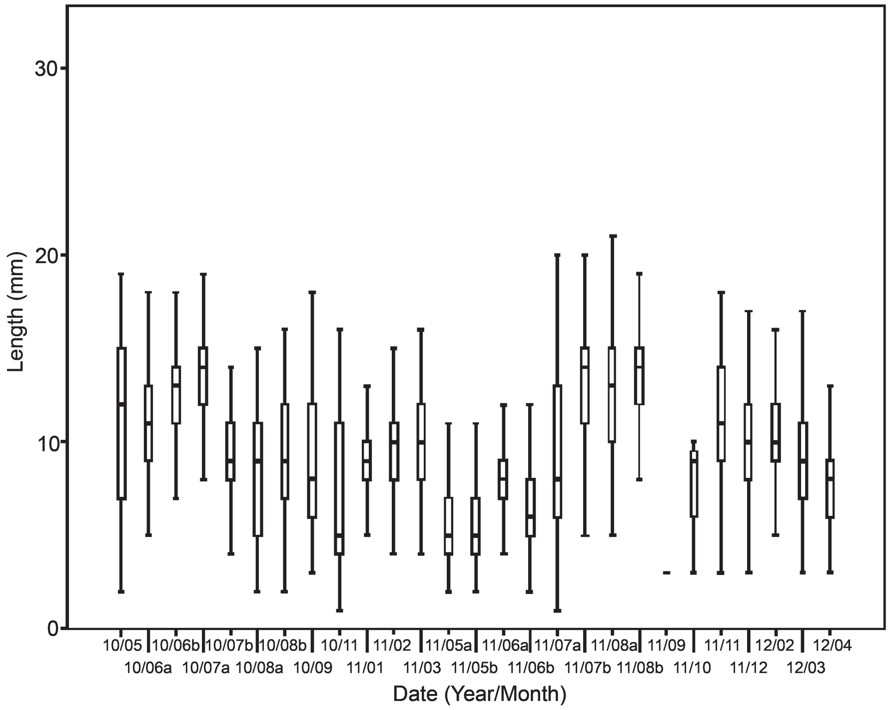


Fig. 7. Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Holmesimysis sculpta.*

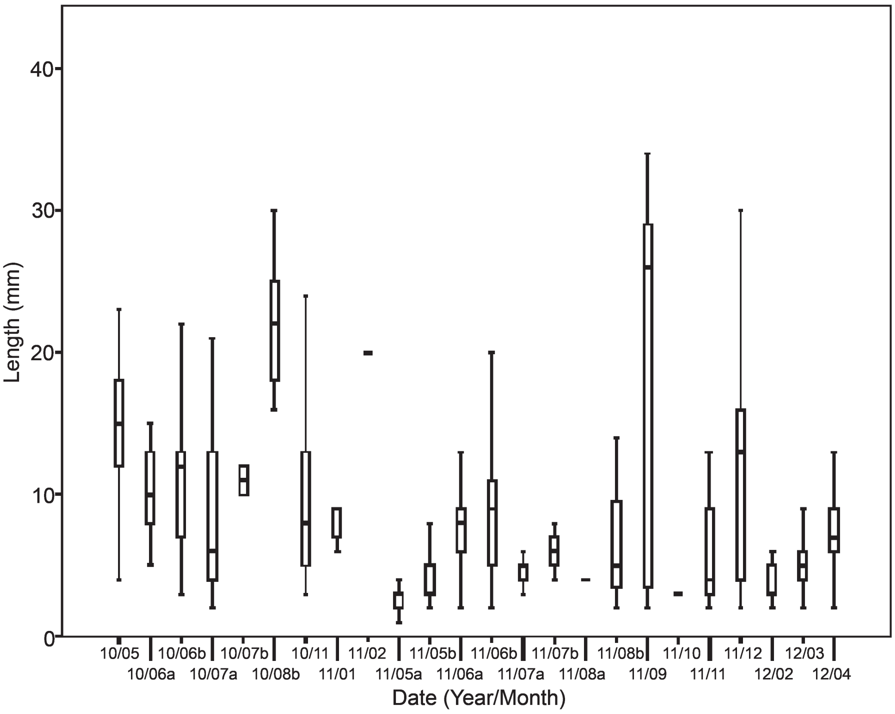


Fig. 8. Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Neomysis rayii.*

et al., 2007; Burnham and Duffus, 2016). Data presented here suggest that there is a similar capacity to depress epibenthic mysid prey although in this case, the prey populations have the capacity to recover. Predatory removal at sufficiently high levels will necessitate at least one summer season of high growth to re-establish swarms that again become a viable prey resource. The implication is that reprieve periods of low foraging for one to three years allowed mysid populations to rebuild, with three years required for reconstruction after the highest foraging years, except in the case of 2011, which remained high after 2010 (see Table 1). This differs from amphipods, which have long maturation times and singular reproductive events for individuals. Life histories and loss of niche space has hindered the repopulation of infaunal prey, despite a release from annual predation (Burnham and Duffus, 2016).

Between 2004 and 2009 there were three sets of consecutive years with descending foraging, where a year of higher foraging is followed by a year of lower whale numbers. For each of these cycles the average and peak number of whales

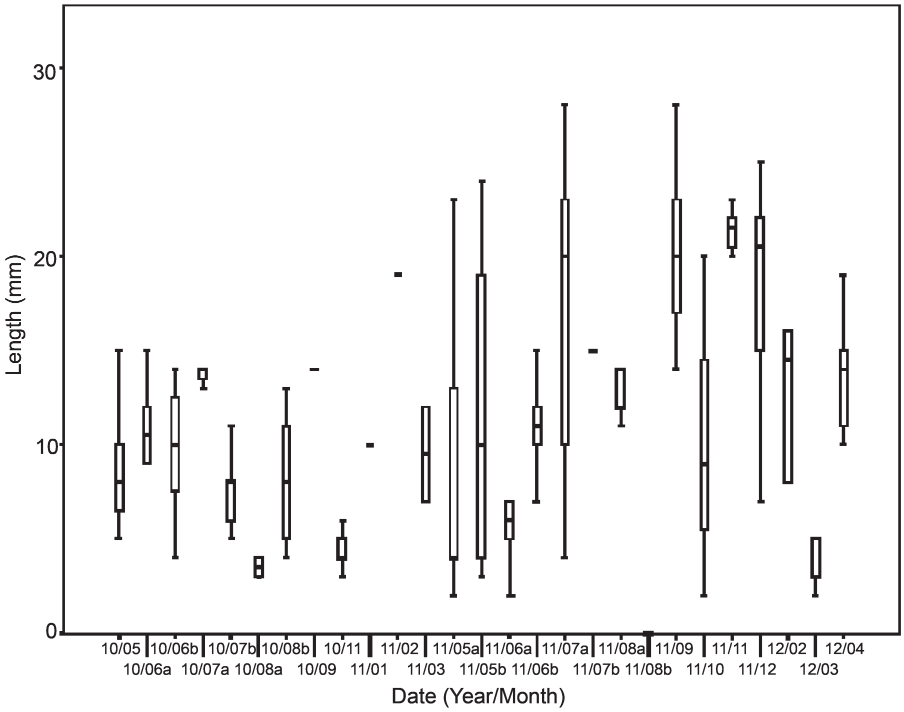


Fig. 9. Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Telacanthomysis columbiae.*

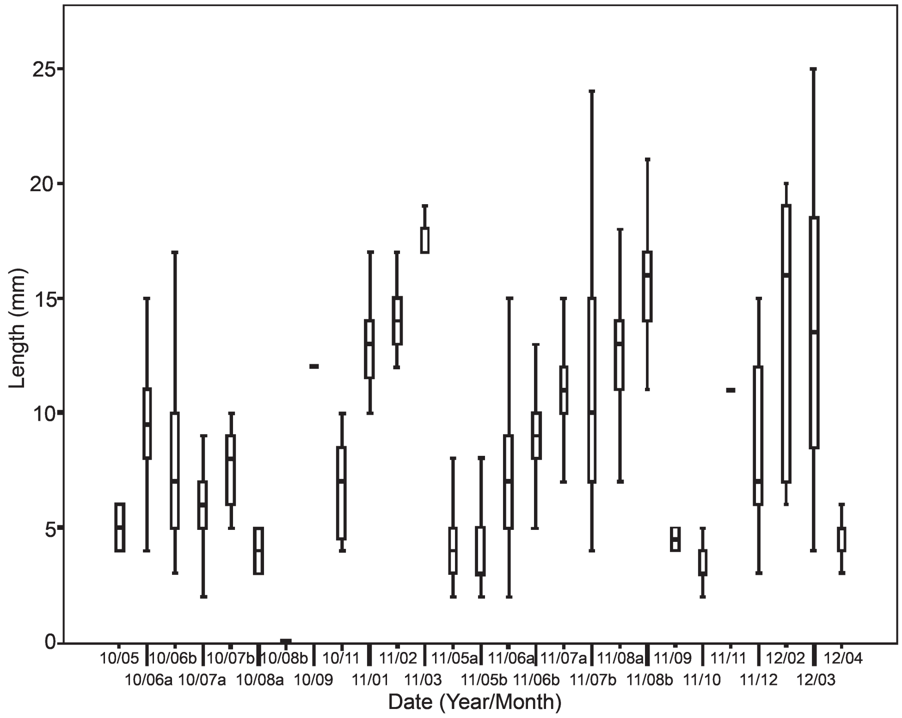


Fig. 10. Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Columbiaemysis ignota.*

for both the high and low year is approximately halved compared to the previous set (Fig. 2). The 2010 and 2011 data (i.e. two years of high numbers of foraging whales) are considered anomalous. Examination of external data revealed nothing unusual in the spring levels of primary production in this area at this time, or compared to coast-wide measurements (Feyrer, 2010b). This may support expanded prey populations, specifically those of *Holmesmysis sculpta*, the dominant species, which breeds overwinter and may have formed very large spring cohorts in the 2010–11 period.

In years where prey reserves do not exceed the 'threshold of interest' of predatory whales (see e.g. Bakun, 2006), lower foraging intensity can create a period of reprieve, allowing prey to reproduce with fewer losses. Once the resource recovers sufficiently, there will be a greater number of foraging whales in the following season(s). The cycling of prey population emulates 'predator-pit topography', where recovery, or 'breakout,' follows periods of prey 'refuge' and predator forced 'carnage' (Bakun, 2006). The data suggest a degree of 'boom-bust' cycling in foraging intensity,

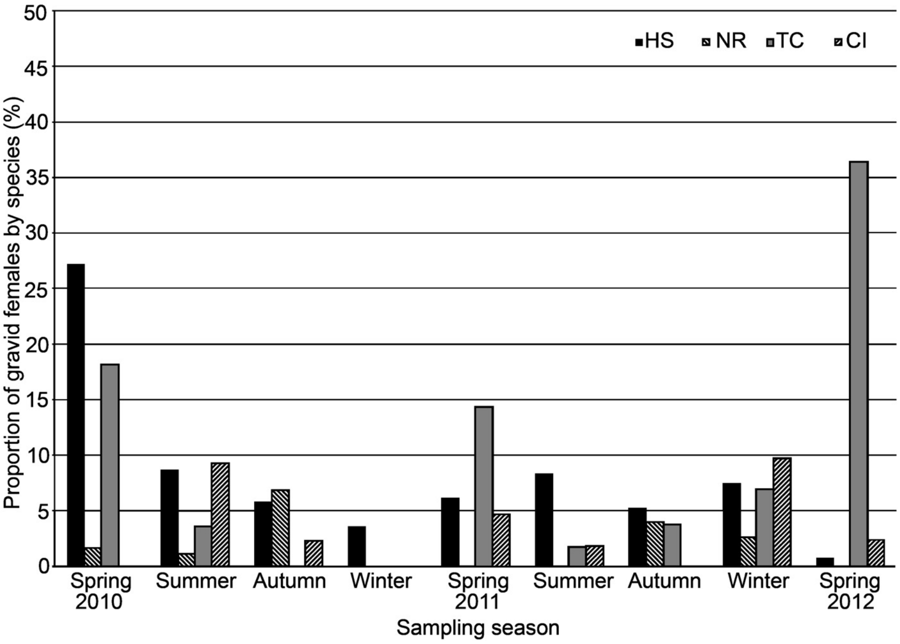


Fig. 11. Seasonal comparison of the percentage of gravid females per species for *H. sculpta* (HS), *N. rayii,*(NR) *T. columbiae* (TC) and *C. ignota* (CI). Spring: March, April, May; Summer: June, July, August; Autumn: September, October, November; Winter: December, January, February.

represented by the average number of whales foraging per survey (Table 1, Fig. 2) as well as the total annual number of foraging days that whales can be sustained by prey resources in Clayoquot Sound (Fig. 2). Years with intensified foraging compared to the global mean (boom) are followed by periods of reduced whale presence (bust) and so 1–3 years of 'refuge' for prey (see Table 1, Fig. 2). On only one occasion during the study period were there two consecutive high foraging years (2010 and 2011); and 2010 had the second highest mean value in the series behind the 2013 value (see Figs 2 and 3). These follow several years of depressed foraging. High foraging intensity was also seen in 2002 after the other extended low period (1999–2001; Fig. 2). Although number of whales does not have a direct relationship to prey presence, foraging pressure from whales has been established in this area as a reliable proxy for mysid abundance, both on a regional and site level. A foraging threshold on the prey-patch scale has been established, with feeding not seen to occur if mysid swarm density was below 2,300 mysids/m^3 (Feyrer and Duffus, 2014).

Skew and kurtosis are unconventional means of assessing the trophic consequences of foraging by apex-predators, but they do describe the temporal procession of foraging pressure within a season. The expectation was for a platykurtic distribution, showing near consistent foraging intensity through a summer based on recurring mysid reproduction. Assuming that the peak foraging date would lag slightly behind mysid brood production, the expectation was a slight positive skew relative to a late summer maximum.

All years, with the exception of 2007, 2010 and 2011, showed a positive skew, where foraging intensity built towards the peak date and then declined rapidly. We suggest that this is likely to be a function of predation i.e. after the heaviest foraging period, mysid numbers collapsed. In the cases of negative skew and a low foraging intensity (e.g. 2007), it is hypothesised that whales may have moved into the site to search for prey but found little and thus moved to other locations. They may or may not return later in the season, pulled by growing stocks in this site, or pushed by mysid collapses in alternate sites. In the case of 2010 (see Fig. 3) and 2011, the negative skew may be attributed to the prey resource being high throughout the summer, which suggests successful foraging was still possible late into the season. These two years show unprecedented mysid presence following a three-year period of depressed foraging (Fig. 2). The whales foraging in Clayoquot Sound are part of a population subgroup, the Pacific Coastal Feeding Group (PCFG; Calambokidis *et al.*, 2010; IWC, 2010), with individuals showing high site fidelity to feeding locales, as well as also foraging in sites adjacent. In our case, it is likely whales assess the relative prey presence in areas extending from Puget Sound to the central British Columbia coast (Calambokidis *et al.*, 2010).

The platykurtic nature of the distributions obscured the pattern of skew somewhat, where several increases in foraging intensity within a season were seen (e.g. 2006, Fig. 4). The leptokurtic years (2000, 2001, 2007, 2008, 2009, 2012, 2013) show predation centred around the peak date. For years with a lower average number of foraging whales, this represents the exploitation of a single brood in an otherwise prey limited environment (e.g. 2009, Fig. 6).

No significant relationship between the number of whales foraging in the last two weeks of a season to the first fortnight of the following season was detected. The interplay between inter- and intra-seasonal demands may be masking any pattern. It is likely here we are comparing low whale numbers after prey has been reduced from a summer of foraging, and then spring-early summer the following year where mysid broods are yet to have become viable prey for gray whales after a winter of little reproduction or growth (Burnham, 2015). In the late spring/early summer mysids are not an attractive resource to gray whales. The initial spring brood does not immediately form large dense swarms that attract whales, so this creates a period of repose for mysids. Broods produced later in the season show higher growth and swarm stabilisation and this attracts increased predation. Although mysid swarms matured as the season progressed, two months of foraging pressure in the mid-season on the progeny of two broods reduces mysid swarms by late summer, becoming once more insufficient as a prey resource. This deduction was supported by both the positive skew in the data and gray whale foraging peaking from mid to late summer (see Table 1). More detailed work on the life cycles of the mysid species present in the area, particularly the four species discussed here, have confirmed this (Burnham, 2015). However, for years with high numbers of foraging whales and a platykurtic distribution (e.g. 2010, 2011) the data suggested that prey was available in large swarms and sufficient biomass to attract whales for an extended period.

On both intra- and inter-seasonal scales, predator presence was linked to prey abundance, although the proliferation of prey was in turn linked to the previous year's predation. Gray whales have shaped their own prey abundance with mediation by the reproductive behaviour of the prey. Reproduction and recovery of mysid populations took place in periods of light foraging, heavy foraging and in the absence of foraging in a period of predator reprieve. These mixed processes each with their own success, go some way to buffer the effect of one summer's prey removals to the next.

The whales themselves have a buffer which allows them to easily move from poor quality to higher quality prey sites. Thus, it is quite likely that other sites to the north and south are linked. The interesting outcome of this study is that where there are physical situations similar to Clayoquot Sound along the west coast, some similar ecological narratives may be occurring. Not every headland/bay system with rocky reefs has records of foraging whales in recent times. This study proposes the possibility that whales may be a cause of longer-term ecological change to these sites where predatory behaviour exceeds prey resilience. Longer time spans of observation and prey analysis are necessary to further this study's findings.

ACKNOWLEDGEMENTS

Thanks to the crew of the Whale Lab past and present. Thoughtful comments made by Jim Sumich on the manuscript were also appreciated. Research was conducted in the traditional territory of the Ahousaht First Nation, with support from the community and the late Chief Earl George. From Ahousaht particular thanks go to Hughie and Keith Clarke and families.

REFERENCES

Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: Navigating the 'predator pit' topographies. *Prog. Oceanogr.* 68: 271–88.

Burnham, R.E. 2015. Reproductive strategies conferring species dominance in marine mysid (Peracarida, Mysida) species in coastal waters off Vancouver Island, BC. *Crustaceana* 88: 1,421–1,438.

Burnham, R.E. and Duffus, D.A. 2016. Gray whale (*Eschrichtius robustus*) predation and the demise of amphipod prey reserves in Clayoquot Sound, British Columbia. *Aquat. Mamm.* 42(2): 123–126.

Calambokidis, J., Laake, J.L. and Klimik, A. 2010. Abundance and population structure of seasonal gray whales in the Pacific Northwest 1978–2008. Paper SC/62/BRG32 presented to the IWC Scientific Committee, June 2010, Agadir, Morocco (unpublished). 50pp. [Paper available from the Office of this Journal].

Coyle, K.O., Bluhm, B., Konar, B., Blanchard, A. and Highsmith, R.C. 2007. Amphipod prey of gray whales in the northern Bering Sea: Comparison of biomass and distribution between the 1980s and 2002–1003. *Deep Sea Res. II* 54: 2,906–18.

Duffus, D.A. 1996. The recreational use of gray whales in southern Clayoquot Sound, Canada. *Appl. Geogr.* 16: 179–90.

Dunham, J.S. and Duffus, D.A. 2001. Foraging patterns of gray whales in central Clayoquot Sound, British Columbia, Canada. *Mar. Ecol. Prog. Ser.* 223: 299–310.

Dunham, J.S. and Duffus, D.A. 2002. Diet of gray whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia, Canada. *Mar. Mammal Sci.* 18(2): 419–37.

Feyrer, L.J. 2010a. Differences in embryo production between sympatric species of mysids (family *Mysidae*) in the shallow coastal waters off Vancouver Island, BC. *Mar. Biol.* 157(11): 2,461–5.

Feyrer, L.J. 2010b. The foraging ecology of gray whales in Clayoquot Sound: Interactions between predator and prey across a continuum of scales. Masters Thesis, Department of Geography. University of Victoria, Victoria, British Columbia.

Feyrer, L.J. and Duffus, D.A. 2014. Threshold foraging by gray whales in response to fine scale variations in mysid density. *Mar. Mam. Sci.* 31(2):19.

Hatler, D.F. and Darling, J.D. 1974. Recent observations of the gray whale in British Columbia. *Can. Field Nat.* 88: 449–59.

Highsmith, R.C., Coyle, K.O., Bluhm, B.A. and Konar, B. 2006. Gray whales in the Bering and Chukchi seas. pp.303–313. *In*: J.A. Estes, D.P. DeMaster., D.F. Doak, T.M. Williams and R..L. Brownell, Jr. (Eds) *Whales, Whaling, and Ocean Ecosystem*s. University of California Press; Berkeley, CA:

International Whaling Commission. 2010. Chair's Report of the 62nd Annual Meeting. Annex G. Report of the Standing Working Group on the Aboriginal Whaling Management Plan (AWMP). *Ann. Rep. Int. Whal. Commn 2010*: 80–87. [Retrieved on 20 April 2014 from *https://iwc.int/annual-reports-iwc*]

Kathman R.D., Austin W.C., Saltman J.C. and Fulton J.D. 1986. Identification manual to the *Mysidacea* and *Euphausiacea* of the northeast Pacific. *Can. Spec. Publ. Fish. Aquat. Sci.* 93: 411pp.

Laskin, D., Duffus, D.A. and Bender, D.J. 2010. Mysteries of the not so deep: An investigation into gray whale habitat use along the west coast of Vancouver Island, British Columbia. pp.105–20. *In*: J. Breman (ed.). *Ocean Globe*. ESRI Press. Redlands, California.

Malcom, C.D. and Duffus, D.A. 2000. Comparison of subjective and statistical methods of dive classification using data from a time-depth recorder attached to a gray whale (*Eschrichtius robustus*). *J. Cetacean Res. Manage.* 2(3): 177–82.

Mauchline, J. 1980. The biology of mysids and euphausiids. *Ad. Mar. Bio.* 18: 3–681.

Mulkins, L.M., Jelinski, D.E., Karagatzides, J.D. and Carr, A. 2002. Carbon isotope composition of mysids at a terrestrial-marine ecotone, Clayoquot Sound, British Columbia, Canada. *Estuar. Coast. Shelf. S.* 54(4): 669–75.

Oliver, J.S. and Slattery, P.N. 1985. Destruction and opportunity on the sea floor: effects of gray whale feeding. *Ecol.* 66(6): 1,965–75.

Short, C.J. 2005. A multiple trophic level approach to assess ecological connectivity and boundary function in marine protected areas: a British Columbia example. Masters Thesis, Department of Geography, University of Victoria, Victoria, British Columbia. [Available at: *https://dspace.library.uvic.ca/handle/1828/617?show=full*].

Sokal, R.R. and Rohlf, F.J. 1981. *Biometry: The Principles and Practices of Statistics in Biological Research*. 2nd ed. W.H. Freeman and Co., San Francisco. 895pp.

Stelle, L.L. 2001. Behavioural ecology of summer resident gray whales (*Eschrichtius robustus*) feeding on mysids in British Columbia, Canada. PhD thesis, University of California, Los Angeles California USA. 166pp.

Turpen S., Hunt J.W., Anderson B.S. and Pearce, J.S. 1994. Population structure, growth, and fecundity of the kelp forest mysid *Holmeimysis costata* in Monterey Bay, California. *J. Crustacean Biol.* 14: 657–63.

Wittmann, J.K. 1984. Ecophysiology of marsupial development and reproduction in Mysidacea (*Crustacea*). *Oceanog. Mar. Biol.* 22: 393–428.

Strandings of dolphins in the Adelaide Dolphin Sanctuary, South Australia

S.K. Adamczak[1], C. Kemper[2] and I. Tomo[2]

Contact e-mail: steph.adamczak@gmail.com

ABSTRACT

The Adelaide Dolphin Sanctuary was gazetted in 2005 to protect a resident population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) that lives in a heavily impacted urban environment. This study assesses the numbers and types of strandings before and after the creation of the sanctuary. Monitoring took place during 1987–2013, when 57 events were reported and 53 carcasses were examined by post-mortem. Events were assigned to a circumstance of death that combined post-mortem results and/or anecdotal information. The majority of records were Indo-Pacific bottlenose dolphins ($n = 47$, 82%) but a few common dolphins (*Delphinus delphis*, $n = 7$, 12%) were also documented. Many ($n = 19/46$, 41%) of the Indo-Pacific bottlenose dolphins were 1 year old or less. Strandings averaged 2.19 per annum for all dolphin species and 1.80 for Indo-Pacific bottlenose dolphins. When pre- ($n = 20$) and post-sanctuary ($n = 27$) data were compared for Indo-Pacific bottlenose dolphins, anthropogenic events decreased from 30% ($n = 6/20$) to 7% ($n = 2/27$) and no intentional (illegal) killings or entanglements were recorded after 2004. Unintentional anthropogenic mortalities were primarily boat collisions ($n = 4$ out of 5 cases). Disease was the most frequently recorded circumstance of death ($n = 21$) and although the number of cases increased after 2004, this may have been due to improved pathology investigations. Live strandings were rare during the study ($n = 2$). Despite a significant increase in overall dolphin mortalities pre- and post-sanctuary, the number of human-induced mortality events decreased significantly. Continued monitoring and post-mortems of carcasses is recommended for managing dolphins in the sanctuary.

KEYWORDS: AUSTRALASIA; INDO-PACIFIC BOTTLENOSE DOLPHIN; SANCTUARIES; REGULATIONS; CONSERVATION

INTRODUCTION

Cetaceans are iconic species that are protected by law in most western countries yet are still under threat due to human activities. Unintentional mortalities can result from entanglement in fishing and other gears and from vessel collisions, both of which are believed to be leading causes of cetacean mortality worldwide (e.g. Reeves *et al.*, 2013; Thomas *et al.,* 2016; Van Waerebeek *et al.*, 2007). In order to mitigate these interactions, some countries have introduced legislation to reduce vessel speeds (Read, 2000; ASCOBANS, 2015) and reduce and monitor bycatch through improved fisheries reporting (Read, 2000). The creation of marine protected areas in which there are effective mitigation measures can also assist cetacean conservation (Hoyt, 2005; Gormley *et al.*, 2012). Marine protected areas specifically designed to protect cetaceans have increased since the early 2000s (Hoyt, 2005).

Ecosystem-based management is the most effective strategy for marine protected areas, including those focused on cetaceans (Hoyt, 2005). This approach attempts to meet the needs of the environment while addressing the impacts of human activities (Hooker and Gerber, 2004). Cetaceans can benefit from these integrative strategies if the protected area is properly managed (Bearzi, 2012). Although cetaceans have not historically been the focus of protected areas, management plans have increasingly included them as important components of the ecosystem. Examples include the Moray Firth Special Area of Conservation in Scotland (Cheney *et al.*, 2014) and the Pelagos Sanctuary in the Mediterranean (Hoyt, 2005). In 2005, the Adelaide Dolphin Sanctuary Act (2005) was established to protect a resident population of Indo-Pacific bottlenose dolphins and its habitat, including Barker Inlet and adjacent waters of Gulf St. Vincent (DEWNR, 2007).

Management of the Adelaide Dolphin Sanctuary (ADS) adopts an integrative and passive management approach, meaning that the sanctuary is monitored but not heavily regulated as activities such as shipping and fishing are still allowed (DEWNR, 2008). Community engagement and education on the ADS raise awareness of conservation issues and well-trained volunteers act as wardens of the sanctuary. Wardens assist with boat patrols, perform land-based and boat-based surveys of dolphins and conduct surveys on human attitudes toward the sanctuary. Non-government organisations have also been actively involved in studying and protecting the dolphins. The lead agency in sanctuary management is the South Australian Department of Environment and Water, with support from other government departments (DEWNR, 2008).

The target species of the ADS is the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*). However, common bottlenose dolphins (*Tursiops truncatus*) and common dolphins (*Delphinus delphis*) are also frequently recorded in South Australia. Common bottlenose dolphins inhabit the open ocean coast outside Gulf St. Vincent and common dolphins occur within the gulf but away from the coast (Kemper *et al.*, 2008). About 30 resident Indo-Pacific bottlenose dolphins live in the sanctuary, with an additional 20 transients from nearby regions at any one time (Kemper *et al.,* 2008).

A South Australian stranding network began in the early 1990s and has resulted in a database that contains almost 2,000 records. These data have been summarised in several publications related to circumstance and cause of death (Kemper *et al.*, 2005; Tomo *et al.*, 2010; Segawa

---

[1] *School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, New York, USA.*
[2] *South Australian Museum, North Terrace, Adelaide, South Australia, Australia 5000.*

and Kemper, 2015). The most frequent anthropogenic circumstance/cause of death was entanglements in fishing and aquaculture nets and lines, which accounted for 17% of all cetacean mortalities examined by the South Australian Museum (SAM) (Kemper *et al.*, 2005). Common dolphin entanglement mortalities in the purse seine South Australian Sardine Fishery numbered 377 in one year, prior to the adoption of a code of practice (Hamer *et al.*, 2008). In addition, many entanglements have occurred as a result of the tuna feedlot industry (Kemper and Gibbs, 2001). Other types of unintentional anthropogenic mortalities, such as boat collisions, were much less frequent than entanglements in South Australia (Segawa and Kemper, 2015). Intentional (illegal) killings accounted for only 5% of mortality from 1881 to 2000 and some regions, including Adelaide, were noted as problematic (Kemper *et al.*, 2005). Non-anthropogenic mortalities made up 58% of records, with disease, live strandings and other natural causes being noted (Segawa and Kemper, 2015). Tomo *et al.* (2010) considered that lung nematode infections were an important cause of mortality in common dolphins, especially during 2005–2006. In 2013, an Unusual Mortality Event (UME) occurred in Gulf St. Vincent, which was linked to morbillivirus infection in bottlenose dolphins (Kemper *et al.*, 2016).

There has been no published assessment of dolphin mortalities focusing on the Adelaide region. The present study analyses patterns of live strandings and mortalities of Indo-Pacific bottlenose dolphins in the ADS. It provides a baseline for future comparison and a preliminary assessment of the efficacy of management by comparing circumstance of death before and after the sanctuary was created.

METHODS

The ADS is located on the eastern shore of Gulf St. Vincent and includes the lower reaches of the Port River, Barker Inlet and coastal waters to the north (Fig. 1; DEWNR, 2007). The 118km^2 sanctuary incorporates mangroves, tidal flats, salt marshes, seagrass beds and tidal creeks (DEWNR, 2007). The adjacent terrestrial environment is urbanised and industrial. The metropolitan centre of Adelaide (population 1.2 million) is nearby and the banks of the Port River contain important infrastructure, such as a wastewater treatment plant (Fig. 1). The port is the busiest in South Australia, with 2,000 large vessel (approximately 50 to 300m length overall) movements annually (DEWNR, 2008). Water depth ranges from 2 to 16m and the tidal range in the Gulf St. Vincent is approximately 3m (Kämpf *et al.*, 2009). A study conducted by Bossley *et al.* (2017) separated the estuary into two areas. The 'Outer Estuary' was designated as the portion of the estuary in contact with Gulf St. Vincent, which shared similar water quality and the 'Inner Estuary' was the area exposed to a high amount of anthropogenic inputs such as wastewater and heat effluent (Fig. 1; Bossley *et al.*, 2017).

Dolphin strandings, including live strandings and carcasses, were recorded from the sanctuary region during 1987–2013 by SAM. Of 57 documented events, 53 carcasses were collected for post-mortem examination. Species identifications were verified using photographs (in the case of dolphins not collected) and skulls of those collected. When insufficient information was available to identify species, the terms 'bottlenose dolphin' (*Tursiops* sp.) or 'dolphin' were applied.

The SAM and associates improved the pathology findings gained from post-mortems after 2004 when a wildlife pathologist (IT) joined the team. Routine procedures included external and internal examination and photographs, body measurements, gross and histopathology and bacteriological and virological testing. Reproductive organs were collected to determine sexual maturity status and stomach contents were examined for diet and ingested foreign bodies. In most cases, full skeletons were collected and prepared by warm-water maceration.

Relative age was determined for necropsied dolphins using developmental features, body length, sexual maturity and physical maturity of the skeleton (Kemper and Gibbs, 2001). For dolphins that were not collected, neonates could be identified when photographs showed foetal folds and calves could be identified if body length was available. Estimated age of Indo-Pacific bottlenose dolphins was determined by counting incremental layers in the dentine of decalcified, thin-sectioned and stained teeth (Evans *et al.*, 2011). Two teeth were examined for each dolphin and three sets of estimates were made by at least two readers. A mean was calculated to obtain an overall age estimate for each dolphin. The number of GLGs (growth layer group) deposited per annum was assumed to be one.

Strandings were assigned to one of eight categories relating to the reported circumstances surrounding them and results of post-mortem, if performed. These categories were:

(1) Intentional Killing: Intentional harm by humans causing death, such as shotgun or knife wounds.

(2) Other Unintentional: Unintentional/accidental anthropogenically-related deaths such as boat-strikes or propeller wounds.

(3) Entanglement: Dolphin removed from fishing or aquaculture gear or remains of gear found on carcass.

(4) Probable Entanglement: Evidence of entanglement (net marks and body slit or mutilated by human or physiological evidence of entanglement) but without the presence of gear.

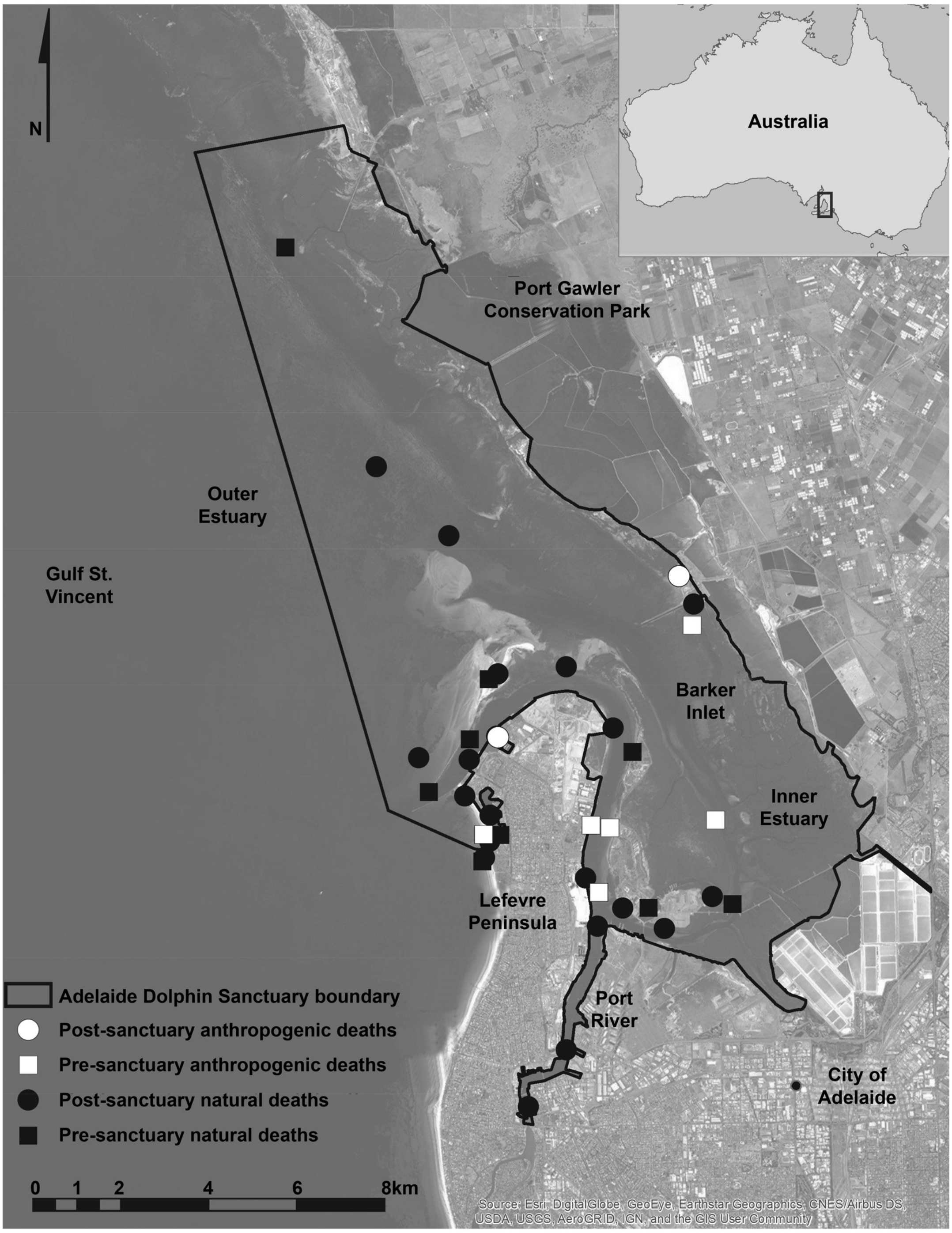
(5) Disease: Deaths related to disease, such as pneumonia or infections.

(6) Other Natural: Natural deaths not related to disease, such as starvation, choking on shark and neonatal death.

(7) Live Stranding: Seen alive on the beach and either died there or was euthanised.

(8) Unknown: No cause of death could be identified.

The first four categories were considered anthropogenic circumstances because they were directly and demonstrably related to human activities. The Other Unintentional category is comprised of accidental mortalities resulting from human activities, such as injuries incurred from boats (Kemper *et al.*, 2005). The categories Disease, Other Natural and Live Stranding were treated as a natural circumstance of death, although the authors note that anthropogenic pollutants can lead to immunosuppression in cetaceans (Isobe *et al.*, 2011).



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Fig. 1. Map of study area showing Indo-Pacific bottlenose dolphin strandings divided into non-anthropogenic mortalities (Stranding, Other Natural, Disease) pre-sanctuary ($n = 9$) and post-sanctuary ($n = 20$) and anthropogenic mortalities (Other Unintentional, Entanglement, Intentional Killing) pre-sanctuary ($n = 6$) and post-sanctuary ($n = 2$).

Statistical tests were computed using the default statistics package in R (R Development Core Team, 2016). Pearson's Chi-square test was used to compare sexes and anthropogenic versus non-anthropogenic strandings, both pre-and post-sanctuary. An F-test showed that there were unequal variances between pre- and post-sanctuary annual counts of events, therefore a non-parametric Wilcoxon signed rank test was used. Cases classified as unknown were not included in statistical analyses.

RESULTS

The total number of strandings recorded within the sanctuary during 1987–2013 was 57 (Table 1). Most individuals were bottlenose dolphins ($n = 48$), of which the majority ($n = 47$) were verified as Indo-Pacific bottlenose dolphins. Strandings were clustered around the Lefevre Peninsula and the western part of Barker Inlet (Fig.1), where there was considerable human activity. Six out of the seven common dolphins were outside Barker Inlet and the Port River. There appeared to be no clear geographic pattern of strandings related to pre- and post-sanctuary, nor anthropogenic and non-anthropogenic circumstances (Fig. 1), although sample size is small. The assumption made in this paper is that carcasses were found close to where the dolphins died.

Of the Indo-Pacific bottlenose dolphins aged by tooth preparations, the oldest was 23 years and individuals 1 year

Table 1

Strandings of dolphins in the Adelaide Dolphin Sanctuary before (1987–2004) and after (2005–13) its gazetting. Number of carcasses that were not collected are in parentheses and included in the number to the left.

Species	1987–2004	2005–3
T. aduncus	20 (0)	27 (2)
Tursiops sp.	1 (1)	0 (0)
D. delphis	4 (0)	3 (0)
Unidentified dolphin	27 (3) 1.59/year	30 (2) 3.75/year

Table 2

Number of Indo-Pacific bottlenose dolphins in five relative age classes before (1987–2004) and after (2005–13) the Adelaide Dolphin Sanctuary was gazetted. Estimated ages were calculated for 34 dolphins using tooth structure. Range of ages for each relative age group refer to both time periods.

Relative age group	1987–2004	2005–13	Range of estimated age
Neonate	6	5	< 3 months
Calf	2	6	3 months to 1 year
Juvenile	5	8	≤ 1–15 years
Subadult	0	1	6 years
Adult	7	6	13–23 years
Total	**20**	**26**	

old or less represented the majority (*n* = 19/46, 41%) of dolphins collected both pre-and post-sanctuary (Table 2). Strandings for each relative age group did not differ between these time periods. In addition, of the dolphins that could be sexed, 28 were male and 19 were female, not statistically different from an equal sex ratio ($\chi^2 = 3.8$, $p > 0.05$).

Table 3 summarises the results for Indo-Pacific bottlenose dolphins during the period of study (annual means and raw numbers). There was a slight overall increase in annual counts of strandings, with the highest number occurring in 2013 (Fig. 2). When the means of the annual counts for 1987–2004 (1.11) and 2005–2013 (3.00) were compared, the result was statistically significant (W = 40.5, $p < 0.05$). However, because 2013 was exceptional due to an UME and 4 of the 8 deaths recorded that year were attributed to disease the test was performed a second time, excluding that year. The revised annual mean for 2005–2012 (2.25) was not significantly different from that pre-sanctuary (W = 40.5, $p > 0.05$).

The mean annual number of strandings assigned to anthropogenic factors for Indo-Pacific bottlenose dolphins during 1987–2013 was 0.31. When pre- and post-sanctuary data were compared, there was a significant difference in the proportion of anthropogenic and non-anthropogenic strandings ($\chi^2 = 5.028$, $p < 0.05$). The number of anthropogenic cases decreased (*n* = 6 pre-sanctuary – annual mean = 0.33, *n* = 2 post-sanctuary – annual mean = 0.22) while non-anthropogenic cases increased (*n* = 9 pre-sanctuary, *n* = 20 post-sanctuary). No Probable Entanglements were recorded during the study period. Prior to 2005, the category Intentional Killing comprised two dolphins shot with shotguns, both in 1998, and there was one reported entanglement in a fishing line in 1987. There were no reported cases of Intentional Killing or Known Entanglement in the period 2005–2013.

The mean annual number of Other Unintentional cases was slightly higher post-sanctuary (0.17 vs 0.22 but with very small sample sizes (Table 3). During the whole study period, the majority (4/5) of Other Unintentional events were boat-related, usually evidenced by propeller wounds. The remaining event classified as Other Unintentional involved a fish hook and sinker found in a dolphin's mouth in 2000.

The mean number of Other Natural strandings increased post-sanctuary (0.22 vs 0.44) as did Live Stranding events (0.06 vs 0.11) but in all cases sample sizes are very small and do not lend themselves to statistical analysis (Table 3). One dolphin had a small number of shotgun pellets embedded in its blubber, but its death was attributed to multi-organ infection that did not appear to be directly related to the shooting. The mean number of disease-related events increased post-sanctuary (0.22 vs 1.89) dominated by the UME in 2013 (Table 3). Most (11/21) Disease events were caused by infections, of which 3 were lung infections and 4 were multi-organ infections, while other events in this category included numerous illnesses ranging from renal failure to cardiac failure.

DISCUSSION

Despite the recent rise in popularity of cetacean-based marine protected areas (Hoyt, 2005), there has been limited

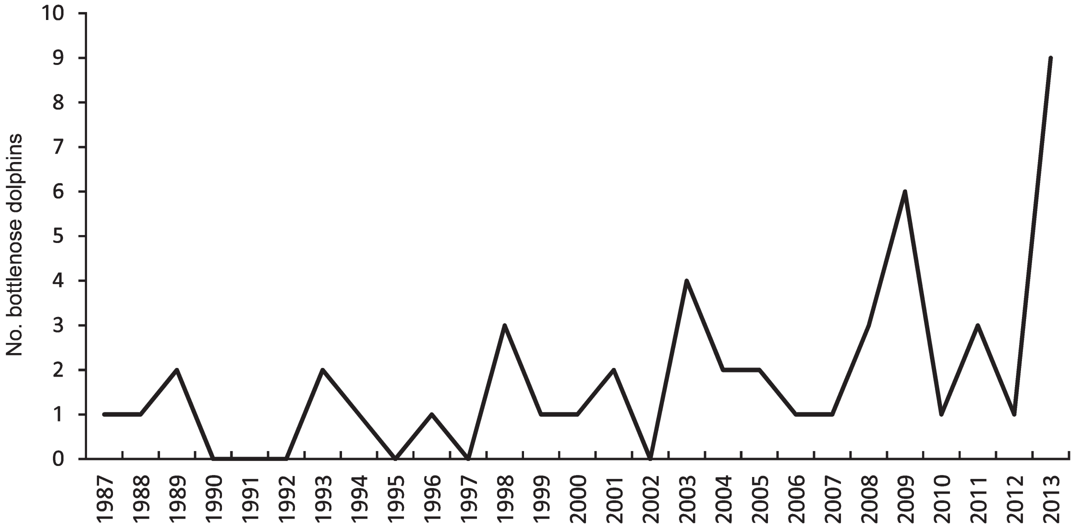


Fig. 2. Number of Indo-Pacific bottlenose dolphin strandings each year in the Adelaide Dolphin Sanctuary, South Australia.

Table 3

Number of Indo-Pacific bottlenose dolphins related to circumstance of death in the Adelaide Dolphin Sanctuary, South Australia before (*n* = 20) and after (*n* = 27) gazetting.

Circumstance of death	1987–2004	2005–13
Unknown	5	5
Anthropogenic		
Intentional killing	2	0
Entanglement	1	0
Other unintentional	3	2
Non-anthropogenic		
Disease	4	17
Other natural	4	2
Live stranding	1	1

research evaluating their effect (Hooker and Gerber, 2004; Cheney *et al*., 2014). It is argued that cetaceans can benefit from protected areas (Hooker and Gerber, 2004; Bearzi, 2012), but studies have reported conflicting results (Gormley *et al*., 2012; Cheney *et al*., 2014). It is essential that an appropriate level of monitoring is in place to allow robust evaluation as to whether mitigation measures are working and to inform changes required if they are found not to be working.

Increased public awareness, and therefore reporting effort, is another possible bias and this is important to consider when using opportunistically collected data (Segawa and Kemper, 2015).

This initial study of ADS strandings is a first step in this process. Some time-related factors also influence the ability to use the present dataset to examine changes. For example, the post-2005 dataset was skewed by 2013, when an UME occurred (Kemper *et al.,* 2016). In addition, an increase in bottlenose dolphin abundance within the sanctuary area around 2004 has been reported (Bossley *et al*., 2017) that affects statistics related to the proportion of animals in a population that may be affected by anthropogenic factors. There is also the possibility that increased effort may affect trend investigations using strandings data.

In summary, it can be noted that in terms of the present dataset, no significant changes were found in most parameters examined before and after creation of the sanctuary. However, it is recognised that the sample sizes are small, the time period is relatively short and there are issues related to effort (and numbers of animals present) that render our dataset at present not adequate to detect what may be small changes. Notwithstanding this, the reduction in strandings associated with anthropogenic factors provides preliminary evidence that the ADS may be having some positive effect.

Actual and potential threats within the ADS

Notwithstanding sample size issues, the data presented here provide information on some of the types of threats that need to be considered within the ADS, including:

(1) deliberate harm;

(2) injuries/death arising from depredation;

(3) entanglement in lines;

(4) vessel collisions; and

(5) factors that may make animals more susceptible to disease, such as contaminants.

It is encouraging that no Intentional Killings have been recorded since they were initially reported in 1998. In 2000, a multi-disciplinary team was established to investigate mortalities and promote the need for public vigilance regarding intentional harm to dolphins. This may have acted as a deterrent, though some dolphins have been shot north of the ADS. The motivation for killing dolphins is not known but studies from elsewhere have shown that fishers may react aggressively to actual or perceived depredation including frightening fish away from lines and nets (Notarbartolo di Sciara and Bearzi, 2002; Lauriano *et al.*, 2004; Loch *et al.*, 2009).

Recreational line fishing is a popular activity in the ADS (DEWNR, 2008). Elsewhere it has been identified as a major concern for inshore dolphins (Wells *et al.*, 1998; Powell and Wells, 2011). In the present study, one dolphin died with a fish hook and sinker in its mouth and this could have been a result of depredation of fish from recreational fishing activities. Studies have shown that this type of foraging activity can spread through a population rapidly (Donoghue *et al.*, 2002; Cunningham-Smith *et al.*, 2006). Although this event occurred in 2000 and similar mortality events have not been recorded since, dolphins in the ADS may still be partaking in this behaviour. Depredation, begging and provisioning behaviours tend to increase when prey are depleted (Wells, unpublished data in Powell and Wells, 2011). Studies of stomach contents have found atypical prey items (i.e. chicken bones) in some dolphins from the ADS and surrounding waters, possibly due to anthropogenic influences (Gibbs, pers. comm.) and there are unpublished cases of illegal provisioning.

With respect to entanglement deaths, only one dolphin (out of the 47 investigated) was identified as being killed from entanglement throughout the 27-year period. This is in contrast to the results from state-wide studies that identified entanglements as a leading cause of death in South Australian cetaceans (Kemper *et al.*, 2005; Segawa and Kemper, 2015). However, many non-fatal entanglements in fishing lines and other gear have been recorded in the sanctuary (Bossley, pers. comm.) and the dolphins either shed the gear or were assisted by authorities in doing so. Entanglements that result in dolphin mortality are more likely due to nets (Kemper *et al.,* 2005), which are legal in the northern part of the ADS, however the reported entanglement in this study involved fishing line.

Deaths associated with vessel collisions are more prevalent than entanglements in our dataset both before and after 2005. In fact it is the highest cause of anthropogenic deaths in our dataset although absolute numbers are low. In addition, non-fatal vessel injuries have been recorded in studies elsewhere (Wells *et al.*, 2008; Bechdel *et al.*, 2009). Four of the five cases categorised as Other Unintentional involved severe propeller injuries. Dolphins in the sanctuary are susceptible to vessel collisions because there is much boating and shipping activity (DEWNR, 2007).

Dolphin deaths associated with disease showed a substantial increase (mean annual values of 0.22 vs 1.89) after 2004 (Table 3). However, this was probably due at least in part to (a) improved diagnosis when a veterinary pathologist joined the team; and (b) the 2013 UME referred to above. In South Australia as a whole, disease comprised a large proportion of known circumstance of death for stranded cetaceans (Kemper *et al.*, 2005), and in New Zealand the low proportion of disease-related events was attributed to inadequate pathological testing (Stockin *et al.*, 2009). Many of the ADS dolphins had infectious diseases, including chronic and acute, and multi-organ infections. Some of the cases involved lung infections, which is common for cetaceans (Jepson *et al.*, 2000; Kemper *et al.*, 2005). Reduced resistance to disease can be associated with human-related factors such as pollution.

Mitigation measures

Legislation protecting dolphins in the ADS is the same as throughout South Australia. The National Parks and Wildlife Act (Protected Animals – Marine Mammals Regulations 2010) outlines safe distances from dolphins when swimming or operating a vessel and declares that provisioning is illegal. Furthermore, the Adelaide Dolphin Sanctuary Act (2005) amended the National Parks and Wildlife Act (1972) to increase the fine for intentionally harming a marine mammal from $10,000 to $100,000 or two years' imprisonment. Commercial fishing is permitted in some parts of the sanctuary and recreational fishing is managed through the Fisheries Management Act (2007). Strict enforcement of the law is the most likely reason for the decrease in anthropogenically-related strandings in the sanctuary.

This is facilitated by ADS staff and volunteers undertaking daily boat and land compliance patrols throughout the sanctuary to ensure that regulations are being followed and to inform sanctuary-users of proper protocol in the presence of dolphins (DEWNR, 2008; Gibbs, pers. comm.). This presence helps to deter would-be violators as well as educate people in correct behaviour. Staff and volunteers also remove debris from the water to reduce possible entanglements or ingestion of foreign objects by dolphins (DEWNR, 2008). There is an intense programme of education and outreach that raises awareness of the dolphins and the need for their protection (DEWNR, 2008; Gibbs, pers. comm.).

Continued monitoring of dolphin mortalities in the ADS is essential for sanctuary management. In addition, studies documenting the types and patterns of non-fatal entanglements are needed. Quantifying and mapping human use of the sanctuary, especially boating, and recreational and commercial fishing, may help to link activities to dolphin mortalities.

ACKNOWLEDGEMENTS

Since 2009, funding for small cetacean strandings and mortalities has been made available to the South Australian Museum by the Adelaide Mount Lofty Natural Resources Management Board. Adelaide Dolphin Sanctuary (DEW) staff and volunteers were instrumental in collecting carcasses and data on the dolphins studied and we thank them for this effort. We thank other DEW staff, especially Deb Kelly, who have supported the study over many years. We thank the Dolphin Trauma Group, especially Mike Bossley for his ongoing support for the project and Roger Byard for conceiving the idea to form the group. We thank the Australian Marine Wildlife Research and Rescue Organisation. Mark Hill (veterinarian) assisted with necropsies in the early days of the study and provided logistical support for the programme. We thank Susan Gibbs for her assistance, David Stemmer and previous collection managers at the SAM for the enormous effort involved in processing and archiving specimens. Volunteers have assisted the programme in many ways. We thank Tomoyo Segawa Fellowes for compiling the database upon which the study was based. Maria Bellis (Forensic Science SA) was instrumental in preparing histology slides during the early years of the study. Tooth ageing was assisted by Elena Trentin, Mauro Talamonti and Stefania Milano. We would also like to thanks Peter Shuaghnessy, Dr. Mike Bossley and Robert Cerrato for their comment on earlier drafts.

REFERENCES

ASCOBANS. 2015. Report of the ASCOBANS expert workshop on the requirements of legislation to address monitoring and mitigation of small cetacean bycatch. Report to the 22nd ASCOBANS Advisory Committee Meeting, The Hague, Netherlands, 29 September–1 October 2015. 39pp. [Available at: *http://www.ascobans.org*]

Bearzi, M. 2012. Cetaceans and MPAs should go hand in hand: A case study in Santa Monica, California. *Ocean Coast Manage.* 60:56–9.

Bechdel, S.E., Mazzoil, M.S., Murdoch, M.E., Howells, E.M., Reif, J.S., McCulloch, S.D., Schaefer, A.M. and Bossart, G.D. 2009. Prevalence and impacts of motorized vessels on bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida. *Aquat. Mamm.* 35(3):367–77.

Bossley, M., Steiner, A., Rankin, R.W. and Bejder, L. 2017. A long-term study of bottlenose dolphins (*Tursiops aduncus*) in an Australian industrial estuary: Increased sightings associated with environmental improvements. *Mar. Mam. Sci.* 33: 277–90.

Cheney, B., Corkrey, R., Durban, J.W., Grellier, K., Hammond, P.S., Islas-Villanueva, V., Janik, V.M., Lusseau, S.M., Parsons, K.M., Quick, N.J., Wilson, B. and Thompson, P.M. 2014. Long-term trends in the use of a protected area by small cetaceans in relation to changes in population status. *Glob. Ecol. Con.* 2:118–28.

Cunningham-Smith, P., Colbert, D.E., Wells, R.S. and Speakman, T. 2006. Evaluation of human interactions with a provisioned wild bottlenose dolphin (*Tursiops truncatus*) near Sarasota Bay, Florida and efforts to curtail the interactions. *Aquat. Mamm.* 32:346–56.

Department of Environment, Water and Natural Resources. 2007. Dolphin Reference Paper 1: Dolphins. Adelaide Dolphin Sanctuary. 40pp. [Available at: *www.naturalresources.sa.gov.au/files/.../public/.../ads-reference-paper-dolphins-rep.pdf*]

Department of Environment, Water and Natural Resources. 2008. Adelaide Dolphin Sanctuary: Management Plan. Adelaide Dolphin Sanctuary. 25pp. [Available at: *www.naturalresources.sa.gov.au/files/.../public/.../cons-gen-dolphinsanctmanagplan.pdf*]

Donoghue, M., Reeves, R.R. and Stone, G. 2002. Report on the workshop on interactions between cetaceans and longline fisheries held in Apia, Samoa. November 2002. New England Aquatic Forum Series Report 03-1. 44pp.

Evans, K., Kemper, C., McKenzie, J. and McIntosh, R. 2011. Age determination of marine mammals using tooth structure. Marine Mammal Aging Facility, South Australian Museum. 70 pp. [Available at: *http://www.samuseum.sa.gov.au/research/biological-sciences/mammals/marine-mammal-ageing-facility*].

Gormley, A.M., Slooten, E., Dawson, S., Barker, R.J., Rayment, W., du Fresne, S. and Bräger, S. 2012. First evidence that marine protected areas can work for marine mammals. *J. Appl. Ecol.* 49:474–80.

Hamer, D.J., Ward, T.M. and McGarvey, R. 2008. Measurement, management and mitigation of operational interactions between the South Australian Sardine Fishery and short-beaked common dolphins (*Delphinus delphis*). *Biol. Conserv.* 141(11):2865–78.

Hooker, S.K. and Gerber, R. 2004. Marine reserves as a tool for ecosystem-based management: The potential importance of Megafauna. *Bioscience*. 54(1):27–39.

Hoyt, E. (ed.) 2005. *Marine Protected Areas for Whales, Dolphins and Porpoises: A World Handbook for Cetacean Habitat Conservation*. Earthscan, London. 516pp.

Isobe, T., Oshihoi, T., Hamada, H., Nakayama, K. and Yamada, T.K. 2011. Contamination status of POPs and BFRs and relationship with parasitic infections in finless porpoises (*Neophocaena phocaenoides*) from Seto Inland Sea and Omura. *Marine Poll. Bull.* 63:564–71.

Jepson, P.D., Baker, J.R., Kuiken, T., Simpson, V.R., Kennedy, S. and Bennett, P.M. 2000. Pulmonary pathology of harbour porpoises (*Phocoena phocoena*) stranded in England and Wales between 1990 and 1996. *Vet. Rec*. 146(25):721–28.

Kämpf, J., Brokensa, C. and Bolton, T. 2009. Hindcasts of the fate of desalination brine in large inverse estuaries: Spencer Gulf and Gulf St. Vincent, South Australia. *Desalination and Water Treatment* 2:325–33.

Kemper, C.M. 2004. Osteological variation and taxonomic affinities of bottlenose dolphins, *Tursiops* spp., from South Australia. *Aust. J. Zool*. 52:29–48.

Kemper, C.M. and Gibbs, S.E. 2001. Dolphin interactions with tuna feedlots at Port Lincoln, South Australia and recommendations for minimising entanglements. *J. Cetacean Res. Manage.* 3(3):283–92.

Kemper, C.M., Flaherty, A., Gibbs, S.E., Hill, M., Long, M. and Byard, R.W. 2005. Cetacean captures, strandings and mortalities in South Australia 1881–2000, with special reference to human interactions. *Aust. Mammal.* 27(1):37–47.

Kemper, C.M., Bossley, M. and Shaughnessy, P.D. 2008. Marine mammals of Gulf St Vincent, Investigator Strait and Backstairs Passage. Chapter 25. pp.339–352. *In*: S.A. Shepherd, S. Bryars, I.R. Kirkegaard, P. Harbison and J.T. Jennings (eds*.). Natural History of Gulf St Vincent*. Royal Society of South Aust. (Inc.), Adelaide, Australia. 123pp.

Kemper, C.M., Tomo, I., Bingham, J., Bastianello, S.S., Wang, J., Gibbs, S.E., Woolford, L., Dickson, C. and Kelly, D. 2016. Morbillivirus-associated Unusual Mortality Event in South Australian bottlenose dolphins is largest reported for southern hemisphere. *R. Soc. Open Sci.* 3: 160838.

Lauriano, G., Fortuna, C.M., Moltedo, G. and Notarbartolo di Sciara, G. 2004. Interactions between common bottlenose dolphins (*Tursiops truncatus*) and the artisanal fisher in Asinara Island National Park (Sardinia): assessment of catch damage and economic loss. *J. Cetacean Res. Manage.* 6(2): 165–73.

Loch, C., Marmontel, M. and Simões-Lopes. 2009. Conflicts with fisheries and intentional killing of freshwater dolphins (Cetacea: Odontoceti) in the Western Brazilian Amazon. *Biodivers. Conserv*. 18:3979–88.

Notarbartolo di Sciara, G. and Bearzi, G. 2002. Cetacean direct killing and live capture in the Mediterranean Sea. Section 5.1–5.4. *In*: G. Notarbartolo di Sciara (ed.) *Cetaceans of Mediterranean and Black Seas: State of Knowledge and Conservation strategies*. A report to ACCOBAMS Secretariat, Monaco, February 2002. 4pp.

Powell, J.R. and Wells, R.S. 2011. Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Mar. Mammal Sci.* 27(1):111–29.

R Development Core Team. 2016. *R*: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available at: *http://www.R-project.org/*].

Reeves, R.R., McClellan, K. and Werner, T.B. 2013. Marine mammal bycatch in gillnet and other entangling net fisheries, 1990 to 2011. *Endang. Species Res.* 20: 71–97.

Read, A.J. 2000. Potential mitigation measures for reducing the by-catches of small cetaceans in ASCOBANS Waters. Report to ASCOBANS. 22pp. [Available at: *http://www.eurocbc.org/Dr%20A%20J%20READ%20Report%20to% 20ASCOBANS%2027_12_2000.PDF*]

Segawa, T. and Kemper, C. 2015. Cetacean strandings in South Australia (1881–2008). *Aust. Mammal.* 37:51–66.

Song, K.J. 2014. Status of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Jeju Island, Korea. *Pac. Sci.* 68(4):555–62.

Stockin, K.A., Duignan, P.J., Roe, W.D., Meynier, L., Alley, M. and Fettermann, T. 2009. Causes of mortality in stranded common dolphin (*Delphinus* sp.) from New Zealand waters between 1998 and 2008. *Pac. Conserv. Biol.* 15:217–27.

Thomas, P.O., Reeves, R.R. and Brownell, J., R. L. 2016. Status of the world's baleen whales. *Mar. Mammal Sci.* 32(2): 682–734.

Tomo, I., Kemper, C.M. and Lavery, T.J. 2010. Eighteen-year study of South Australian dolphins shows variation in lung nematodes by season, year, age class and location. *J. Wildlife Dis.* 46(2):488–98.

Van Waerebeek, K., Baker, A.N., Félix, F., Gedamke, J., Iñiguez, M., Sanino, G.P., Secchi, E., Sutaria, D., van Helden, A. and Wang, Y. 2007. Vessel collisions with small cetaceans worldwide and with large whales in the Southern Hemisphere, an initial assessment. *LAJAM*. 6(1):43–69.

Wells, R.S., Hoffman, S. and Moors, T.L. 1998. Entanglement and mortality of bottlenose dolphins, *Tursiops truncatus*, in recreational fishing gear in Florida. *Fish. Bull.* 96(3):647–50.

Wells, R.S., Allen, J.B., Hoffman, S., Bassos-Hull, K., Fauquier, D.A., Barros, N.B., DeLynn, R.E., Sutton, G., Socha, V. and Scott, M.D. 2008. Consequences of injuries on survival and reproduction of common bottlenose dolphins (*Tursiops truncatus*) along the west coast of Florida. *Mar. Mammal Sci.* 24(4):774–94.