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Contents

Editorial

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

Two Journal issues have been published in 2017 – this one and also the sixteenth volume in the series.

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

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G.P. DONOVAN
Editor

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Photo-identification comparison of humpback whale (*Megaptera novaeangliae*) flukes from Antarctic Area IV with fluke catalogues from East Africa, Western Australia and Eastern Australia

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ABSTRACT

Early 'Discovery mark' data together with recent photo-identification, acoustic, genetic and satellite-radio tag data revealed linkages between humpback whales migrating from breeding grounds (C) off East Africa and the Area III feeding area, from Western Australian breeding grounds (D) and the Antarctic Area IV feeding area and the East Australian breeding grounds (E1) and Antarctic Area V feeding area. These data also revealed low levels of intermingling between (E1) and (D) humpback whales in the Antarctic Area IV feeding area consistent with these being separate populations. Greenpeace photographed the ventral tail flukes of 30 individual humpback whales in the Antarctic Area IV feeding area (70°E–130°E) from 2 to 9 January 2008, between 62°47'S and 64°14'S latitude and 80°00'E and 112°57'E longitude. Comparisons of the Antarctic Area IV Greenpeace fluke catalogue ($n = 30$) with existing reconciled fluke catalogues from East Africa ($n = 842$), Western Australia ($n = 1,558$) and Eastern Australia ($n = 1,964$), yielded no photo-identification matches. An analysis of the frequencies of whales seen and not seen in Antarctica, East Africa, Western Australia and Eastern Australia relative to the frequencies expected to have been seen and not seen, based on the estimated population sizes and the sizes of the catalogues, provided evidence that the Antarctic whales photographed are from a different population to the East African and East Australian populations. There was weak evidence supporting the hypothesis that the Antarctic whales are from the Western Australian population but insufficient data were available to determine a clear outcome. A comparison of the Antarctic Area IV Greenpeace catalogue ($n = 30$) with other existing African, Indian Ocean, Western and Eastern Australian and/or Antarctic catalogues, together with increased sampling across the humpback whale feeding season in Antarctica and along the Western and Eastern Australian coastline during their winter migration, is likely to provide further evidence of the migratory destination of these humpback whales. It will also add to our limited knowledge of the extent of population overlap within the Antarctic Area III, IV and V feeding areas.

KEYWORDS: HUMPBACK WHALE; PHOTO-IDENTIFICATION; MIGRATORY MOVEMENTS; ANTARCTIC; AFRICA; AUSTRALASIA; FEEDING AREAS; BREEDING GROUNDS; MANAGEMENT AREAS

INTRODUCTION

'Discovery marks' from the 1930s to the 1950s revealed linkages between humpback whales from East Africa (C) breeding grounds and Antarctic Area III feeding area (0°E–70°E), between humpback whales from the Western Australian breeding grounds (D) and Antarctic Area IV feeding area (70°E–130°E), and humpback whales from the Eastern Australian breeding grounds (E1) and Antarctic Area V feeding area (130°E–170°W). Discovery mark data also revealed low levels of interchange of individual humpback whales from breeding grounds D and E1 with Antarctic feeding Area IV and V (Rayner, 1940; Chittleborough, 1965; Dawbin, 1966; IWC, 2011; IWC, 2012).

Recent genetic evidence reports linkages between humpback whales migrating along the West Australian (D) coast and Antarctic Area IV feeding area (Pastene *et al.*, 2013) and low levels of interchange between breeding populations of Western Australia (D) and Eastern Australia (E1) (Anderson, 2013; Schmitt *et al.,* 2014a). Only two previous anecdotal photo-identification matches support linkages between Western Australia and Antarctic Area IV feeding area and mingling between breeding populations of Western Australia (D) and Eastern Australia (E1). One match supports the linkage between Western Australian breeding grounds (D) and Antarctic Area IV feeding area (Gill and Burton, 1995). The lateral body of a humpback whale was photographed on 3 September 1989 at 32°S, 116°E off Perth on the southwest coast of Western Australia during the southern migration and was subsequently matched to a photograph of the lateral body of the same individual humpback whale sighted and photographed on 14 February 1993 at 64°S, 101°E, in the Antarctic Area IV feeding area

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(Gill and Burton, 1995; Fig. 1). A single match supports interchange between humpback whales from Eastern Australia (E1) and Western Australia (D) (Kaufman *et al.,* 2011). A humpback whale tail fluke photograph obtained off North Stradbroke Island (28°S, 154°E) on 15 September 1987 was matched to a fluke photograph obtained off Perth (32°S, 116°E) on 10 October 1995 (Kaufman *et al.,* 2011; Fig. 1). Satellite-radio tag tracking of an individual humpback whale supports linkages between East Africa (C) and Antarctic Area III feeding area (Fossette *et al.,* 2014). Similarly, only one individual humpback whale satellite-radio tag track (Gales *et al.,* 2009; Fig. 1) supports the presence (Andrews-Goff, pers. comm.; Franklin *et al.,* 2017) of East Australian whales in the Antarctic Area IV feeding area. Recent acoustic evidence also reports low levels of interchange between humpback whales from breeding Areas D and E1 (Noad *et al.,* 2000).

This study uses the first large photo-identification dataset to investigate linkages and interchange between breeding grounds C off East Africa, D off Western Australia and E1 off Eastern Australia and the Antarctic Area IV feeding area. The outcome of a photo-identification comparison between a catalogue of individual humpback whales photographed in the Antarctic Area IV feeding area (2008, n = 30), and three large existing regional fluke catalogues from East Africa (2000–2006, n = 842), Western Australia (1990–2007, n = 1,558) and Eastern Australia (1992–2005, n = 1,964) is reported. A novel analysis of the photo-identification data (see statistical analysis below) was used to investigate linkages between each of the three breeding grounds and the Antarctic Area IV feeding area, and the results are discussed.

Table 1

Date and location of humpback whales photographed by Greenpeace in Antarctic IWC Management Area IV feeding area

Whale	Date (dd/mm/yy)	Latitude Deg. mins (S)	Longitude Deg. mins (E)
001	02/01/08	63.34	112.57
002	02/01/08	63.33	112.54
003	02/01/08	63.34	112.57
004	02/01/08	63.34	112.57
005	02/01/08	63.34	112.57
006	02/01/08	63.48	111.47
007	03/01/08	63.25	105.39
008	03/01/08	63.27	104.52
009	03/01/08	63.27	104.52
010	03/01/08	63.25	105.39
011	04/01/08	63.02	102.08
012	07/01/08	62.47	87.04
013	07/01/08	62.47	87.04
014	07/01/08	62.47	87.04
015	07/01/08	62.47	87.04
016	07/01/08	62.47	87.04
017	07/01/08	62.47	87.04
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024	07/01/08	62.47	87.04
025	07/01/08	62.47	87.04
026	07/01/08	62.47	87.04
027	07/01/08	62.47	87.04
028	07/01/08	62.47	87.04
029	09/01/08	64.14	80.01
030	09/01/08	64.14	80.01

METHODS

Photo-identification and fluke catalogues

The Greenpeace International vessel *Esperanza* undertook a non-lethal research program in Antarctica from 7 November 2007 to 8 February 2008. As part of this program, photographs were taken of humpback whales in the Antarctic Area IV feeding area (70°E–130°E) from 2 to 9 January 2008 in locations ranging between 62°47'S and 64°14'S, 112°57'E and 80°00'E (see Table 1 and Fig. 1). The resulting Greenpeace Antarctic Area IV (ANT) catalogue of ventral humpback whale tail fluke photographs consists of n = 30 photo-identified individual humpback whales.

The Wildlife Conservation Society and the American Museum of Natural History Cetacean Conservation and Research Program have conducted photo-identification studies of humpback whales off East Africa since 2000 (Cerchio *et al*., 2008a; 2008b). Photography of humpback whale pods was conducted off Madagascar (C3, 16°S, 50°E) between 2000 and 2006. The resulting East African (EAF) fluke catalogue for the period 2000–2006 consists of n = 842 unique individuals. Only the Madagascar (C3) catalogue was used for this study.

The Centre for Whale Research Western Australia has conducted photo-identification studies of humpback whales off Western Australia since 1990 (Jenner *et al.,* 2001). Photography of humpback whale pods was conducted at Exmouth Gulf (21°40'S, 114°10'E), Dampier (20°20'S, 116°45'E) and the Kimberley region (15°50'S, 123°30'E) between 1990 and 2007. The reconciled Western Australian (WA) fluke catalogue for the period 1990–2007 consists of n = 1,558 unique individuals.

The Oceania Project conducted vessel-based photo-identification of humpback whale pods and individual whales in Hervey Bay, Queensland (25°S, 153°E) between 1992 and 2005 (Franklin *et al*., 2011, Franklin 2012, Franklin 2014). The reconciled Eastern Australian (EA) fluke catalogue for the period 1992–2005 consists of n = 1,964 unique individuals.

The sampling sites and the reconciled fluke catalogues are summarised in Table 2 and the locations of the photo-identification sampling sites and IWC breeding grounds and feeding areas are shown in Fig. 1.

Photo-identification sampling sites for this study: Madagascar (16°S, 50°E); Exmouth Gulf (21°40'S, 114°10'E), Dampier (20°20'S, 116°45'E) and Kimberley (15°50'S, 123°30'E); Hervey Bay (25°S, 153°E). Antarctic Area IV sampling sites for this study (shown as circles in Fig. 1, also see Table 1): (g) 2-Jan-08, (60°S, 112°E), 6 flukes; (h) 3-Jan-08, (63°S, 105°E), 4 flukes; (i) 4-Jan-08, (63°S, 102°E), 1 fluke; (j) 7-Jan-08, (63°S, 87°E), 17 flukes; (k) 9-Jan-08, (64°S, 80°E), 2 flukes.

Other photo-identification and satellite-tag locations mentioned in the text: (a) 3-Sep-89 off Perth, (32°S, 116°E) one lateral body photo; (b) 14-Feb-93, (64°S, 101°E), one lateral body photo (Gill and Burton, 1995); (c) sat-tag commenced, 10-Oct-08, (37°S, 150°E), (d) sat-tag ceased, 3-Feb-09, (61°S, 101°E) (Gales *et al*., 2009, Andrews-Goff,

Table 2

Summary of East African, Western Australian and Eastern Australian sampling sites (SITE) and the population tail fluke catalogues (POP) of individual humpback whales used in this study.

East Africa (EAF)		Western Australia (WA)		Eastern Australia (EA)	
Site	Flukes (*n*)	Site	Flukes (*n*)	Site	Flukes (*n*)
Madagascar (C3)	842	Exmouth, Dampier and Kimberley	1,558	Hervey Bay	1,964
Total (POP)	842		1,558		1,964

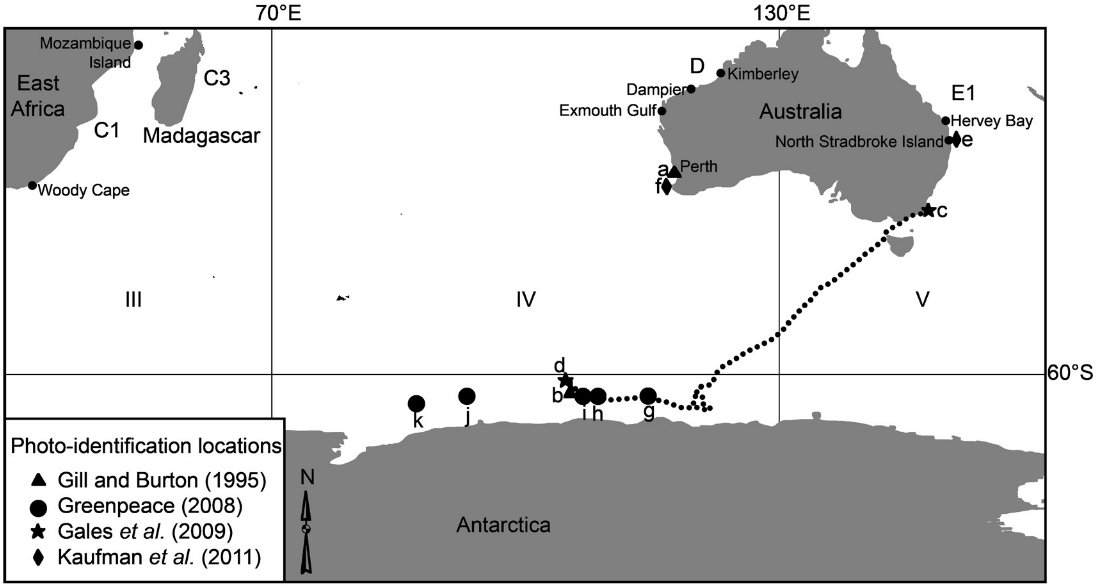

Fig. 1. East African, Western Australian and Eastern Australian photo-identification sampling sites, used in this study; IWC breeding grounds C1, C3, D and E1 and Antarctic feeding Areas III (0°–70°E), IV (70°E–130°E) and V (130°E–170°W); and other photo-identification locations mentioned in text.

pers. comm. and Franklin *et al.*, 2017); (e) 15-Sep-87 (28°S, 154°E) off North Stradbroke Island, one fluke, (f) 10-Oct-95 (32°S, 116°E) one fluke (Kaufman *et al.,* 2011).

Statistical analysis

A novel analysis (first described in Franklin *et al.,* 2012) was conducted to investigate the photo-identification data from Antarctic Area IV (ANT) fluke catalogue and each of the large regional photo-identification datasets from East African (EAF), Western Australian (WA) and the Eastern Australian (EA) fluke catalogues.

The analysis tested the question: are the data available for each region consistent with the hypothesis that the whales sighted in the vicinity of the Antarctic Area IV are from a single population? (single population hypotheses).

The following rationale was used to design the analysis:

(a) If the whales sighted in Antarctic Area IV were members of the EAF, WA or EA population (Table 2), the proportion of the ANT catalogue expected to be matched to the EAF, WA or EA catalogue would be equal to the proportion of the EAF, WA or EA population that were in the EAF, WA or EA catalogue and alive and available for capture in Antarctic Area IV. For example, if one third of the East African population were in the EAF catalogue and alive at the time Antarctic Area IV was sampled, a third of the ANT catalogue could be expected to be matched to the EAF catalogue (single population hypotheses).

(b) Alternatively, if the whales sighted in Antarctic Area IV were not members of the EAF, WA or EA population, the proportion of the ANT catalogue expected to be matched to the EAF, WA or EA catalogue would be less than the proportion of the EAF, WA or EA population alive and in the EAF, WA or EA catalogue (separate population hypothesis).

Given the above rationale and the estimates described below, the analysis may be based on a test of association in a 2 × 2 cross-table of frequencies constructed as *'not seen'* or *'seen'* in Antarctic Area IV by *'not seen'* or *'seen'* in East Africa, Western Australia or Eastern Australia (Table 3).

Looking at these data and estimates, the expected numbers of matches, $\hat{m}_{\text{POP-ANT}}$, may be derived from the equal proportions rationale presented above, $m_{\text{POP-ANT}}/n_{\text{ANT}} = n_{\text{POP}}/N_{\text{POP}}$, and calculated as $\hat{m}_{\text{POP-ANT}} = (n_{\text{POP}} * n_{\text{ANT}})/N_{\text{POP}}$. This is both the standard way of calculating the expected frequencies under a null hypothesis of independence in a cross-table (row total by column total over grand total) and a simple transformation of the Lincoln-Petersen Estimator, $\hat{N}_{\text{P}} = (n_1 * n_2)/m_2$. The expected frequencies for each of the other cells were obtained in the standard way. Note that the null hypothesis of independence in the Table 3 corresponds to the single population hypothesis described above.

A one-tailed test of association is appropriate because the alternative hypothesis is that the observed frequency of whales seen at both locations was fewer (and never more)

Table 3

Scheme for cross-tables: East Africa, Western Australia/Eastern Australia (POP) – Antarctic IWC Management Area IV (ANT)

	East Africa/Western Australia/Eastern Australia (POP)		
Antarctic IWC Management Area IV (ANT)	Not seen	Seen	Total
Not seen	$N_{POP} - n_{ANT} - n_{POP} + m_{POP\text{-}ANT}$	$n_{POP} - m_{POP\text{-}ANT}$	$N_{POP} - n_{ANT}$
Seen	$n_{ANT} - m_{POP\text{-}ANT}$	$m_{POP\text{-}ANT}$	n_{ANT}
Total	$N_{POP} - n_{POP}$	n_{POP}	N_{POP}

N_{POP} = Population estimate at 2008 for East Africa, Western Australia and Eastern Australia.

n_{POP} = Estimate of number of living whales in 2008 from the East African, Western Australian and Eastern Australian catalogues.

$m_{POP\text{-}ANT}$ = Number of whales matched between East Africa, Western Australia or Eastern Australia and Antarctic IWC Management Area IV.

n_{ANT} = Number of whales identified in Antarctic IWC Management Area IV.

than the expected frequency under the null hypothesis. A one-tailed *p*-value from Fisher's Exact Test was used. This test is preferred over the asymptotic Pearson Chi-square test when expected frequencies are small (Everitt, 1992).

The analysis required estimates of the East African, Western Australian and Eastern Australian populations (N_{POP}) for 2008 and estimates of the number of individuals in the POP catalogues that were alive in early 2008 and potentially available for capture in Antarctic Area IV (N_{POP}).

RESULTS

Comparison of the Antarctic Area IV catalogue (*n* = 30) to the East African (*n* = 842), Western Australian (*n* = 1,558) and Eastern Australian (*n* = 1,964) catalogues found no matches (locations are shown in Fig. 1 above).

Analysis: Antarctic Area IV – East Africa

An estimated population of 7715 was obtained for East Africa. This was based on the estimate of the East African C3 population in 2006 at 6,737, CV = 0.31 (Cerchio *et al.,* 2008a). However, to allow for growth between 2006 and 2007 and to take into account that the 2006 estimate may only be an estimate of a sub-region of the C population, as suggested by Cerchio *et al.* (2008a), the upper bound estimate of 7,715, CV = 0.24 was used as a minimum estimate for the East African (C) population in early 2008.

The 842 individuals recorded in the EAF catalogue between 2000 and 2006, were assumed to have been captured at a constant rate of 120.3 whales per annum. Application of an estimated mortality rate of 4% per annum (Clapham *et al.* 2001; Zerbini *et al*., 2010), yielded an estimated 748 whales in the catalogue that were alive and available for capture in Antarctic Area IV in early 2008.

Table 4 reports the frequencies of whales 'not seen' and 'seen' near the Antarctic Area IV by 'not seen' and 'seen' in East Africa based on the above estimates together with the size of the Antarctic Area IV catalogue (*n* = 30) and the number of Antarctic Area IV to East Africa matches (*n* = 0). The expected frequencies shown were derived on the assumption of independence corresponding to a hypothesis that the whales seen in both places were members of the same population.

Table 4

Estimated numbers and expected frequencies of whales 'not seen' and 'seen' in Antarctica IWC Management Area IV by 'not seen' and 'seen' in East Africa

		East Africa		
Antarctic Area IV	Frequency	Not seen	Seen	Total
Not seen	Observed	6,937	748	7,685
	Expected	6,939.9	745.1	7,685
Seen	Observed	30	0	30
	Expected	27.1	2.9	30
Total		6,967	748	7,715

The one-tailed p-value from Fisher's exact test for the data in Table 4 was *p* = 0.047, indicating that the Antarctic and East Africa data were likely to be from separate populations. With 2.9 matches expected under the single population null hypothesis, it is highly unlikely that no matches would be found unless the data were on whales from separate populations. The null hypothesis would not have been rejected if 1 match had been found (*p* = 0.197).

Analysis: Antarctic Area IV – Western Australia

The estimated Western Australian population of 26,100 in early 2008 was based on the 2007 estimate of Salgado Kent *et al.* (2012) of 26,100 (95% CI = 20,152–33,272). Note: See IWC (2012) for discussion of potential bias of the results in Salgado Kent *et al.* (2012).

The 1,558 individuals recorded in the WA catalogue between 1990 and 2007 were assumed to have been captured at a constant rate of 86.6 whales per annum. Application of an estimated mortality rate of 4% per annum (Clapham *et al*., 2001; Zerbini *et al*., 2010, yielded an estimated 1,127 whales in the catalogue that were alive and available for capture in Antarctic Area IV in early 2008.

Table 5 reports the frequencies of whales 'not seen' and 'seen' near the Antarctic Area IV by 'not seen' and 'seen' in Western Australia based on the above estimates together with the size of the Antarctic Area IV catalogue (*n* = 30) and the number of Antarctic Area IV to Western Australia matches (*n* = 0). The expected frequencies shown were derived on the assumption of independence corresponding to a hypothesis that the whales seen in both places were members of the same population.

The one-tailed p-value from Fisher's exact test for the data in Table 5 was p = 0.266, indicating insufficient evidence (i.e. P > 0.05) to reject the null hypothesis that the Antarctic and WA data were from the same population. However, the finding of no matches weakens the argument that the Antarctic data were from the WA population: even a single

Table 5

Estimated numbers and expected frequencies of whales 'not seen' and 'seen' in Antarctica IWC Management Area IV by 'not seen' and 'seen' in Western Australia.

		Western Australia		
Antarctic Area IV	Frequency	Not seen	Seen	Total
Not seen	Observed	24,943	1,127	26,070
	Expected	24,944.3	1,125.7	26,070
Seen	Observed	30	0	30
	Expected	28.7	1.3	30
Total		24,973	1,127	26,100

match (p = 0.626) would have strengthened the case for a single population. The relatively small Antarctic catalogue and the relatively small proportion of the estimated WA population expected to be alive and in the WA catalogue (4.32%) makes for an indefinite conclusion.

Analysis: Antarctic Area IV – Eastern Australia

The Eastern Australian population in early 2008 was estimated at 9,592 whales based on the Noad *et al.* (2011) estimate of 7,090 in 2004 with an assumed rate of increase of 10.6% per annum.

The 1,964 individuals recorded in the EA catalogue between 1992 and 2005, were assumed to have been captured at a constant rate of 140.3 whales per annum. Application of an estimated mortality rate of 4% per annum (Clapham *et al*., 2001, Zerbini *et al*., 2010), yielded an estimated 1,527 whales in the catalogue that were alive and available for capture in Antarctic Area IV in early 2008.

Table 6 reports the frequencies of whales 'not seen' and 'seen' near the Antarctic Area IV by 'not seen' and 'seen' in Western Australia based on the above estimates together with the size of the Antarctic Area IV catalogue ($n = 30$) and the number of Antarctic Area IV to Western Australia matches ($n = 0$). The expected frequencies shown were derived on the assumption of independence corresponding to a hypothesis that the whales seen in both places were members of the same population.

The one-tailed p-value from Fisher's exact test for the data in Table 6 was p = 0.005, indicating that the Antarctic and EA data were from separate populations. With 4.8 matches expected under the single population null hypothesis, it is highly unlikely that no matches would be found unless the data were on whales from separate populations. The null hypothesis would not have been rejected had even one match had been found (p = 0.037).

Table 6

Estimated numbers and expected frequencies of whales 'not seen' and 'seen' in Antarctica IWC Management Area IV by 'not seen' and 'seen' in Eastern Australia

		Eastern Australia		
Antarctic Area IV	Frequency	Not seen	Seen	Total
Not seen	Observed	8,035	1,527	9,562
	Expected	8,039.8	1,522.2	9,562
Seen	Observed	30	0	30
	Expected	25.2	4.8	30
Total		8,065	1527	9,592

DISCUSSION

This study is the first to utilise large humpback whale photo-identification datasets for comparison against a small catalogue from the Antarctic Area IV feeding area to investigate linkages between Area IV feeding area and East Africa, Western Australia and Eastern Australia. The data support the hypothesis that humpback whales feeding in Antarctic Area IV are a separate population from the East Africa and Eastern Australia populations. However, as the East African and Eastern Australian data used in this study are each from one sampling site, there is a possibility that comparison of the Antarctic flukes with other African and East Australian catalogues may yield matches. Consequently, we cannot discount the likelihood that some East African and Eastern Australian humpbacks may feed in the Antarctic Area IV feeding area (see Franklin *et al.,* 2017). In contrast, there is much more recent evidence that some Eastern Australian humpbacks feed in Antarctic Area V in and around the Balleny Islands (Franklin *et al.,* 2008; Franklin *et al.,* 2012; Constantine *et al.,* 2014; Schmitt *et al.,* 2014b).

The limited data from Western Australia and the small Antarctic Area IV catalogue used in this study provided weak evidence to reject the null hypothesis that humpback whales feeding in Antarctic Area IV are from the Western Australian population. Both early 'Discovery mark' data and recent photo-identification data provide support for the hypothesis that Western Australian humpback whales feed in Antarctic Area IV (Rayner, 1940; Chittleborough, 1965; Dawbin, 1966; Gill and Burton, 1995). Moreover, recent genetic data supports linkages between Western Australia (D) and Antarctic Area IV feeding area (Pastene *et al.,* 2013). Consequently, the most likely interpretation of available photo-identification data in this study is that the humpback whales feeding in Antarctic Area IV are from the Western Australian population.

Both early Discovery mark data and recent photo-identification, satellite-tag, genetic and acoustic data support the hypothesis of low levels of overlap, in the Antarctic Area IV feeding area, between Eastern Australian (E1) humpback whales and Western Australian (D) humpback whales (Rayner, 1940; Chittleborough, 1965; Dawbin, 1966; Gales *et al.,* 2009; Andrews-Goff, pers. comm.; Kaufman *et al*., 2011; Anderson, 2013; Schmitt *et al.,* 2014a; Franklin *et al.,* 2017).

The timing and location of sampling in Antarctic Area IV feeding area is likely an important factor in determining the linkages between tropical breeding grounds and Antarctic Area IV feeding area. The humpback whale satellite-radio tagged off Eden in October 2008 (Franklin *et al.,* 2017) travelled down into Antarctic Area IV feeding area during February 2009 whereas the sampling for this study in Antarctica was during January. Moreover, there is a temporal staggering of sexual and maturational classes of humpback whales during the migration to and from Antarctica (Chittleborough, 1965; Dawbin, 1966, 1997; Franklin, 2012). Consequently, sampling in the Antarctic Area IV feeding area throughout December, January and February may yield more useful results for comparison with coastal humpback whale tail fluke catalogues.

Collection of further photo-identification data of humpback whales in Antarctic Area III, IV and V feeding areas with sampling across the season will assist in further investigation of the linkages between the Antarctic feeding areas and tropical breeding grounds of humpback whales in both the Indian and Pacific Ocean basins, as well as rates of interchange between these different breeding populations during their period in the feeding areas.

The Greenpeace Antarctic Area IV catalogue should also be compared to any other existing West African, East African, Indian Ocean, Australian and/or Antarctic catalogues, as this is likely to provide further data on the migratory destination of these humpback whales and add to our limited knowledge of the extent of breeding population overlap within the Antarctic Area III, IV and V feeding areas.

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REFERENCES

Anderson, M.J. 2013. Genetic connectivity within Eastern Australian humpback whales and their relationship to adjacent South Pacific and Indian Ocean stocks. PhD thesis, Southern Cross University, Lismore, NSW. [Available at: *http://epubs.scu.edu.au/theses/362/*].

Cerchio, S., Ersts, P., Pomilla, C., Loo, J., Razafindrakoto, Y., Leslie, M., Andrianrivelo, N., Mindon Dushane, J., Murray, A., Collins, T. and Rosenbaum, H. 2008a. Revised estimation of abundance for breeding stock C3 of humpback whales, assessed through photographic and genotypic mark-recapture data from Antongil Bay, Madagascar, 2000–2006. Paper SC/60/SH32 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 20pp. [Paper available from the Office of this Journal].

Cerchio, S., Findlay, K., Ersts, P., Minton, G., Bennet, D., Meÿer, M., Razafindrakoto, Y., Kotze, D., Oosthuizen, H., Leslie, M., Andrianarivelo, N. and Rosenbaum, H. 2008b. Initial assessment of exchange between breeding stocks C1 and C3 of Humpback whales in the western Indian ocean using photographic mark recapture data, 2000–2006. Paper SC/60/SH33 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 15pp. [Paper available from the Office of this Journal]

Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J Mar. Fresh. Res*. 16: 33–128.

Clapham, P.J., Robbins, J., Brown, M., Wade, P. and Findlay, K. 2001. A note on plausible rates of population growth for humpback whales. *J. Cetacean Res. Manage.* (Suppl.) 3: 196–7.

Constantine, R., Steel, D., Allen, J., Anderson, M., Andrews, O., Baker, C.S., Beeman, P., Burns, D., Charrassin, J.-B., Childerhouse, S., Double, M., Ensor, P., Franklin, T., Franklin, W., Gales, N., Garrigue, C., Gibbs, N., Harrison, P., Hauser, N., Hutsel, A., Jenner, C., Jenner, M.-N., Kaufman, G., Macie, A., Mattila, D., Olavarría, C., Oosterman, C., Paton, D., Poole, M., Robbins, J., Schmitt, N., Stevick, P., Tagarino, A., Thompson, K. and Ward, J. 2014. Remote Antarctic feeding ground important for east Australian humpback whales. *Mar. Biol.* 161:1087–1093. [Available at: *http://dx.doi.org/10.1007/s00227-014-2401-2*].

Dawbin, W.H. 1966. The seasonal migratory cycle of humpback whales. pp.145–170 *In*: K.S. Norris (ed.) *Whales, Dolphins and Porpoises.* University of California Press, Berkeley, California. xv+789pp.

Dawbin, W.H. 1997. Temporal segregation of humpback whales during migration in southern hemisphere waters. *Mem. Qld. Mus*. 42 (1):105–38.

Everitt, B.S. 1992. *The Analysis of Contingency Tables*. 2nd Edn, Chapman and Hall/CRC. 164pp.

Fossette, S., Heide-Jørgensen, M.-P., Jensen, M.V., Kiszka, J., Bérubé, M., Bertrand N. and Vély M. 2014. Humpback whale (*Megaptera novaeangliae*) post breeding dispersal and southward migration in the western Indian Ocean. *J Exp. Mar. Biol. Ecol.* 450:6–14.

Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M. M., Hauser, N., Donoghue, M., Russell, K., Mattila, D. K., Robbins, J., Oosterman, A., Leaper, R., Baker, C. S., and Clapham, P. 2008. Migratory movements of humpback whales (*Megaptera novaeangliae*) between eastern Australia and the Balleny Islands, Antarctica, confirmed by photo-identification. Paper SC/60/SH2 presented to the IWC Scientific Committee, June 2008, Santiago, Chile. 12pp (unpublished). [Paper available from the Office of this Journal].

Franklin, T., Franklin W., Brooks, L., Harrison, P., Baverstock, P. and Clapham, P. 2011. Seasonal changes in pod characteristics of eastern Australian Humpback whales (*Megaptera novaeangliae*), Hervey Bay 1992–2005. *Mar. Mammal Sci.*, 27(3): e134–e152 (July 2011). [Available at: doi: 10.1111/j.1748-7692.2010.00430.x].

Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M.M., Hauser, N., Donoghue, M., Russell, K., Mattila, D.K., Robbins, J., Oosterman, A., Leaper, R., Harrison, P., Baker, S.C. and Clapham, P. 2012. Antarctic waters (Area V) near the Balleny Islands are a summer feeding area for some Eastern Australian (E(i) breeding group) humpback whales (*Megaptera novaeangliae*). *J. Cetacean Res. Manage.* 12: 321-27.

Franklin, T. 2012. The social and ecological significance of Hervey Bay Queensland for eastern Australian humpback whales (*Megaptera novaeangliae*). PhD thesis, Southern Cross University, Lismore, NSW. 245pp. [Available at: *http://epubs.scu.edu.au/theses/357/*].

Franklin, W. 2014. Abundance, population dynamics, reproduction, rates of population increase and migration linkages of eastern Australian Humpback whales (*Megaptera novaeangliae*) utilising Hervey Bay, Queensland. PhD thesis Southern Cross University, Lismore, NSW. 396pp. [Available at: *http://epubs.scu.edu.au/theses/422/*].

Franklin, W., Franklin, T., Gibbs, N., Childerhouse, S., Garrigue, C., Constantine, R., Brooks, L., Burns, D., Paton, D., Poole, M. M., Hauser, N., Donoghue, M., Russell, K., Mattila, D.K. Robbins, J., Anderson, M., Olavarria, C., Jackson, J., Noad, M., Harrison, P., Baverstock, P., Leaper, R., Baker, S.C. and Clapham, P. 2014. Photo-identification confirms that humpback whales (*Megaptera novaeangliae*) from eastern Australia migrate past New Zealand but indicates low levels of interchange with breeding grounds of Oceania. *J. Cetacean Res. Manage.* 14 (1): 133–40.

Franklin, W., Franklin, T., Andrews-Goff, V., Paton, D.A. and Double, M. 2017. Movement of two humpback whales (*Megaptera novaeangliae*) satellite-radio tagged off Eden, NSW and matched by photo-identification with the Hervey Bay catalogue. *J. Cetacean Res. Manage.* 17: 29–33.

Gales, N., Double, M., Robinson, S., Jenner, C., Jenner, M., Kink, E., Gedamke, J., Paton, D. and Raymond B. 2009. Satellite tracking of southbound east Australian Humpback whales (*Megaptera novaeangliae*): challenging the feast or famine model for migrating whales. Paper SC/61/SH17 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 11pp. [Paper available from the Office of this Journal]

Gill, P.C. and Burton, C.L.K. 1995. Photographic resight of a humpback whale between Western Australia and Antarctic Area IV. *Mar. Mammal Sci.* 11: 96–100.

International Whaling Commission. 2011. Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales, 4–7 April 2006, Hobart, Tasmania. *J. Cetacean Res. Manage.* (Special Issue 3): 1–50.

International Whaling Commission. 2012. Report of the Scientific Committee. Annex H. Report of the Sub-Committee on Other Southern Hemisphere Whale Stocks. *J. Cetacean Res. Manage.* (Suppl.). 13: 192–216.

Jenner, K.C.S., Jenner, M.N. and Mccabe, K.A. 2001. Geographical and temporal movements of humpback whales in western Australian waters. *APPEA J*: 749–65.

Kaufman, G., Coughran, D., Allen, J. M., Burns, D., Burton, C., Castro, C., Childerhouse, S., Constantine, R., Franklin, T., Franklin, W., Forestell, P., Gales, R., Garrigue, C., Gibbs, N., Jenner, C., Paton, D., Noad, M., Robbins, J., Slooten, E., Smith, F. and Stevick, P. 2011. Photographic evidence of interchange between east Australia (BS E-1) and West Australia (BS-D) Humpback whale breeding populations. Paper SC/63/SH11 presented to the IWC Scientific Committee, June 2011, Tromsø, Norway (unpublished). 13pp. [Paper available from the Office of this Journal]

Noad, M.J., Cato, D.H., Bryden, M.M., Jenner, M.N. and Jenner, K.C.S. 2000. Cultural revolution in whale songs. *Nature* 408: 537–37.

Noad, M. J., Dunlop, R. A., Paton, D. and Cato, D. H. 2011. Absolute and relative abundance estimates of Australian east coast humpback whales (*Megaptera novaeangliae*). *J. Cetacean Res. Manage.* (Special Issue 3): 243–52.

Pastene, L.A., Kitakado, T., Goto, M. and Kanda, N. 2013. Mixing rates of humpback whales of Stocks D, E and F in the Antarctic. Paper SC/65a/SH13 presented to the IWC Scientific Committee, June 2013, Jeju Island, Republic of Korea (unpublished). 11pp. [Paper available from the Office of this Journal]

Rayner, G.W. 1940. Whale marking: progress and results to December 1939. *Discovery Rep.* 19: 245–84.

Salgado Kent, C.P., Jenner, C., Jenner, M., Bouchet, P. and Rexstad, E. 2012. Southern Hemisphere Breeding Stock D humpback whale population estimates from North West Cape, Western Australia. *J. Cetacean Res. Manage.* 12(1): 29–38.

Schmitt, N.T., Double, M.C., Jarman, S.N., Gales, N., Marthick, J.R., Polanowski, A.M., Baker, C. Scott, Steel, D., Jenner, K.C.S., Jenner, M., Gales, R., Paton, D., and Peakall, R. 2014a. Low levels of genetic differentiation characterize Australian humpback whale (*Megaptera novaeangliae*) populations. *Mar. Mammal Sci.* 30: 221–41.

Schmitt, N.T., Double, M.C., Baker, C.S., Gales, N., Childerhouse, S., Polanowski, A.M., Steel, D., Albertson, R., Olavarria, C., Garrigue, C., Poole, M., Hauser, N., Constantine, R., Paton, D., Jenner, C.S, Jarman, S.N. and Peakall, R. 2014b. Mixed-stock analysis of humpback whales (*Megaptera novaeangliae*) on Antarctic feeding grounds. *J. Cetacean Res. Manage.* 14 (1):141–57.

Zerbini, A.N., Clapham, P.J. and Wade, P.R. 2010. Assessing plausible rates of population growth in humpback whales from life-history data. *Marine Biology* 157(6): 1225–1236.

Age estimation for bowhead whales (*Balaena mysticetus*) using aspartic acid racemisation with enhanced hydrolysis and derivatisation procedures

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ABSTRACT

Accurate determination of the ages of individual whales is key to developing effective conservation strategies for the bowhead whale (*Balaena mysticetus*). Previous attempts to develop reliable methods of age determination for this species have included using body length and baleen length measurements, baleen carbon cycling analysis, assessments of corpora accumulation, and aspartic acid racemisation (AAR; conversion of L to D enantiomers) measurements. Each of these methods has its limitations. The primary objective of this study was to improve the AAR analysis technique for determining age in bowhead whales in order to obtain consistent, reproducible results for D/L ratios for estimated ages. Using a modified AAR method, lenses from 68 bowhead whales were analysed and ages estimated. A comparison of the results to previous ageing by corpora counting or baleen carbon cycling methods for 11 of the whales showed smaller standard errors for the AAR analyses. The modified AAR methods applied in this study increase the precision of D/L measurements and provide improved bowhead whale AAR results.

KEYWORDS: BOWHEAD WHALE; AGE DETERMINATION

INTRODUCTION

Conservation can be hindered by a lack of knowledge regarding the health of individuals, population demography and the extent to which threats are identified and managed (Reynolds *et al.,* 2005). The future long-term survival of bowhead whales (*Balaena mysticetus*) and other ice-adapted species will, in particular, be influenced by the direct effects of climate change (and resultant changes in human activities) on reproduction, longevity, and other life history parameters. The reliable age estimation of individual bowhead whales is important for the evaluation of such effects and the informing of conservation and management decisions.

For most marine mammals, age is calculated by counting growth layer groups (GLGs) in teeth (Hohn, 2009). However, GLG counting is not applicable for bowhead whales or other baleen whales (Suborder Mysticeti; Order Cetacea). Aspartic acid racemisation (AAR) of the lens nucleus provides an alternative method of ageing when no teeth are present. During gestation, two enantiomers (L and D) of aspartic acid with D/L ratios that are slightly greater than zero at the genesis of formation, are laid down in the nucleus of the lens where no metabolic activity occurs (Bada *et al.*, 1980). Thus, additional conversion of L to D aspartic acid in the lens nucleus takes place only due to racemisation over time following birth. The racemisation rate constant of aspartic acid enantiomers (K_{asp}) can be ascertained using the Arrhenius equation, which accounts for the effect of temperature on that constant and, therefore, on the reaction rate.

Although the use of AAR has shown considerable promise and led to several published analyses for age estimation of bowhead whales (Bada *et al.,* 1980; George *et al.,* 1999; Rosa *et al.,* 2004, 2013; Wetzel *et al.,* 2007), analytical problems have previously been encountered when using this method. The most troubling of these issues includes reproducibility of the D/L ratio as a consequence of the AAR analytical protocols, instrument response fluctuations, sample/standard instability and natural variability in living animals. Consequently, our primary goal was to examine and refine the amino acid analysis method used in previous studies of bowhead whales (Bada *et al.,* 1980; George *et al.,* 1999; Rosa *et al.,* 2004; 2013; Wetzel *et al.,* 2007) and other species (Olson and Sunde, 2002) to enhance precision of bowhead whale age estimates, and thus the value of those estimates to inform conservation and management decisions. Our results include the first age estimates for 57 whales not previously aged by any method.

MATERIALS AND LABORATORY METHODS

Sample acquisition

For decades, scientists with the North Slope Borough, Department of Wildlife Management (NSB-DWM), have worked closely with Alaska Native hunters to examine bowhead whales taken during subsistence hunts. During this period, a range of bowhead tissue samples were collected and archived, and basic biological data documented for each whale. Included in these collections were bowhead whale eyes from individuals spanning the breadth of age and reproductive status (fetus through adults), which had been preserved (frozen, intact). For this study, 68 archived bowhead eyes were selected from whales ranging in size and

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possible ages for AAR analysis. All available fetal eyes were analysed for this study. While a range of age classes was selected as specimens for this study, we do not consider the dataset to be representative of the population age structure (i.e. it is not a random sample). The primary objectives of the paper were to investigate improvements of the AAR method for estimating the age of bowhead whales over a range of size classes and to estimate ages for a large number of whales not previously aged.

Eye lens removal and analysis of extracts

The methods employed for acquisition of lens nuclei were similar to those described by George *et al.* (1999), Olson and Sunde (2002) and Rosa *et al.* (2004; 2013). For each eye, the lens nucleus was removed and trimmed. One half of the nucleus was retained frozen in a clean glass vial, and the other half was analysed.

Sample extracts were hydrolysed and derivatised using methods modified from those previous studies. Analyses for D and L isomers of aspartic acid were done in triplicate on a HyperClone reverse phase C18 column (120A, 250 × 4mm, 5micron; Phenomenex, Torrance, CA, USA) using a high performance liquid chromatograph (HPLC; Agilent Technologies, Santa Clara, CA, USA), equipped with an autosampler and scanning fluorescence detector (λ_{ex} = 230nm; λ_{em} = 445nm). The HPLC flow rate was 1.5 ml/min, the column temperature was set to 30ºC and methanol (A), acetonitrile (B) and N-acetyl-L-cysteine (NAC) buffer (C) were used as eluants.

Hydrolysis

George *et al* (1999) and others have followed the methodological lead of J.L. Bada, to estimate age for large whales (e.g. Bada *et al.,* 1980). In general, previous work on bowhead amino acid racemisation employed a lens hydrolysis protocol using 6M HCL at 100ºC for 6 hours of hydrolysis. For this study, we evaluated a range of hydrolysis times and temperatures to optimise this step for bowhead lens amino acid preparation. Specifically, our study found that stable hydrolysis occurred using 6M HCl at 80ºC for 8 hours. With shorter hydrolysis time periods and/or higher temperatures, inconsistent hydrolysis was observed. Neither 80ºC nor 100ºC are temperatures of hydrolysis that could affect the aspartic acid D/L ratio (Goodfriend, 1997; Goodfriend and Myer, 1991).

Standards

The calibration of the D/L ratios measured by HPLC included eight different ratios of D and L isomer standards of aspartic acid which were analysed in triplicate for each set of 10 sample analyses. The standard ratios (D:L) used included: 0.5:99.5, 1:99, 2:98, 5:95, 10:90, 20:80, 30:70, and 50:50. We paid particular attention to designing a robust initial calibration followed by bracketing each set of three samples (all samples were run in triplicate) with a 5:95 D/L standard to confirm instrument and sample stability. The ability to generate stable and consistent calibration curves eliminates the need for daily adjustments or modelling instrument calibration responses (George *et al.*, 1999; Rosa *et al.*, 2004)

All standards in this study were corrected for trace cross contamination of the D isomer in the L isomer aspartic acid standard and vice versa. For each standard calibration curve analysis, we required the regression coefficient of determination (R^2) to be at least 0.99; otherwise a new standard calibration mixture was made and analysed until an acceptable R^2 value was achieved.

Derivatisation

Previous studies (e.g. George *et al.*, 1999; Olsen and Sunde, 2002; Rosa *et al.*, 2004) conducted derivatisations in which the amino acid sample extract was diluted 1:1000 with distilled water, and a subsample of the dilution was placed in a centrifuge with 10μl of OPA-NAC (ortho-phthaldialdehyde and N-acetyl-L-cysteine). This mixture was shaken for 20 seconds, and centrifuged for 15 minutes, at which time 475 μl of 0.05 M sodium acetate buffer was added. Finally, 200 μl of this solution was analysed by HPLC using methanol and sodium acetate for mobile phase at 1ml/min.

In contrast to the multi-step process described above, our study followed a different approach (Kaufman and Manley, 1998). We used OPA-IBLC (ortho-phthaldialdehyde and N-isobutyryl-l-cysteine) instead of OPA-NAC; our amino acid extract was rehydrated with 0.01M HCL and sodium azide (antibacterial) at 0.04 ml/mg lens and was subsequently was placed on the HPLC where derivatisation was performed in a single step within the autosampler syringe. Conducting the derivatisation in a single step within the syringe eliminates the possibility of inconsistencies or errors being introduced at each step of a separate derivatisation processes due to contamination and technician error. This in-needle derivatisation followed by immediate HPLC analysis greatly decreases chemical stability problems that have been observed with previous methods (George *et al.*, 1999; Olsen and Sunde, 2002; Rosa *et al.*, 2004).

STATISTICAL METHODS

Age estimation

Estimates of $(D/L)_i$ for the *i*th whale and $(D/L)_0$ are used to estimate age according to the equation

$$\mathrm{Age}_i = \frac{\log\{(1+(D/L)_i)/(1-(D/L)_i)\} - \log\{(1+(D/L)_0)/(1-(D/L)_0)\}}{2K_{asp}}$$

(Masters *et al.*, 1977; Bada *et al.*, 1980; George *et al.*, 1999). The $(D/L)_0$ value was estimated using an inverse variance weighted average of five values. The first value is 0.0250 (SE = 0.0013) from Rosa *et al.* (2013). This is estimated from a regression model using D/L data mostly for young whales of known ages (using corpora counts, baleen growth increments and fetal data). The remaining values are means of triplicate D/L measurements for four fetuses included in the present dataset. These values ranged from 0.0256 to 0.0293 with standard errors ranging from 0.0001 to 0.0005. The final estimated $(D/L)_0$ value used in the age equation is 0.0286 (SE = 0.0000629). For the *i*th whale, the observed data value of $(D/L)_i$ is taken to be the average of our three replicated measurements. We used K_{asp} = 0.000145 (SE 0.000145) from Rosa *et al.* (2013).

Variance estimation used a hybrid parametric and non-parametric bootstrap approach (Davison and Hinkley, 1997). The variance and 95% confidence interval were estimated separately for each whale. Also, separately, for each whale, we re-sampled the three independent D/L measurements uniformly with replacement. Within each bootstrap iteration we also employed parametric re-sampling of $(D/L)_0$ and K_{asp}. The approximate correlation between the estimates of $(D/L)_0$ and K_{asp} is minimal (i.e. 2×10^{-10}), so this was ignored during re-sampling. Together, these bootstrap sampled quantities were used to generate one bootstrap pseudo-estimate of Age_i. We used 10,000 bootstrap replications for each whale. Confidence intervals were generated using the percentile method.

Growth curve estimation

We used age estimates from 238 whales to estimate growth curves. Of these, 182 were previously aged using AAR, corpora counts, and baleen ageing methods (Lubetkin *et al.*, 2008; George *et al.*, 2011; IWC data[6]). We fit the two-stage von Bertalanffy II (1938) model to estimate sex-specific growth curves. We included 68 whales with ages estimated in the current study, which includes 11 whales aged here that had also previously been aged. Altogether, these amount to all bowhead ages we know to exist, except 4 cases excluded as obvious outliers (96B1, 98B25, 00B16, 01KK1), one case with reported standard deviation equal to 0 (95B8F), one whale of unknown sex (00B8) and one pseudohermaphrodite (81WW2). Lubetkin *et al.* (2012) also removed outliers. Like those authors, when more than one estimated age was available for a whale we used the inverse variance weighted mean. We also adopted the same modelling approach used by Lubetkin *et al.* (2012) except that we did not account for the growth spurt they modelled. Although the growth spurt is biologically plausible, we found that the simpler model had superior Bayes Information Criterion and seem to yield as good a fit with less complexity.

RESULTS

Age estimation

Table 1 provides estimated ages, bootstrap standard errors and bootstrap 95% confidence intervals for the age data for 68 bowhead whales. Negative age estimates can occur because the D/L values include measurement uncertainty and there may be minor model misfit and/or underestimation of uncertainty at the extreme lower range of our data. Such estimates should be interpreted as 'very young'. Three of the negative estimates are for foetuses and the fourth whale is probably a yearling (8.4m).

The most striking aspect of these results is that there is further evidence that some bowhead lifetimes may extend nearly 200 years or beyond. This is consistent with previous findings from other researchers (George *et al.,* 1999). Past recoveries of harpoons and bomb lances in landed

Table 1

Whale ID, length in meters (L), sex, age estimates (years), 95% confidence interval limits (%), standard error (SE).

Whale	L	Sex	Age	2.5	97.5	SE	Whale	L	Sex	Age	2.5	97.5	SE
81WW2	17.7	P*	73.3	55.6	100.1	11.6	05B21	8.8	F	12.9	9.8	17.9	2.1
96B5	14.9	F	121.5	91.7	167.9	19.5	05B25	13.2	F	14.8	11.2	20.5	2.4
97B5	10.1	F	4.9	3.7	6.7	0.8	05S5	16.5	F	47.3	36.0	64.6	7.4
97B7	13.2	F	13.0	9.9	18.0	2.1	05S7	18.0	F	81.5	61.7	112.2	13.1
97B8	13.6	F	18.5	14.0	25.7	3.0	06B6	13.3	M	28.0	21.0	38.7	4.5
97B10	16.7	F	58.2	43.9	80.4	9.3	06B10	6.3	F	1.3	1.0	1.9	0.2
97B12	15.3	M	67.4	51.1	92.7	10.7	06B18	14.4	M	54.6	41.4	75.3	8.7
98B4	13.1	F	22.0	16.7	30.1	3.5	07B8	14.9	M	87.3	66.1	120.7	14.0
98B5	15.1	M	95.4	72.1	130.9	15.2	07B9	14.3	F	31.4	23.7	43.3	5.1
98B10	13.0	F	13.7	10.4	19.0	2.2	07B9F*	4.1	F	–2.2	–3.1	–1.6	0.4
98B20	11.8	F	16.2	12.2	22.3	2.6	07B10	16.1	F	37.8	28.5	51.9	6.1
98B21	15.2	M	48.5	36.6	66.6	7.7	07B11	15.0	M	77.9	58.8	107.4	12.6
98WW2	14.1	F	20.9	15.7	28.8	3.3	07B12	14.8	F	32.1	24.4	44.2	5.1
02B2	16.7	F	51.9	39.4	71.8	8.3	07B13	16.6	M	88.5	66.9	121.3	14.2
02B3	19.2	F	106.3	80.5	145.8	16.9	07B16	14.4	F	28.4	21.5	38.9	4.5
02B5	8.5	F	4.7	3.6	6.5	0.8	07G3	15.3	F	39.8	29.7	55.6	6.6
02B17	9.3	F	7.4	5.6	10.1	1.2	07G4	15.2	F	29.1	21.9	40.3	4.7
02B21	10.0	F	12.5	9.4	17.3	2.0	07S1	10.0	M	9.4	7.1	12.8	1.5
02B22	8.1	F	1.6	1.2	2.3	0.3	07S2	8.3	F	7.4	5.5	10.3	1.2
03B6	13.9	F	19.3	14.5	26.6	3.2	07S3	10.7	M	17.7	13.3	24.5	2.9
03B9	16.4	F	68.3	51.6	93.4	11.0	07S4	15.2	F	34.8	26.3	47.7	5.5
04B4	14.2	F	22.1	16.8	30.3	3.5	08B14	13.6	F	27.3	20.8	37.7	4.4
04B5	16.8	F	80.0	60.3	110.9	12.9	08S3	19.1	F	187.6	141.7	258.1	30.2
04B5F*	4.1	F	0.7	0.5	1.1	0.1	09KK1F*	1.6	F	–3.2	–4.5	–2.4	0.5
04B8	13.6	F	23.9	18.2	32.8	3.8	10B15	12.5	M	20.0	15.1	27.5	3.2
04B9	14.9	F	18.5	14.0	25.6	3.0	11B3	17.5	F	55.9	42.4	77.1	9.0
04G2	8.7	F	4.3	3.2	5.9	0.7	11B4	7.8	F	2.5	1.2	4.1	0.7
04KK1	15.8	M	123.2	93.1	169.2	19.9	11B5	16.0	F	37.0	27.9	50.5	5.9
04KK2	6.7	M	0.0	–0.2	0.2	0.1	11B6	16.9	F	71.0	53.4	98.6	11.5
04KK3	8.4	F	7.0	5.2	9.8	1.2	11B7	15.4	F	157.2	119.5	217.2	25.1
04WW4	16.8	F	68.3	51.8	94.3	11.0	12B15	8.4	F	–0.6	–1.3	–0.2	0.3
05B8	8.2	M	1.7	1.1	2.5	0.4	12S2	13.6	M	23.2	17.6	32.3	3.8
05B11	12.1	F	18.6	13.9	25.6	3.0	12S2F*	3.8	F	–1.6	–2.4	–1.1	0.4
05B12	14.2	F	28.1	21.2	39.1	4.5	12S3	8.1	F	1.1	0.5	1.8	0.3

*F=foetus; P=pseudohermaphrodite.

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[6] IWC Datasets 'AARAges06.txt' and 'ages.060927.csv' available from the IWC Secretariat, 135 Station Road, Impington, Cambridge, CB24 9NP, United Kingdom [*http://www.iwc.int*].

whales also point to very long lifespans (George and Bockstoce, 2008).

The ages of 11 of the 68 whales assessed in this study have previously been estimated by other researchers using corpora counting (n = 9) and baleen isotope cycle analysis (n = 2) ageing techniques. Table 2 compares this study's estimates to other ageing results with the same whales. Although sample sizes for comparisons of age estimates using these different techniques are very small, it appears that the AAR estimate generated from this study is consistent with the two whales for which a baleen cycle age estimate had been determined (Lubetkin *et al.,* 2008). However, the corpora counting age estimates of George *et al.* (2011) for the same whales are generally higher than the age estimates determined from this AAR study.

Growth curve estimation

Fig. 1 shows a plot of the age estimates for the whales in this study, and 164 additional whales previously aged by other researchers. Each whale is represented by a circle (the point estimate) and a horizontal bar (spanning the 95% confidence interval for the corresponding age estimate). Red bars correspond to females, and males are represented by blue. The whales aged in our study are shown with heavier lines than for the whale ages from other researchers. The black lines in Fig. 1 show the fitted sex-specific von Bertalanffy II (1938) growth curves with female whales being larger than males of the same age.

It is worth noting that the confidence intervals in Fig. 1 are not used in the curve fitting, nor are they an output of it. They are merely to provide additional information about the age estimates using the best available information. Although they are broadly comparable, there may be some differences between methods, as examined in Table 2.

DISCUSSION

Considerable effort has gone into development and application of methods to age bowhead whales. Several approaches have emerged; each has some limitations. From the simplest to the most sophisticated, these methods assess body length, baleen length, baleen carbon cycling, number of corpora lutea and corpora albicantia, and AAR.

Measuring body length is not an effective method for estimating age. The correlation between body length and age in bowheads is poor, especially for older whales, and the relationship is sex-specific (Rosa *et al.,* 2011; George *et al.,* 1999). This phenomenon is well illustrated by the growth curves shown in Fig. 1.

Baleen length has also been used to estimate age. However, baleen is continuously worn down as bowheads grow older, and wear rates need to be estimated to apply the technique; hence, baleen length correlates best with age for whales under 10 years old (Lubetkin *et al.,* 2012) and is much less reliable for older individuals. Similarly, baleen carbon cycling analysis can only be reliably used for young whales (Lubetkin *et al*., 2008).

Corpora counting cannot be used for immature animals and is obviously not applicable for males. Resulting age estimates in mature female whales can have high standard errors similar to those from the earlier AAR age studies for bowheads (e.g. Olsen and Sunde, 2002; George *et al.,* 1999; 2011). To appropriately apply corpora ageing techniques, it is necessary to know life history and other parameters including age of sexual maturity, age of onset of senescence (or even whether there is senescence), ovulation rate (and potential changes thereof), and whether corpora albicantia persist through the life of the animal (Olsen and Sunde, 2002). Even so, the correlation of age estimates between corpora counting and AAR methods is surprisingly high for

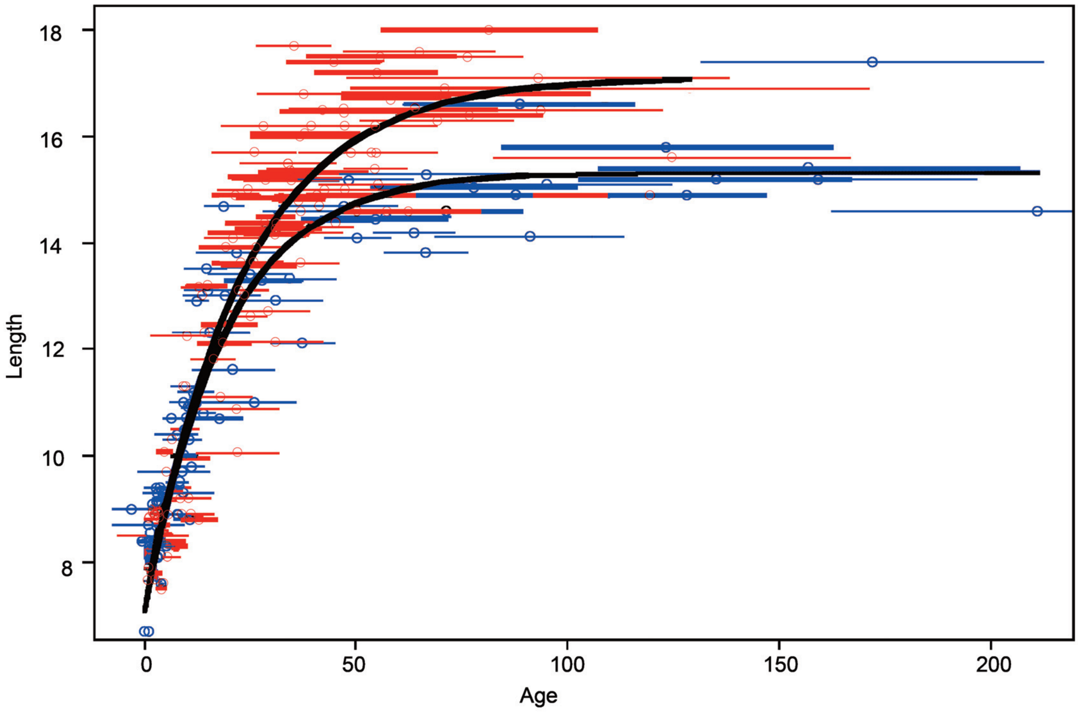

Fig. 1. Fitted von Bertalanffy growth curves. Each whale is represented by a circle (the point estimate) and a horizontal bar (spanning the 95% confidence interval). Red bars correspond to females and blue bars to males. The whales aged in this study are represented by thicker lines.

Table 2

Comparison of age estimates from other studies using alternative aging methods. L08 refers to Lubetkin *et al.* (2008). G11 refers to George *et al.* (2011). DAA refers to data available from the International Whaling Commission under its Data Availability Agreement (DAA).

Whale	Age	SE	Method	Citation
02B17	7.4	1.2	AAR	Here
	6.8	1.1	Baleen	DAA
02B2	51.9	8.3	AAR	Here
	79	18	Corpora	G11
	65.9	12.0	Corpora	DAA
02B21	12.5	2.0	AAR	Here
	11.7	2.3	Baleen	L08
02B3	106.3	16.9	AAR	Here
	139	38	Corpora	G11
	114.1	23.5	Corpora	DAA
03B9	68.3	11.0	AAR	Here
	102	26	Corpora	G11
	85.0	15.9	Corpora	DAA
04B8	23.9	3.9	AAR	Here
	31	6	Corpora	G11
04B9	18.5	3.0	AAR	Here
	43	8	Corpora	G11
05B12	28.2	4.6	AAR	Here
	38	7	Corpora	G11
96B5	121.4	19.5	AAR	Here
	125	38	Corpora	G11
	114.1	23.5	Corpora	DAA
97B10	58.2	9.3	AAR	Here
	65	14	Corpora	G11
	55.2	9.3	Corpora	DAA
97B8	18.5	3.0	AAR	Here
	31	6	Corpora	G11
	27.5	5.1	Corpora	DAA

mature female bowhead whales and CVs are sometimes comparable (George *et al.,* 2011).

In summary, alternative methods to AAR for age determination all have noteworthy drawbacks when applied to whole populations of bowhead whales. AAR appears to be the most promising method for population level assessments of age-specific life history parameters.

The alternative methods of age estimation mentioned above are fundamentally based on biological processes of individual whales (which can vary across a population based on health status, nutrition, and other factors). In contrast, AAR analysis is based on the rate of a chemical reaction governed only by physical-chemical processes, and as such, there is less inherent variation in response among individuals due to biotic factors (Bada *et al.,* 1980; George *et al.,* 1999; Rosa *et al.,* 2004; 2013; Wetzel *et al.,* 2007).

Although earlier studies using AAR provided valuable contributions to the development of a chemical analysis method for ascertaining ages of mysticetes, the modifications to the previously used AAR method offer improvement of an important tool for determining age. The specific AAR method modifications identified and applied in this study include (a) species specific hydrolysis time and temperature that optimises the preparation of the bowhead lens proteins for further AAR analysis; (b) using alternate amino acid derivatising reagents and (c) elimination of the separate amino acid derivatisation steps to reduce technician error and sample contamination, which helps to ensure stable and consistent results for greatly improved reproducibility.

The methodological changes provided D/L data that are remarkably consistent, and hence provide age estimates with greater precision than has been reported for other studies (Table 3). The average coefficients of variation (CVs) and ranges of CVs in this study were notably lower than those generated by four other AAR studies for estimating age of bowhead or minke whales (*Balaenoptera acutorostrata*). The use of this AAR modified method to provide estimates that have improved precision can enhance the value of ageing data and may help scientists to establish reliable age-specific vital rates (e.g. age at sexual maturation; reproductive rates; age-specific survival; longevity) of both sexes and all ages of bowhead whales. In turn, this may help resource managers consider possible changes in bowhead life history parameters in a changing Arctic environment. Moreover, having an accurate and precise ageing technique and a fitted growth curve for both sexes can help scientists and managers better understand whether particular demographic groups are most vulnerable to ship strikes and entanglements; assess changes over time in the extent to which fishing, shipping and other threats (e.g. contaminants) affect particular age groups; and proactively inform effective mitigation actions before consequences of threats become critical.

The benefits of using AAR assays to estimate age do not end with bowhead whales. The approach can be applied to other hard-to-age homeotherms (e.g. other mysticetes, birds, deep sea invertebrates) of ecological or economic importance to help provide improved life history information for better-informed management and conservation decisions.

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Table 3

Comparison of the CVs of estimated average ages, CVs of ranges of ages, and method differences from five AAR whale studies.

	George *et al.* (1999)	Olsen and Sunde (2002)	Rosa *et al.* (2004)	Rosa *et al.* (2012)	Wetzel *et al.* (this study)
Hydrolysis time and temperature	6 hrs @ 100°C	6 hrs @ 90°C	6 hrs @ 100°C	6 hrs @ 100°C	8 hrs @ 80°C
Derivatisation reagents	OPA-NAC	OPA-NAC	OPA-NAC	OPA-NAC	OPA-IBLC
Multi-step derivatisation	Yes	Yes	Yes	Yes	No
Average age estimate CVs	55%	78%	90%	34%	17%
Range of age estimate CVs	17–600%	22–245%	17–432%	16–143%	15–24%

sharing their expertise on bowheads. The bowhead samples were collected under NMFS Permit #17350 to the NSB Department of Wildlife Management.

REFERENCES

Bada, J.L., Brown, S. and Masters, P.M. 1980. Age determination of marine mammals based on aspartic acid racemization in the teeth and lens nucleus. *Rep. int. Whal. Commn* (Special Issue 3): 113–118.

Davison, A.C. and Hinkley, D.V. 1997. *Bootstrap Methods and Their Applications*. Cambridge University Press, Cambridge, England. 582pp.

George, J.C. 2009. Growth, morphology and energetics of bowhead whales (*Balaena mysticetus*). Doctoral Dissertation, University of Alaska Fairbanks. 168pp.

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*) using 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 Biology* (31):751–4.

George, J.C., Follmann, E., Zeh, J., Sousa, M., Tarpley, R. and Suydam, R. 2011. A new way to estimate whale age using ovarian corpora counts. *Can. J. Zool.* 89: 840–52.

Goodfriend, G.A. 1997. Aspartic acid racemization and amino acid composition of the organic endoskeleton of the deep-water colonial anemone *Gerardia*: determination of longevity from kinetic experiments. *Geochimica et Cosmochimica Acta*. 61:1,931–9.

Goodfriend, G.A. and Meyer, V.R. 1991. A comparative study of the kinetics of amino acid racemization/epimerization in fossil and modern mollusk shells. *Geochimica et Cosmochimica Acta*. 55:3,355–67.

Hohn, A.A. 2009. Age estimation. pp.11–17. *In:* W.F. Perrin, B. Würsig and J.G.M. Thewissen (eds.) *Encyclopedia of Marine Mammals*. Elsevier Inc., San Diego, CA. 1,352pp.

Kaufman, D.S. and Manley, W.F. 1998. A new procedure for determining DL amino acid ratios in fossils using reverse phase liquid chromatography. *Quat. Geochronology*. 17:987–1,000.

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.

Lubetkin, S.C., Zeh, J. and George, J. 2012. Statistical modeling of baleen and body length at age in bowhead whales. *Can. J. Zool*. 90(8):915–31.

Masters, P.M., Bada, J.L. and Zigler, J.S. 1997. Aspartic acid racemization in the human lens during ageing and in cataract formation. *Nature.* 268:71–3.

Olson, E. and Sunde, J. 2002. Age determination of minke whales (*Balaenoptera acutorostrata)* using the aspartic acid racemization technique. *Sarsia*. 87:1–8.

Reynolds, J.E., Perrin, W.F., Reeves, R.R., Ragen, T.J. and Montgomery, S. (eds.) 2005. *Marine Mammal Research: Conservation Beyond Crisis*. Johns Hopkins University Press, Baltimore, Maryland. 223pp.

Rosa, C., George, J. C., Zeh, J., Botta, O., Zauscher, M., Bada, J. and O'Hara, T. M. 2004. Update on age estimation of bowhead whales (*Balaena mysticetus*) using aspartic acid racemization. Paper SC/56/BRG6 presented to the IWC Scientific Committee, June 2004 Sorrento, Italy (unpublished). 15pp. [Paper available from the Office of this Journal]

Rosa, C., Zeh, J., George, J.C., Botta, O., Zauscher, M., Bada, J. and O'Hara, T.M. 2011. Age estimates based on aspartic acid racemization for bowhead whales (*Balaena mysticetus*) harvested in 1998–2000. Paper SC/63/BRG5 presented to the IWC Scientific Committee, June 2011, Tromsø, Norway (unpublished). 14pp. [Paper available from the Office of this Journal].

Rosa, C., Zeh, J., George, J. C., Botta, O., Zauscher, M., Bada, J. and O'Hara, T.M. 2013. Age estimates based on aspartic acid racemization for bowhead whales (*Balaena mysticetus*) harvested in 1998–2000 and the relationship between racemization rate and body temperature. *Mar. Mamm. Sci*. 29:424–45.

Von Bertalanffy, L. 1938. A quantitative theory of organic growth (Inquiries on growth laws, II). *Hum. Biol.* 10(2):181–213.

Wetzel, D.L., Mercurio, P., Reynolds, J.E. and George, J.C. 2007. The pursuit of precise and accurate methods to determine ages of bowhead whales (*Balaena mysticetus*). Paper presented at 17th Biennial Conference on the Biology of Marine Mammals, Cape Town, South Africa, November–December 2007.

New data on Soviet catches of blue (*Balaenoptera musculus*) and right whales (*Eubalaena japonica*) in the North Pacific

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ABSTRACT

Details are provided on 17 previously unreported catches of blue whales, and 93 catches of North Pacific right whales, all taken illegally by the former USSR. The blue whale catches were made between mid-July and mid-September 1972 in the eastern North Pacific at distances of from 96 to 626 nautical miles from the US west coast (Oregon and Washington); they highlight the inadequacy of the International Observer Scheme, as implemented in 1972, to report or detect illegal whaling. These previously unknown blue whale catches bring the Soviet total to 1,638 for the period 1948–1972. The 93 right whale catches were made during the period 1951–62 around the Kuril Islands, which brings the known total of takes of this species from 1935–1971 to 775 (including 10 taken for scientific research and officially reported at the time).

KEYWORDS: WHALING–MODERN; NORTH PACIFIC; BLUE WHALE; NORTH PACIFIC RIGHT WHALE; KURIL ISLANDS; OBSERVER SCHEME; SOVIET WHALING

INTRODUCTION

It is now well-established that the former USSR conducted a global campaign of illegal whaling for three decades after 1945 (e.g. Yablokov, 1994; Ivashchenko and Clapham, 2014). Since this revelation, extensive efforts have been undertaken to correct the falsified catch record and related information reported by the USSR to the International Whaling Commission (IWC) via the Bureau of International Whaling Statistics (BIWS). The catch record was revised using 'true' catch data that had been retained either by former whaling industry biologists or available in public archives in the Russian Federation. Using the true data, Ivashchenko *et al.* (2013) reported corrected catch totals for Soviet whaling operations (1948–79) in the North Pacific. These included 1,621 blue whales, *Balaenoptera musculus* (of which only 858 were officially reported to the IWC), as well as 681 North Pacific right whales, *Eubalaena japonica* (none of which were reported).

Here, we provide details of previously unreported catches of 17 blue whales and 93 right whales, made by Soviet whaling fleets; we also provide updated totals for Soviet catches of these two species in the North Pacific. The new data were discovered in previously unread Soviet whaling industry reports, as noted below.

METHODS AND MATERIALS

As described previously, true catch data for Soviet whaling operations were summarised in formerly secret industry reports that were declassified after Yablokov (1994) revealed the USSR's illegal whaling. For the North Pacific, these reports were primarily found in Russian public archives; the types and limitations of the reports are described in detail in Ivashchenko *et al.* (2013).

The data summarised here come from a total of 12 scientific reports or whaling station logbooks, all unpublished, that had not previously been seen by the authors; details are provided below.

RESULTS AND DISCUSSION

Blue whales

Data on the 17 blue whale catches were discovered in the joint scientific report for the *Vladivostok* and *Dalniy Vostok* whaling fleets for the 1972 whaling season (Isakov *et al.*, 1973).

The catches are listed in Table 1 below. Since the report gives joint figures for the *Vladivostok* and *Dalniy Vostok*, it is not possible to determine with certainty whether the catches were made by one or both factory fleets. However, although noon position data are known to be not entirely accurate for Soviet fleets (Ivashchenko and Clapham, 2017) they are generally reliable. The positions match those of *Dalniy Vostok* in the original BIWS data to within 2 or 3 degrees longitude; whereas the *Vladivostok* positions in the original IWS data differ by 24 to 45 degrees longitude. It therefore seems most likely that these whales were taken by the *Dalniy Vostok.* The report gives the catch data in a table only, with no further discussion or information in the main text. To our knowledge, there were no other illegal catches made by either factory fleet in 1972, although the numbers for legal catches in 1972 reported to BIWS differed from those given in Ivashchenko *et al.* (2013).

These previously unknown catches bring the total Soviet catch of North Pacific blue whales since 1948 to 1,638; revised figures by year and whaling operation are given in Table 2. Catch locations are shown in Fig. 1; these were at distances from the coasts of Washington and Oregon ranging from 96 to 626 n.miles. For convenience and context, Fig. 2 shows the locations of all Soviet blue whale catches ($n = 236$ animals) for which position data are available.

It is not clear how the Soviet fleet was able to kill blue whales in that season (blue whales were completely

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Table 1

Soviet catches of blue whales in the eastern North Pacific by the *Vladivostok* and *Dalniy Vostok* whaling fleets, 1972. Stomach contents are presumed to be krill in all cases, but this is not specified in the source material (nor were they identified to species).

	Month	Day	Sex	Length (m)	Long.	Lat.	Stomach contents
1	July	17	F	19.6	135 57’ W	44 14’	Small qty krill
2	July	17	M	21.8	135 57’ W	44 14’	Full
3	July	18	M	20.1	133 53’ W	42 44’	Full
4	July	27	M	21.5	128 56’ W	43 40’	Full
5	July	27	M	22.0	128 56’ W	43 40’	Full
6	August	1	M	21.3	127 52’ W	45 16’	Full
7	August	3	F	23.0	126 26’ W	44 02’	Full
8	August	22	F	18.5	134 47’ W	47 29’	Small qty krill
9	August	22	M	21.6	134 47’ W	47 29’	Full
10	August	22	F	24.0	134 47’ W	47 29’	Full
11	August	22	M	20.0	134 47’ W	47 29’	Full
12	August	22	F	20.3	134 47’ W	47 29’	Full
13	August	23	M	17.4	131 59’ W	46 17’	Small qty krill
14	September	2	F	20.7	135 21’ W	45 43’	Full
15	September	2	M	20.5	135 21’ W	45 43’	Full
16	September	2	M	20.0	135 21’ W	45 43’	Full
17	September	13	F	20.0	138 46’ W	44 42’	Full

Table 2

Soviet catches of blue whales in the North Pacific, 1948–78 (revised after Ivashchenko *et al.* 2013, Table 6). Numbers in parentheses are the officially reported catches. Another 29 blue whales were caught by the Soviet factory ship *Aleut* prior to 1948.

Year Station/floating factory	*Aleut*	*Kuril Islands*	*Sovetskaya Rossiya*	*Vladivostok*	*Dalniy Vostok*	*Slava*	Total (reported)
1948	3	–	–	–	–	–	3 (3)
1949	3	–	–	–	–	–	3 (3)
1950	5	2	–	–	–	–	7 (7)
1951	7	9	–	–	–	–	16 (16)
1952	7	17	–	–	–	–	24 (24)
1953	11	10	–	–	–	–	21 (21)
1954	12	23	–	–	–	–	35 (35)
1955	4	27	–	–	–	–	31 (31)
1956	7	45	–	–	–	–	52 (52)
1957	9	44	–	–	–	–	53 (53)
1958	–	14	–	–	–	–	14 (14)
1959	22	19	–	–	–	–	41 (41)
1960	–	14	–	–	–	–	14 (14)
1961	2	15	–	–	–	–	17 (17)
1962	19	11	37	–	–	–	67 (30)
1963	14	1	108	299	88	–	510 (348)
1964	17	–	79	25	67	–	188 (77)
1965	10	–	43	163	–	–	216 (72)
1966	–	–	–	15	45	–	60 (0)
1967	–	–	–	51	43	–	94 (0)
1968	–	–	–	3	28	25	56 (0)
1969	–	–	–	2	15	33	73 (0)
1970	–	–	–	7	12	–	19 (0)
1971	–	–	–	4	3	–	7 (0)
1972	–	–	–	17	–	17 (0)	–
Total	**152**	**251**	**267**	**592**	**301**	**58**	**1,638 (878)**

protected at that time), since 1972 saw the introduction of the IWC’s International Observer Scheme (IOS), which required foreign observers to be placed aboard factory ships. The IOS agreement specifically required that Japan and the USSR exchange observers on each other’s factory ships in the North Pacific and the Antarctic. During the 1972 IWC meeting, the IOS report (IWC, 1972) noted that appointments had been made by the Commission for the North Pacific observers and the exchange was between Japan and the USSR. The USSR provided IOS observers for all three of the Japanese factory ships that operated in the North Pacific in 1972. All of the IOS observers were paid by the government that nominated them but formally reported to the IWC.

At the 1973 IWC meeting, the IOS report (IWC, 1973) provided the details from the observers from the summer of 1972 in the North Pacific. Mr. S. Imazeki, a government supervisor on Japanese factory ships in the Antarctic, was assigned to the *Dalniy Vostok* and was aboard the vessel from June to September 1972. Mr M. Mizuno, an officer of a Japanese factory ship in the Antarctic, was assigned to the Soviet factory ship *Vladivostok* for the period June to

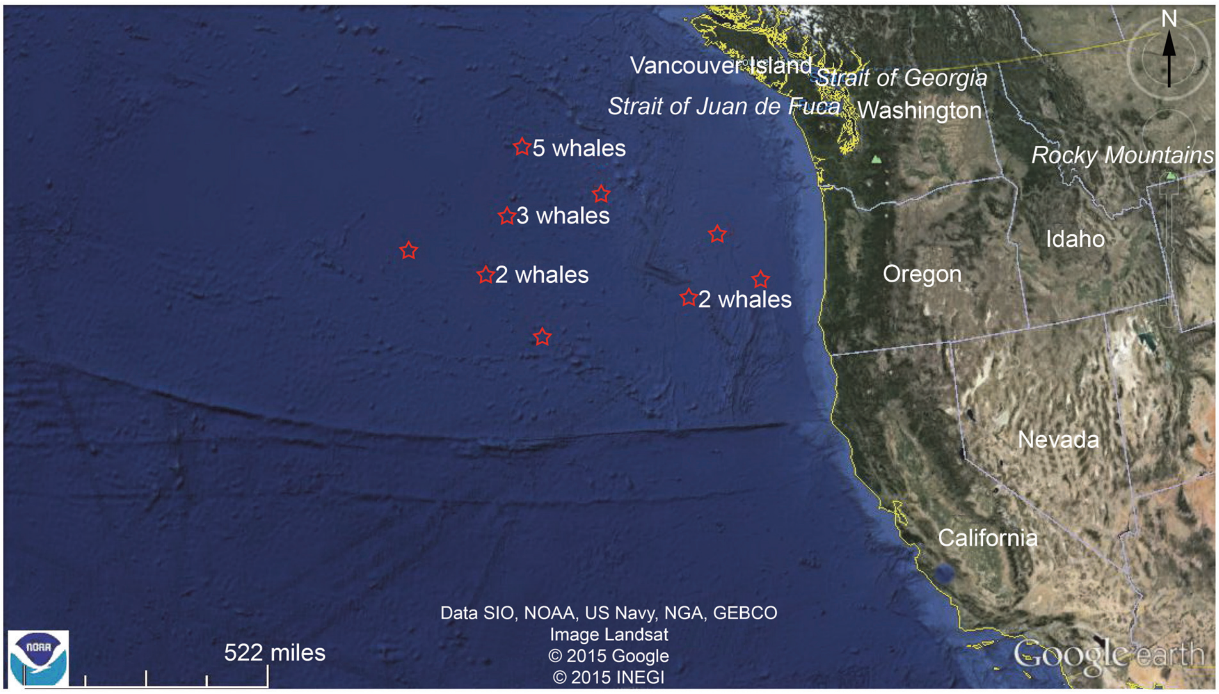

Fig. 1. Locations of previously unreported Soviet blue whale catches in 1972. Stars with no text represent single animals.

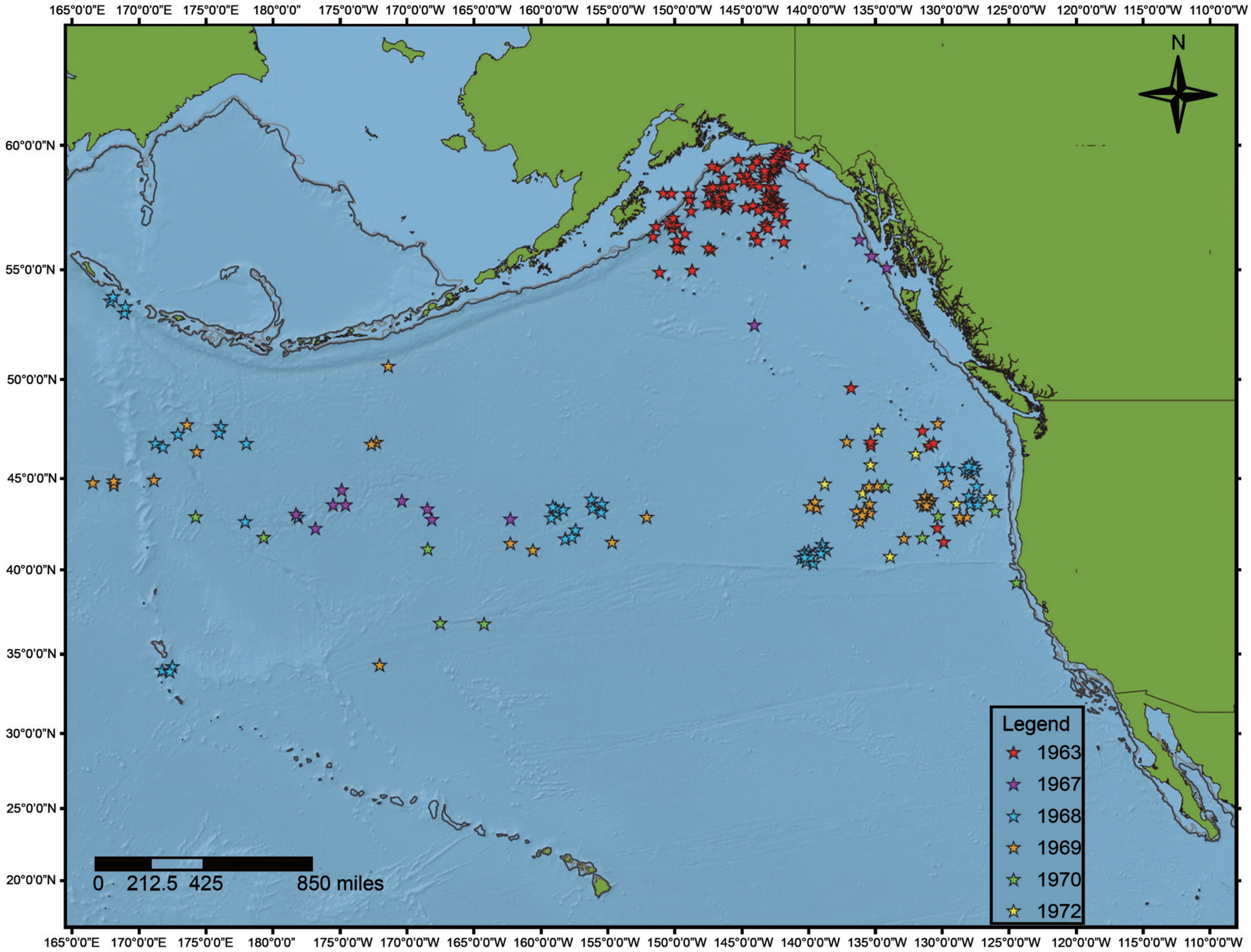

Fig. 2. Locations of all Soviet blue whale catches (*n* = 236) for which position data exist.

September 1972. Both observers were aboard when the blue whale catches were made. All of the IOS observers were provide with copies of the Convention and Schedule and a memorandum outlining their duties. They were asked to deal with serious infractions immediately and inform the Commission as soon as possible but 'no serious infractions were reported'. Imazeki reported only that six undersized whales were taken (five fin and one sei whale), and Mizuno reported that two undersized whales were landed (one fin and one sei whale). The infractions reported are minor compared to the catch of blue whales which had been protected in the North Pacific since the 1966 season[3]. It is possible that this small number of blue whales were processed at night when the observers were sleeping, but this also shows the limitation of the IOS. Therefore, as has been noted by others (Mikhalev *et al.*, 2009), it is clear from the blue whale takes reported here that illegal catches continued at some level despite implementation of the IOS.

North Pacific right whales

All of the 93 'new' right whale catches summarised here were made by the Soviet land whaling stations in the Kuril Islands (Fig. 3) between 1951 and 1962 (Table 3).

More detailed information on 34 of these whales was found in logs of catches kept by the land stations; these logs were later deposited in public archives. Details are summarised in Table 3, which for the sake of completeness also includes 10 right whales (not included in the overall total of 34) killed for scientific research in 1955 and officially reported to the IWC. Location data are available for some catches; the accuracy of this information is unknown but it likely provides a good general guide to where whales were taken within the Kurils.

Lengths are given for most of the whales, and range from 10.75m (described in the report concerned as a calf, although from its length we would consider it to be more than one year of age) to 11 whales with lengths equal to or more than 17m. Weights are also given for many animals, although it is not clear how these were calculated. In the report on 10 whales taken for scientific research in 1955, Klumov (1962) notes that, where possible, the weight of individual whales was calculated by weighing body parts as the animals were butchered, although apparently no allowance was made for loss of blood. Therefore, weights given are certainly underestimated; Lockyer (1976) suggested by at least 6% for baleen whales based upon limited data. There is no information on how weights were calculated for whales killed in other years, but the fact that Table 3 includes instances of whales that are heavier than others despite being of shorter length implies that the whaling stations were not

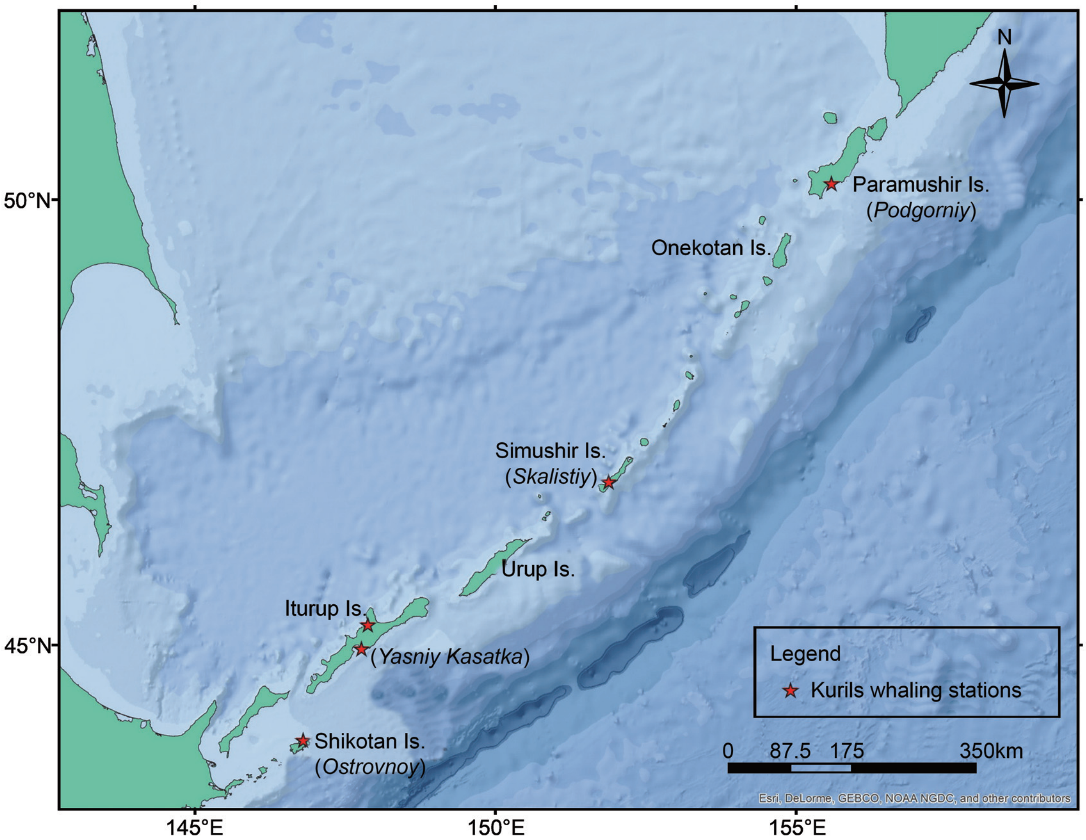

Fig. 3. Location of Soviet shore whaling stations in the Kuril Islands.

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[3] At the 1965 Commission meeting, no objections were made by any of the Contracting Governments present, including the USSR, for the binding amendment proposed to paragraph 4(1) of the Schedule under which "it is forbidden to kill or to attempt to kill blue whales in the North Pacific Ocean and its dependent waters north of the Equator for five years beginning with the 1966 season". In a statement by the USSR delegation at the Special Meeting of Commissioners from North Pacific Member Nations, which took place in Honolulu, Hawaii, from 14 to 17 February 1966, they stated 'it supports the resolution [*sic*] of the Commission forbidding the taking of blue whales in the North Pacific for five years from the 1966 season' (IWC, 1967, p.72). At the 1970 meeting of the IWC Scientific Committee, it was recommended 'that the present ban on killing blue and humpback whales be extended for at least three years beginning with the 1971 season' (IWC, 1971, p.21). The Contracting Governments at the 1970 Commission meeting agreed with the Scientific Committee and extended the existing North Pacific ban on killing blue whales.

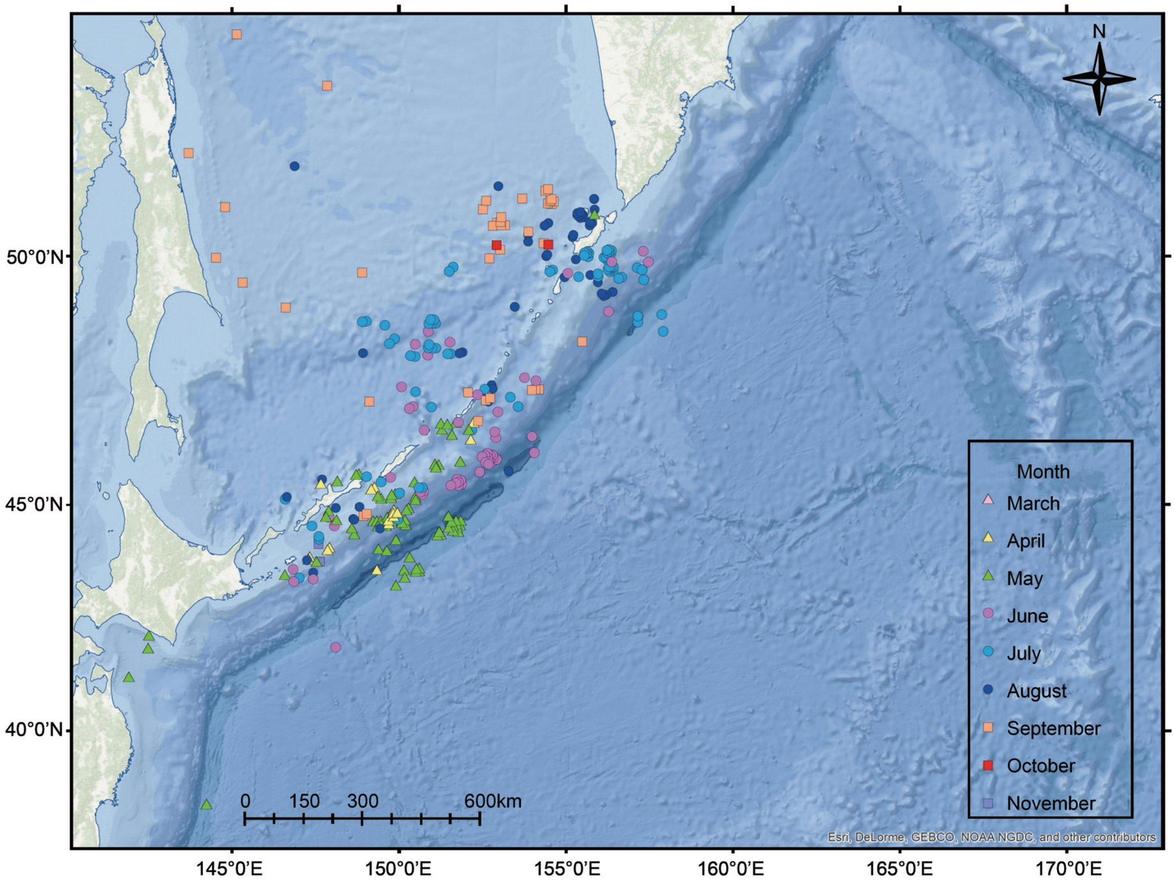

Fig. 4. Locations of Soviet catches or sightings of right whales in the Kuril Islands and Okhotsk Sea (where known) for the period 1951–1968.

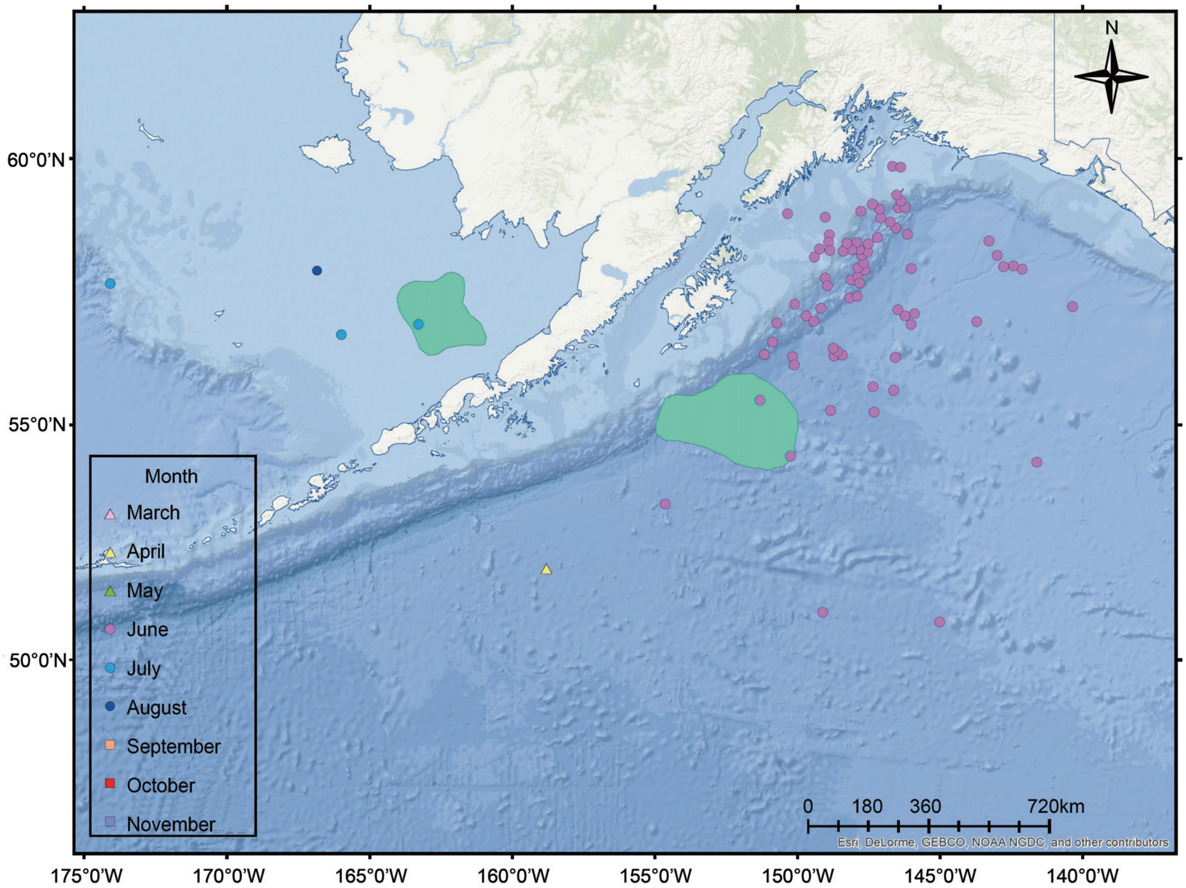

Fig. 5. Locations of Soviet catches of right whales in the 1960s off Alaska in the eastern North Pacific (where known). The two green 'blobs' were identified as catch areas in the 1960s by Doroshenko (2000). See Ivashchenko and Clapham (2012) for further details and discussion.

Table 3

Catches of North Pacific right whales from the Kuril Islands, 1951–63. When 'Kurils' is given as the area, the specific land station is unknown. All 10 catches made in 1955 were previously reported to the IWC as being for scientific research; others represent previously unpublished data.

Year	Month	Day	Area	Lat. N	Long. E	No. whales	Length (m)	Blubber thickness (cm)	Details	Source
1951	June	19	Podgorniy	–	–	1	14.5	20	Product weight = 23.4t	Anon (1957a)
1951	June	28	Podgorniy	–	–	1	17.3	26	Product weight = 40.2t	Anon (1957a)
1951	July	9	Podgorniy	–	–	1	11.8	16.2	Product weight = 15.8t	Anon (1957a)
1951	July	10	Podgorniy	–	–	1	13.2	21.6	Product weight = 18.5t	Anon (1957a)
1951	July	12	Podgorniy	–	–	1	12.2	17	Product weight = 16t	Anon (1957a)
1951	July	16	Podgorniy	–	–	1	17.2	23	Product weight = 44.9t	Anon (1957a)
1951	July	18	Podgorniy	–	–	1	15	20.4	Product weight = 40.2t	Anon (1957a)
1953	April	–	Kurils	46.70	152.23	1	15.9	16.5	Weight = 46.1t	Anon (1953)
1953	May	–	Kurils	43.48	146.58	1	14.9	19.1	Weight = 44.6t	Anon (1953)
1953	June	–	Kurils	44.72	147.90	1	14.3	16	Weight = 60.2t	Anon (1953)
1953	June	–	Kurils	44.53	148.07	1	18.1	14	Weight = 93.9t	Anon (1953)
1953	July	–	Kurils	43.42	147.02	1	17.2	19	Weight = 67.7t	Anon (1953)
1953	August	–	Kurils	43.80	147.25	1	16.9	24.2	Weight = 70.5t	Anon (1953)
1953	August	–	Kurils	43.53	147.43	1	11.7	12.3	Weight = 37.6t	Anon (1953)
1953	August	–	Kurils	44.92	148.12	1	11.3	11.7	–	Anon (1953)
1954	May	–	Kurils	–	–	1	14.8	–	–	Anon (1954)
1954	June	–	Kurils	43.33	146.85	1	13.2	–	–	Anon (1954)
1954	June	–	Kurils	43.38	147.43	1	15.2	–	Weight = 55t	Anon (1954)
1954	July	–	Kurils	–	–	1	15.6	–	Weight = 56t	Anon (1954)
1955	May	17	Kurils	45.13	149.77	1	18.3	–	Pregnant female (1.9m embryo)	Klumov (1962)
1955	June	1	Kurils	46.38	152.90	1	17	–	Mature male; weight = 66.134t	Klumov (1962)
1955	June	19	Kurils	47.02	150.42	1	16.3	–	Lactating female; weight = 58.59t	Klumov (1962)
1955	July	13	Kurils	49.73	157.28	1	17.06	–	Mature male; weight = 53.485t	Klumov (1962)
1955	July	22	Kurils	49.57	156.58	1	17.4	–	Lactating female with calf; weight = 106.5t	Klumov (1962)
1955	July	22	Kurils	49.70	154.52	1	10.75	–	Male calf	Klumov (1962)
1955	August	10	Kurils	50.78	155.35	1	16.6	–	Mature male; weight = 63.13t	Klumov (1962)
1955	August	10	Kurils	50.37	155.20	1	16.6	–	Mature male	Klumov (1962)
1955	August	11	Kurils	51.08	155.85	1	11.35	–	Immature female, possibly just weaned	Klumov (1962)
1955	August	28	Kurils	50.00	154.42	1	17.8	–	Pregnant female (4.4m embryo)	Klumov (1962)
1955	–	–	Kurils	–	–	13	–	–	No further information	Klumov (1956)
1956	June	–	Kasatka	–	–	1	16.6	11.8	Female; weight = 80t	Anon (1956)
1956	–	–	Podgorniy	–	–	10	–	–	No further information	Klumov (1957)
1956	–	–	Skalistiy	–	–	35	–	–	No further information	Klumov (1957)
1957	May	–	Skalistiy	–	–	1	17.8	25	Weight = 76t	Anon (1957b)
1957	May	–	Skalistiy	–	–	1	19.0	25	Weight = 106.7t	Anon (1957b)
1957	May	–	Skalistiy	–	–	1	14.3	15?	Weight = 42.6t	Anon (1957b)
1957	May	–	Skalistiy	–	–	1	15.7	19.5	Weight = 59.5t	Anon (1957b)
1957	June	–	Podgorniy	–	–	1	–	–	Weight = 64.2t	Anon (1957b)
1957	–	–	Kurils	–	–	1	–	–	No information	Anon (1957c)
1958	May	–	Yasniy	–	–	1	17.5	15.8	Weight = 70.0t	Anon (1958)
1958	May	–	Yasniy	–	–	1	14.5	13.5	Weight = 53.2t	Anon (1958)
1958	June	–	Skalistiy	–	–	1	16.0	21.5	Weight = 54?t	Anon (1958)
1959	May	–	Kasatka	–	–	1	18.4?	25.2	Weight = 114t; length decimal difficult to read	Anon (1959)
1960	–	–	Kurils	–	–	1	–	–	Weight = 60.8t	Anon (1960)
1961	–	–	Kurils	–	–	2	–	–	Combined weight = 64.0t	Anon (1961)
1962	April	–	Kurils	–	–	1	–	–	Weight = 20.3t	Anon (1962)

calculating weight based upon a standard length-weight formula. It is possible that some estimate of total weight was derived from the weight of products obtained.

With these caveats in mind, the catches contain some remarkably large animals. The four heaviest whales were: (1) 18.1m, 93.9 tons, sex unreported, taken in June 1953; (2) 17.4m female, 106.5 tons, July 1955; (3) 19m, 106.7 tons, sex unreported, May 1957; and (4) 18.4m (the decimal is difficult to read in the report), weight listed as 114 tons, sex unreported. In previously reported data on Soviet catches of North Pacific right whales, Ivashchenko and Clapham (2012) reported several animals whose length exceeded 18m.

Catches of an additional 46 right whales were found in a scientific report (Klumov, 1957) summarising research conducted in the year 1956 in the Kuril Islands (including at the five Soviet Kuril shore whaling stations which were operated by Japan prior to World War 2). In an unnumbered table on page 11 of the report, 46 right whales are broken down by sex (24 males, 22 females); these were all examined at the Soviet Kuril whaling stations, with most (35 animals) taken by the Skalistiy land station on Simushir Island in the central Kurils. There was no further information on the biological details of these catches.

The new data bring the known total of right whale catches by the USSR for the period 1935–1971 to 771 (including the 10 taken for scientific research in 1955). Table 4 breaks these catches down by year and area; this is as complete an accounting as available at present. The possibility that some additional data will be found cannot be ruled out, but it is unlikely that there were many more catches than summarised here.

Locations for Soviet right whale catches are known in only some cases. For the sake of completeness, we have

Table 4

Soviet catches of North Pacific right whales by year and area, 1935–71 (revised with new data). ENP = Eastern North Pacific. Unk = Unknown area. Differences in totals between this table and those shown in Ivashchenko and Clapham (2012) and Ivashchenko *et al.* (2013) reflect new data found during the present study.

		Eastern North Pacific				Western North Pacific			
Year	Total catch	Gulf of Alaska	Aleutian Islands	Bering Sea	ENP Pelagic	Okhotsk Sea	Kuril Islands	Kamchatka	Unk
1935	1	–	–	–	–	–	–	1	–
1936	0	–	–	–	–	–	–	–	–
1937	1	–	–	–	–	–	–	1	–
1938	0	–	–	–	–	–	–	–	–
1939	2	–	–	–	–	–	–	2	–
1940	0	–	–	–	–	–	–	–	–
1941	0	–	–	–	–	–	–	–	–
1942	0	–	–	–	–	–	–	–	–
1943	0	–	–	–	–	–	–	–	–
1944	3	–	–	–	–	–	–	–	3
1945	1	–	–	–	–	–	–	–	1
1946	1	–	–	–	–	–	–	–	1
1947	0	–	–	–	–	–	–	–	–
1948	0	–	–	–	–	–	–	–	–
1949	0	–	–	–	–	–	–	–	–
1950	0	–	–	–	–	–	–	–	–
1951	7	–	–	–	–	–	7	–	–
1952	0	–	–	–	–	–	–	–	–
1953	8	–	–	–	–	–	8	–	–
1954	4	–	–	–	–	–	4	–	–
1955	10	–	–	–	–	–	23	–	–
1956	46	–	–	–	–	–	46	–	–
1957	6	–	–	–	–	–	6	–	–
1958	3	–	–	–	–	–	3	–	–
1959	2	–	–	–	–	–	2	–	–
1960	1	–	–	–	–	–	1	–	–
1961	2	–	–	–	–	–	2	–	–
1962	24	–	21	–	–	–	1	–	2
1963	266	253	10	–	3	–	–	–	–
1964	200	87	–	113	–	–	–	–	–
1965	20	20	–	–	–	–	–	–	–
1966	3	3	–	–	–	–	–	–	–
1967	134	3	–	3	–	126	–	–	2
1968	6	–	–	–	–	6	–	–	–
1969	1	–	–	–	1	–	–	–	–
1970	0	–	–	–	–	–	–	–	–
1971	10	–	–	–	–	10	–	–	–
Total	**775**	**366**	**31**	**116**	**4**	**142**	**103**	**4**	**9**

plotted these together with right whale sightings in the Kurils and Okhotsk Sea in Fig. 4; it is not possible to distinguish sightings and catches in the source material. Catches (only) in the eastern North Pacific are plotted in Fig. 5. The distribution and timing of the catches has either been discussed previously (Ivashchenko and Clapham, 2012) or is beyond the scope of the present paper.

REFERENCES

Anon. 1953. Zurnal ucheta dobichi kitov sudami Kuril'skoy kitoboynoy flotilii za 1953g. T.1,2. [Log book of whale catches by the vessels of the Kurils whaling fleet]. *Kuril'skaya Kitoboynaya Flotiliya* 1, 2: 76.

Anon. 1954. Svedeniya o dobiche kitov sudami Kuril'skoy kitoboynoy flotilii za 1954g. [Information about whale catches by the vessels of the Kurils whaling fleet in 1954]. *Kuril'skaya Kitoboynaya Flotiliya*: 93.

Anon. 1956. Zurnal ucheta dobichi kitov sudami Kuril'skoy kitoboynoy flotilii za 1953g. T.1,2 [Log book of whale catches by the vessels of the Kurils whaling fleet]. *Kuril'skaya Kitoboynaya Flotiliya* 1, 2: 76.

Anon. 1957a. Proizvodstvenno-texnicheskiy otchet o rabote kitokambinata Podgorniy for 1948, 1955–57, chimlaboratorii kombinata for 1950–51 and 1953–54. [Production-technology report on work results of the whaling land station Podgorniy during 1948, 1955–57, and chemistry laboratory at the station during 1950–51 and 1953–54]. Vladivostok, Upravlenie Kitoboynikh Flotiliy. 227pp.

Anon. 1957b. Promisloviy otchet Vtoroy Dal'nevostochnoy kitoboinoy flotilii za sezon 1957g. [Whaling report of the Second Far Eastern whaling fleet for 1957 season]. Vladivostok. *Upravlenie Kitoboynikh Flotiliy*: 86pp.

Anon. 1957c. Zurnal ucheta dobichi kitovogo sirtsa sudami 2-oy Dal'nevostochnoy kitoboynoy flotilii za 1957g. [Log book of whale catches by the vessels of the Second Far Eastern whaling fleet in 1957] *Vtoraya Dal'nevostochnaya Kitoboynaya Flotiliya*: 85pp.

Anon. 1958. Zurnal ucheta dobichi kitovogo sirtsa sudami 2-oy Dal'nevostochnoy kitoboynoy flotilii za 1958g. [Log book of whale catches by the vessels of the Second Far Eastern whaling fleet in 1958]. *Vtoraya Dal'nevostochnaya Kitoboynaya Flotiliya*: 114pp.

Anon. 1959. Zurnal ucheta dobichi kitovogo sirtsa sudami 2-oy Dal'nevostochnoy kitoboynoy flotilii za 1959g. [Log book of whale catches by the vessels of the Second Far Eastern whaling fleet in 1959]. *Vtoraya Dal'nevostochnaya Kitoboynaya Flotiliya*: 95pp.

Anon. 1960. Promisloviy otchet 2-oy Dal'nevostochnoy flotilii za 1960g. [Whaling report of the Second Far Eastern whaling fleet in 1960]. Vladivostok, Upravlenie Kitoboynikh Flotiliy. 62pp.

Anon. 1961. Promisloviy otchet 2-oy Dal'nevostochnoy flotilii za 1961god. [Whaling report of the Second Far Eastern whaling fleet in 1961]. Vladivostok, Upravlenie Kitoboynikh Flotiliy. 50pp.

Anon. 1962. Promisloviy otchet 2-oy Dal'nevostochnoy flotilii za 1962god. [Whaling report of the Second Far Eastern whaling fleet in 1962]. Vladivostok, Upravlenie Kitoboynikh Flotiliy. 50pp.

Doroshenko, N.V. 2000. Right whales of the Sea of Okhotsk (history of whaling and its present state). pp.408. *In*: Yablokov, A.V. and Zemsky, V.A. (eds). *Soviet Whaling Data*. Centre for Russian Environmental Policy, Moscow.

Isakov, G.I., Labotsevich, M.I., Koval, E.Z. and Ryabov, B.S. 1973. Otchet nauchnoy gruppy AKF Vladivostok and Dalniy Vostok za 1972 god [Report of the scientific group on board the whaling fleets Vladivostok and Dalniy Vostok for the year 1972]. Vladivostok, Dal'moreproduct. 56pp. [In Russian].

International Whaling Commission. 1967. Chairman's Report of the Seventeenth Meeting. Appendix D. Report of the Special Meeting of Commissioners from North Pacific Member Nations, Honolulu, Hawaii, 14–17 February 1966. [Statement of the Union of Soviet Republics, *sic.*]. *Rep.int.Whal.Commn* 17: 72.

International Whaling Commission. 1971. International Whaling Commission Report 1969–70. Appendix IV. Report of the Scientific Committee [June 1970, London]. *Rep.int.Whal.Commn* 21:24–108.

International Whaling Commission. 1972. Draft Report 1971/72 [International Observer Scheme]. Paper IWC/24/6 presented to the 24th meeting of the International Whaling Commission, London, June 1972. 13pp. [Paper available from the Office of this Journal]

International Whaling Commission. 1973. International Observer Scheme – Report 1972–73. Paper IWC/25/14 presented to the 25th meeting of the International Whaling Commission, London, June 1973. 14pp. [Paper available from the Office of this Journal]

Ivashchenko, Y. and Clapham, P. 2014. Too much is never enough: the cautionary tale of Soviet whaling. *Mar. Fish. Rev.* 76: 1–21.

Ivashchenko, Y. and Clapham, P. 2017. Evaluation of the accuracy of reported noon positions from Soviet whaling factory ships. *J. Cetacean Res.Manage.* 17: 23–28.

Ivashchenko, Y. and Clapham, P.J. 2012. Soviet catches of bowhead (*Balaena mysticetus*) and right whales (*Eubalaena japonica*) in the North Pacific and Okhotsk Sea. *Endangered Species Research* 18: 201–17.

Ivashchenko, Y.V., Clapham, P.J. and Brownell Jr, R.L. 2013. Soviet catches of whales in the North Pacific: revised totals. *J. Cetacean Res. Manage* 13(1): 59–72.

Klumov, S.K. 1956. Predvaritel'niy otchet o rabote expeditsii gj izucheniyu Dal'nevostochnikh kitoobraznikh letom 1955 goda. Preliminary report of the expedition results to study Far Eastern cetaceans during summer 1955. Moskva-Vladivostok, Institut Okeanologii Akademii Nauk SSSR, 149pp.

Klumov, S.K. 1957. Predvaritel'niy otchet o rabote expeditsii gj izucheniyu Dal'nevostochnikh kitoobraznikh letom 1956 goda. Preliminary report of the expedition results to study Far Eastern cetaceans during summer 1956. Moskva-Vladivostok, Institut Okeanologii Akademii Nauk SSSR, 118pp.

Klumov, S.K. 1962. Gladkie (Yaponskie) kity Tikhogo Okeana [The Black right whales in the North Pacific. Sci. Rep. Whales Res. Inst., right whales in the Pacific Ocean]. Tr. Inst. Okeanol. Akad. Nauk Tokyo 21:1–78. SSSR 58:202-97. [In Russian].

Lockyer, C. 1976. Body weights of some species of large whales. *Journal du Conseil International pour l'Exploration de la Mer* 36(3): 259–73.

Mikhalev, Y., Savusin, V.P. and Bushuev, S.G. 2009. Falsification of Soviet whaling data after the introduction of the International Observer Scheme. Paper SC/61/IA20 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 5pp. [Paper available from the Office of this Journal].

Yablokov, A.V. 1994. Validity of Soviet whaling data. *Nature, Lond.* 367(6,459): 108.

Evaluation of the accuracy of reported noon positions from Soviet whaling factory ships

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ABSTRACT

It has generally been assumed that the noon positions reported to the International Whaling Commission (IWC) by Soviet factory ships were accurate, despite that nation's extensive falsification of catch records. In this paper, Soviet whaling industry reports are used to investigate this issue. Comparison of available track data from the reports with information submitted to the IWC through the BIWS shows that the officially reported data provide a reasonably accurate idea of general whaling effort, with minor discrepancies attributable to differences in precision or to geo-referencing. However, the Soviet report tracks sometimes include unreported excursions for the purpose of illegal whaling, and these were omitted from the data sent to the IWC.

KEYWORDS: WHALING–MODERN; USSR; PACIFIC OCEAN; SOUTHERN HEMISPHERE

INTRODUCTION

As is now well established, extensive illegal whaling by the USSR began after World War II and continued for some thirty years (Clapham and Ivashchenko, 2009; Yablokov, 1994). The USSR's numerous violations of whaling regulations included the taking of protected species, under-sized whales, lactating females and calves (Ivashchenko *et al.*, 2011). Ivashchenko and Clapham (2014) estimate that, globally, the Soviet whalers killed approximately 534,119 whales, of which 178,726 were not reported to the IWC.

During this period, the USSR routinely submitted falsified data to the International Whaling Commission (IWC) via the Bureau of International Whaling Statistics (BIWS); they also falsified biological data such as those on sex and length (notably for sperm whales, *Physeter macrocephalus*; Ivashchenko *et al.*, 2013). Using accurate data from formerly secret whaling industry reports, the Soviet catch record has now been largely corrected for both the Southern Hemisphere and the North Pacific (Ivashchenko *et al.*, 2013; Yablokov, 1995; Yablokov *et al.*, 1998). The corrected data are now incorporated into the IWC's catch database (Allison, 2016).

However, a question has remained regarding whether Soviet factory ship noon positions, as reported to the IWC, were also inaccurate. Interviews with former whale biologists who worked on the Soviet factory fleets indicated that these positions were probably generally correct, and Yablokov (1995) provided details of tracks of Soviet factory ships operating in the Southern Hemisphere for certain years. Here, true noon position data from selected Soviet whaling industry reports are compared with locations reported to IWC. The comparisons show that, while the reported positions were largely accurate as far as they went, the USSR failed to include additional excursions made for the purpose of making illegal catches in other areas. They also took additional catches *en route* to and from the Antarctic whaling grounds.

METHODS AND MATERIALS

It is not the intention of this paper to examine every track of every factory fleet, but rather to use some examples from selected fleets and years to assess the general reliability of the data submitted to IWC. In this regard, Yablokov (1995) provided true versus submitted track data for Antarctic whaling operations as a series of paired maps for each whaling season. Despite the inevitably coarse resolution of these maps, they revealed omissions from the officially reported data. There have been no comparisons of track data from Soviet whaling operations in the North Pacific.

Ivashchenko *et al.* (2011; 2013) analysed data from formerly secret Soviet whaling industry scientific, production and inspectors' reports (copies of which were found in Russian archives) to correct catch totals for the North Pacific, and to examine the operational details and economic context of Soviet whaling generally. A partial list of these reports is given in Ivashchenko *et al.* (2013; table 3); however, that listing relates only to the North Pacific, and a few other reports are now available to us which provide information on selected Antarctic operations.

For the most part, only scientific and inspectors' reports contain data on the noon positions of the factory ships concerned: not all of these reports have this information which, when it exists, is in the form of a fold-out map. These maps were scanned and saved as JPEG files, then imported into ArcMap as a raster data set layer and saved as a geo-referenced map. The resulting tracks were compared to information on noon positions as reported by the USSR to the IWC, as contained in the IWC database (Allison, 2016).

A list of the track data referred to in this report, by factory fleet and year, is given in Table 1.

RESULTS AND DISCUSSION

The USSR operated a total of seven whaling factory fleets during the period of illegal catches, from 1948 to 1979 (Ivashchenko *et al.*, 2011). Detailed track data are available for a total of 39 whaling seasons; of these, 15 were from the

Table 1

List of whaling seasons for which data exist to compare the reliability of noon positions reported by Soviet factory ships. 'Antarctic' means whaling seasons where the destination was the Antarctic, though in some cases catches were also made to or from the Southern Ocean whaling grounds, sometimes including north of the equator.

Fleet	Season/ground	Source
Slava	1957/58 Antarctic	Yablokov (1995, pp.25-26)
	1963/64 Antarctic	Yablokov (1995, pp.38-39)
	1968 N Pacific	Vladimirov *et al.* (1968)
	1969 N Pacific	Vladimirov *et al.* (1969)
Aleut	1962 N Pacific	Anonymous (1962)
Sovetskaya Ukraina	1963/64 Antarctic	Yablokov (1995, pp.73-74)
	1965/66 Antarctic	Yablokov (1995, pp.93-94)
	1966/67 Antarctic	Yablokov (1995, pp.98-99)
Yuri Dolgorukiy	1960/61 Antarctic	Yablokov (1995, pp.149-150)
	1961/62 Antarctic	Yablokov (1995, pp.154-155)
	1962/63 Antarctic	Yablokov (1995, pp.164-165)
	1963/64 Antarctic	Yablokov (1995, pp.173-174)
	1964/65 Antarctic	Yablokov (1995, pp.183-184)
	1965/66 Antarctic	Yablokov (1995, pp.192-193)
	1966/67 Antarctic	Yablokov (1995, pp.200-201)
	1967/68 Antarctic	Yablokov (1995, pp.209-210)
	1968-69 Antarctic	Yablokov (1995, pp.217-218)
	1970/71 Antarctic	Yablokov (1995, pp.225-226)
	1971/72 Antarctic	Yablokov (1995, pp.233-234)
Sovetskaya Rossiya	1965 N Pacific	Fig. 1, this paper
	1962/63 Antarctic	Fig. 4, this paper
	1964/65 Antarctic	Fig. 5, this paper
	1965/66 Antarctic	Figs 6 and 7ab, this paper
	1966/67 Antarctic	Yablokov (1995, pp.260-261)
	1967/68 Antarctic	Yablokov (1995, pp.269-270)
	1969/70 Antarctic	Yablokov (1995, pp.280-281)
	1970/71 Antarctic	Yablokov (1995, pp.287-288)
	1971/72 Antarctic	Yablokov (1995, pp.293-294)
Dalniy Vostok	1964 N Pacific	Anonymous (1964, p.80)
	1965 N Pacific	Anonymous (1965, p.66)
	1967 N Pacific	Fig. 2, this paper
	1968 N Pacific	Vladimirov *et al.* (1968)
	1969 N Pacific	Vladimirov *et al.* (1969)
	1970 N Pacific	Fig. 3a, this paper
	1971 N Pacific	Berzin *et al.* (1971)
Vladivostok	1968 N Pacific	Reznichenko and Selyavko (1968)
	1969 N Pacific	Reznichenko and Selyavko (1969)
	1970 N Pacific	Privalikhin *et al.* (1970)
	1971 N Pacific	Berzin *et al.* (1971)

North Pacific, and 24 from the Antarctic. For future reference, these are listed in Table 1. Track data for *Aleut*, the seventh (and oldest) of the Soviet fleets, were found for only one whaling season (1962).

Overall, comparisons of true noon position data with those officially reported to the IWC show that the official data (as far as they went) were in most cases largely accurate, and serve as a reasonably reliable general guide to Soviet whaling effort. However, the reported data were sometimes significantly incomplete, and in particular omitted major sections of track involving excursions by a particular fleet into other areas. These almost certainly represent attempts to avoid suspicion of illegal catches, since many of the omissions involved areas in which catches were prohibited, or which were inhabited largely by protected species. There are numerous examples of this in the paired tracks shown in Yablokov (1995), referenced in Table 1, and additional examples are given below.

Figs 1–5 show examples of reported versus actual track data. Where the tracks are similar, often small differences in locations are likely the result of two factors. Southern Hemisphere locations in the IWC database prior to 1972 are given to the nearest degree, whereas the Soviet industry reports usually provide more precise positions. North Pacific data in the IWC database include degrees and minutes. Second, small differences inevitably result from the geo-referencing process. Consequently, minor differences between tracks are unlikely to be significant in most cases.

However, some of the tracks derived from the Soviet reports include differences which are more difficult to explain, as well as excursions to other areas which are omitted from the officially reported data (it is also known that Soviet catcher boats on occasions worked a long way from the factory ships to which the noon positions refer). Examples are described below.

Reported versus actual tracks for *Sovetskaya Rossiya* in the North Pacific in 1965 (Fig. 1) largely agree, with the exception of an unexplained difference in the eastern Gulf of Alaska. The IWC track shows the fleet heading towards the coast, whereas the track from the fleet scientific report lacks this diversion. We have no explanation for the difference, which is not likely due to the minor factors noted above. Although the tracks largely agree for this whaling operation, it is known from the industry reports that *Sovetskaya Rossiya* spent much of this period illegally whaling. These operations included catches of protected species such as North Pacific right whales (*Eubalaena japonica*), as well as baleen whales generally. Antarctic fleets working in the North Pacific were permitted to hunt only sperm whales. *Sovetskaya Rossiya* caught numerous animals of this species that were below the minimum legal length of 11.6m.

In Fig. 2, the tracks for the *Dalniy Vostok* fleet in 1967 are very similar except for a loop into the central Okhotsk Sea off the eastern coast of Sakhalin Island. Reporting of this excursion might well have raised suspicions, since the region concerned is inhabited largely by gray whales (*Eschrichtius robustus*) and North Pacific right whales, both of which were protected under IWC regulations; indeed, 126 right whales were taken in the area on that expedition (Ivashchenko and Clapham, 2012). The IWC data also show a loop, but in this case it is farther offshore in the central Okhotsk Sea where fin whales (a legally catchable species) were found.

Another case is evident in Fig. 3(a), where the true track shows that the fleet actually worked much farther to the south than they reported to the IWC. In this case, the factory fleet is known to have been illegally taking undersized male and female sperm whales in lower latitudes; reporting the true position might have raised suspicions about the nature of what was being caught there. Reported versus actual (reconstructed) catches of sperm whales associated with these tracks in 1970 are shown in Fig. 3(b).

Such obvious omissions from the reported data indicate excursions for illegal whaling, but it is important to recognise that these omissions occurred only when the fleet was working in areas that might have led to questions regarding the catch. When the fleets were working in areas where legally catchable species could be found, they could whale there illegally without the need to misreport fleet positions. An example is *Sovetskaya Rossiya* in the Gulf of Alaska (Fig. 1, described above).

In Fig. 4, the actual track of *Sovetskaya Rossiya* during the 1962/63 Antarctic whaling season shows two significant deviations from the data reported to IWC. One is a movement to the west of the Antarctic Peninsula, which we are unable to explain. The other is a series of excursions in offshore waters east of Argentina, during which the factory fleet is known to have caught sperm whales. Why the two tracks are different is unclear since the areas in which the fleet actually operated would not have raised any suspicions, and while the catches undoubtedly involved undersized sperm whales, the species itself was legally catchable. An additional confusion arises from the fact that the fleet's production report for the 1962/63 season also gives track data, and these are more similar to those reported to the IWC.

The reported versus actual tracks of *Sovetskaya Rossiya* in 1964/65 (Fig. 5) are largely similar, although the latter shows a significant extension around latitude 35°S towards southwestern Australia. This was likely for the purpose of illegal whaling (whaling for baleen whales was not permitted north of 40°S), but we are unable to determine the species or extent of any catches in this area. Also, a loop south of 60°S and between 80° and 100°E is farther to the south of the IWC track; it is not known if this reflects any real difference in whaling effort or is just an insignificant difference in the precision of what appears in the two sources.

In conclusion, the examples given here show that although the officially reported Soviet factory fleet tracks are generally accurate, there are significant exceptions. Consequently, caution should be employed when using the IWC track data for any detailed analysis.

REFERENCES

Allison, C. 2016. International Whaling Committee summary database, version December 2016. [Available from the Office of the International Whaling Commission, Cambridge, UK] .

Anon. 1962. Promisloviy otchet 2-oy Dal'nevostochnoy flotilii za 1962god. [Whaling report of the Second Far Eastern whaling fleet in 1962]. Vladivostok, Upravlenie Kitoboynikh Flotiliy. 50pp. [In Russian] (Unpublished)

Anon. 1964. Otchet o proizvodstv deyatelnosty kitoboynoy flotilii Dalniy Vostok za promisel 1964. [Report on production activities of the whaling fleet Dalniy Vostok during 1964 season.]. Upravlenie Kitoboinikh Flotiliy, Vladivostok. 81pp. [In Russian] (Unpublished).

Anon. 1965. Otchet o dobiche i realizatsii produktsii kitboynoy flotilii Dal'niy Vostok za promisel 1965 goda. [Report on production and product distribution of the whaling fleet Dalniy Vostok for 1965 season]. Upravlenie Kitoboinikh Flotiliy, Vladovostok. 66pp. [In Russian] (Unpublished).

Berzin, A.A., Blokhin, S.A., Isakov, G.I., Ryabov, V.S. and Lobatsevich, E.I. 1971. Sostoyanie zapasov and raspredelenie kitov v Tikhom Okeane I Antarktike. [State of the resources and distribution of whales in the Pacific Ocean and the Antarctic]. Vladivostok, TINRO. 77pp. [In Russian] (Unpublished).

Clapham, P. and Ivashchenko, Y. 2009. A whale of a deception. *Marine Fisheries Review* 71: 44–52.

Ivashchenko, Y. and Clapham, P. 2014. Too much is never enough: the cautionary tale of Soviet whaling. *Mar. Fish. Rev.* 76: 1–21.

Ivashchenko, Y., Clapham, P. and Brownell, R.L., Jr. 2011. Soviet illegal whaling: The devil and the details. *Mar. Fish. Rev.* 73(3): 1–19.

Ivashchenko, Y. and Clapham, P.J. 2012. Soviet catches of bowhead (*Balaena mysticetus*) and right whales (*Eubalaena japonica*) in the North Pacific and Okhotsk Sea. *Endanger. Species Res.* 18: 201–17.

Ivashchenko, Y.V., Clapham, P.J. and Brownell, R.L., Jr., 2013. Soviet catches of whales in the North Pacific: revised totals. *J. Cetacean Res. Manage.* 13(1): 59–72.

Privalikhin, A.M., Blokhin, S.A. and Isakov, G. 1970. Otchet nauchnikh grup k/f Dalniy Vostok, Vladivostok za promisloviy reis 1970 goda. [Report of the scientific groups from the whaling fleets Dalniy Vostok, Vladivostok for the 1970 whaling season]. Sostoyanie zapasov promislovikh vidov kitov v severnoy chasty Tikhogo okeana [Conditions of whaling reserves in the North Pacific]. TINRO, Vladivostok. 86pp. [In Russian] (Unpublished).

Reznichenko, V. and Selyavko, O. 1968a. Otchet o rabote gosudarstvennoy inspectsii po kitoboynomu promislu na kitoboynoy flotilii Vladivostok za promisel 1968 goda. [Report of the State whaling inspection of the whaling fleet Vladivostok during the 1968 season]. Upravlenie proizvodstvennikh flotiliy 'Dal'moreproduct', Vladivostok. 37pp. [In Russian] (Unpublished).

Reznichenko, V. and Selyavko, O. 1968b. Otchet o rabote gosudarstvennoy inspektsiipo kitoboynomu promislu na kitoboynoy flotilii Vladivostok za promisel 1969 goda. [Report on work of the State whaling inspection on board the whaling fleet Vladivostok for the 1969 season]. Vladivostok, Upravlenie Proizvodstvennikh Flotiliy 'Dal'moreproduct'. 51pp. [In Russian] (Unpublished).

Vladimirov, V.L., Kuzmin, A.A., Nikolaeva, A.N. and Privalikhin, V.I. 1968. Otchet nauchnikh grup k/f Dalniy Vostok i Slava za promisloviy reis 1968g. [Report of the scientific groups from the whaling fleets Dalniy Vostok and Slava during the 1968 whaling season]. In: Sostoyanie zapasov promislovikh vidov kitov v severnoy chasty Tikhogo okeana [Conditions of the whaling species of large whales in the North Pacific]. TINRO, Vladivostok. 76pp. [In Russian] (Unpublished).

Vladimirov, V.L., Kuzmin, A.A., Nikolaeva, A.N., Privalikhin, V.I. and Blokhin, S.A. 1969. Otchet nauchnikh grup k/f Dalniy Vostok i Slava za promisloviy reis 1969g. [Report of the scientific groups from the whaling fleets Dalniy Vostok and Slava for the 1969 season]. Sostoyanie zapasov promislovikh vidov kitov v severnoy chasty Tikhogo okeana [Conditions of whaling species reserves in the North Pacific]. TINRO, Vladivostok. 105pp. [In Russian] (Unpublished).

Yablokov, A. 1995. *Soviet Antarctic Whaling Data*. Center for Russian Environmental Policy, Moscow. 320pp. [In Russian and English].

Yablokov, A.V. 1994. Validity of Soviet whaling data. *Nature, Lond.* 367(6,459): 108.

Yablokov, A.V., Zemsky, V.A., Mikhalev, Y.A., Tormosov, V.V. and Berzin, A.A. 1998. Data on Soviet whaling in the Antarctic in 1947–72 (population aspects). *Russ. J. Ecol.* 29(1): 38–42.

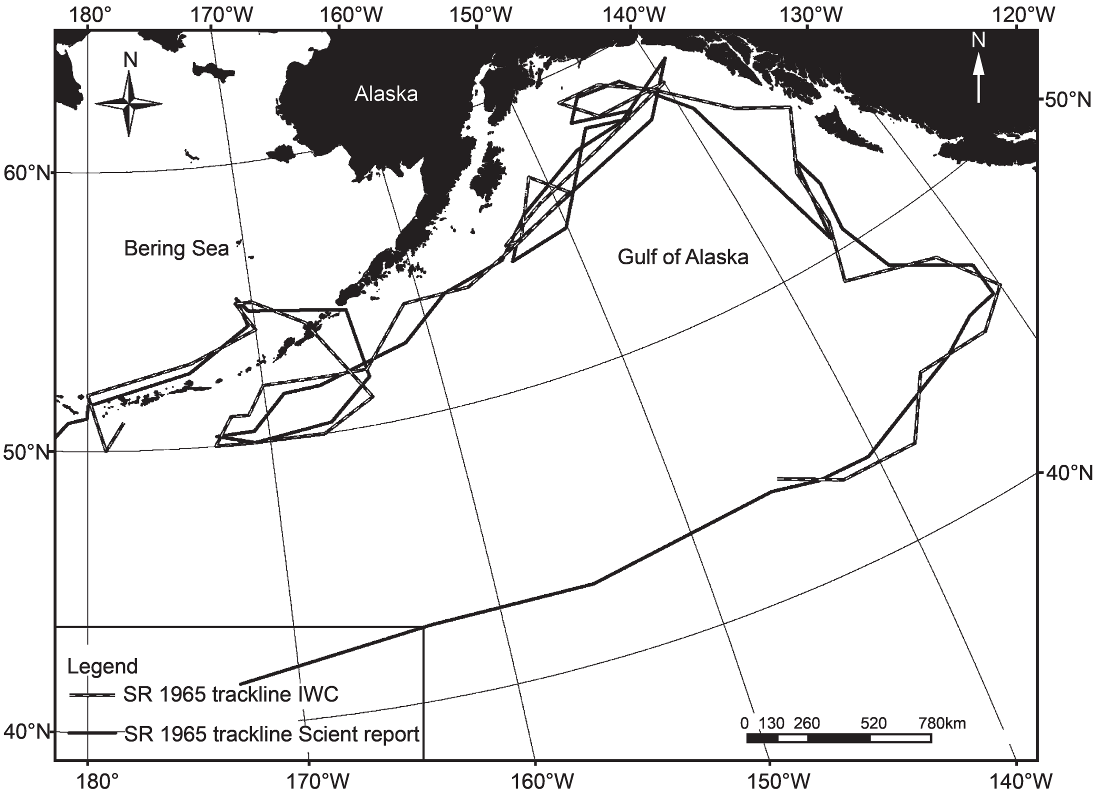

Fig. 1. Reported versus actual track from noon positions of *Sovetskaya Rossiya* (SR) in the North Pacific, 1965. The true track (solid line) was shown in the scientific report for the fleet's 1965 whaling season.

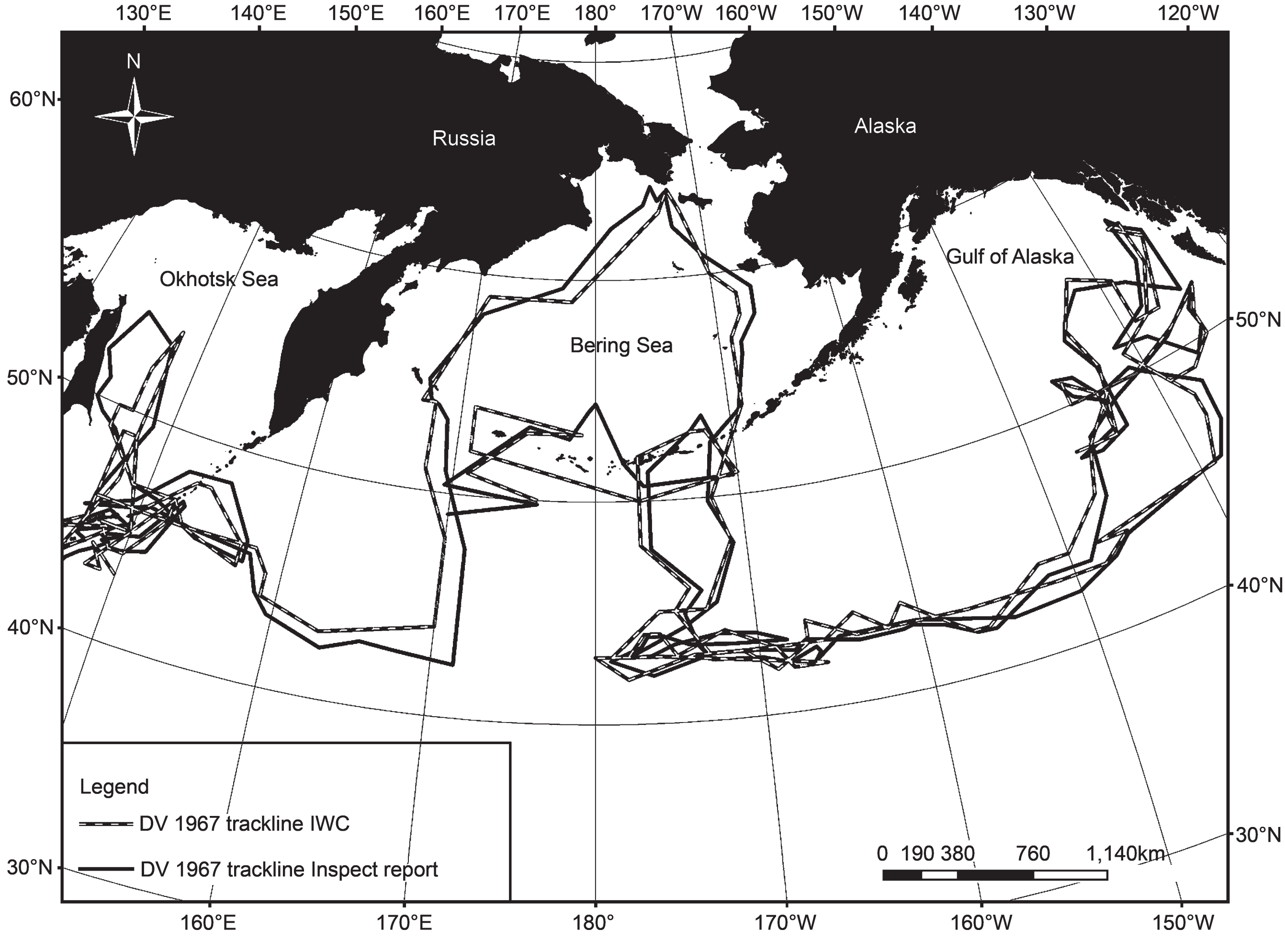

Fig. 2. Reported versus actual track from noon positions of *Dalniy Vostok* (DV) in the North Pacific, 1967. The true track (solid line) was shown in the inspectors' report for the fleet's 1967 whaling season.

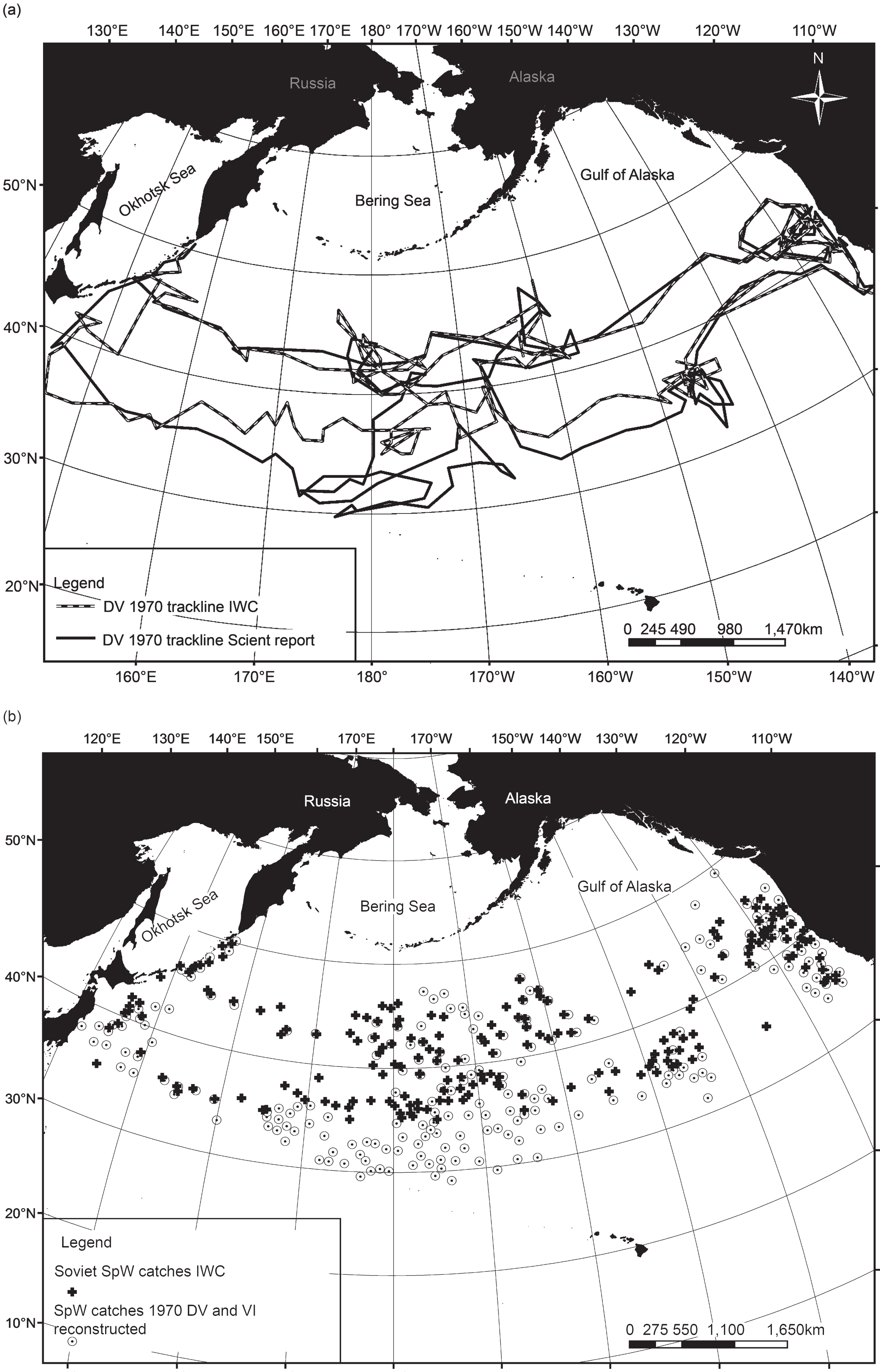

Fig. 3. (a) Reported versus actual track from noon positions of *Dalniy Vostok* (DV) in the North Pacific, 1970. The true track (solid line) was shown in the scientific report for the fleet's 1967 whaling season. See (b) for associated catches. (b). Reported versus actual (reconstructed) catches of sperm whales (SpW) made by the *Dalniy Vostok* fleet in 1970.

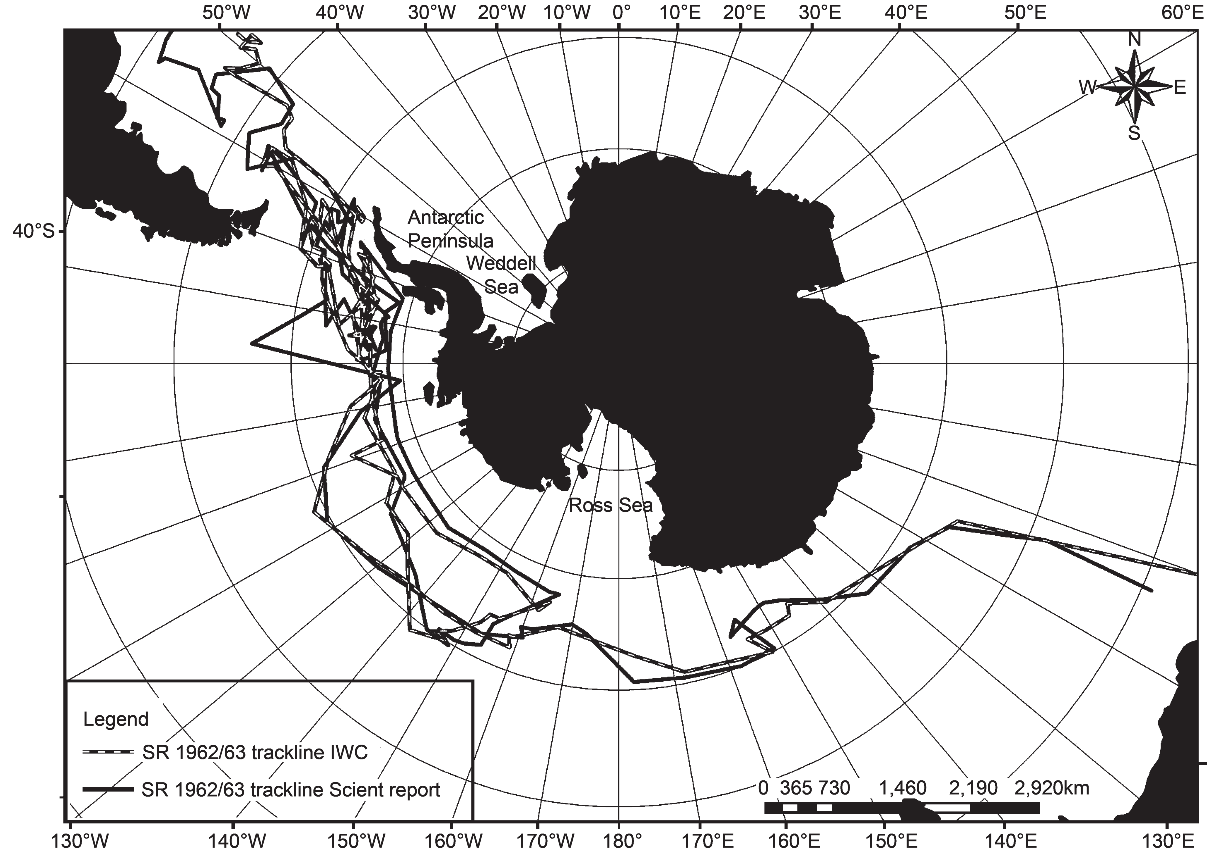

Fig. 4. Reported versus actual track from noon positions of *Sovetskaya Rossiya* (SR) in the Southern Hemisphere, 1962/63. The true track (solid line) was shown in the scientific report for the fleet's 1962/63 whaling season.

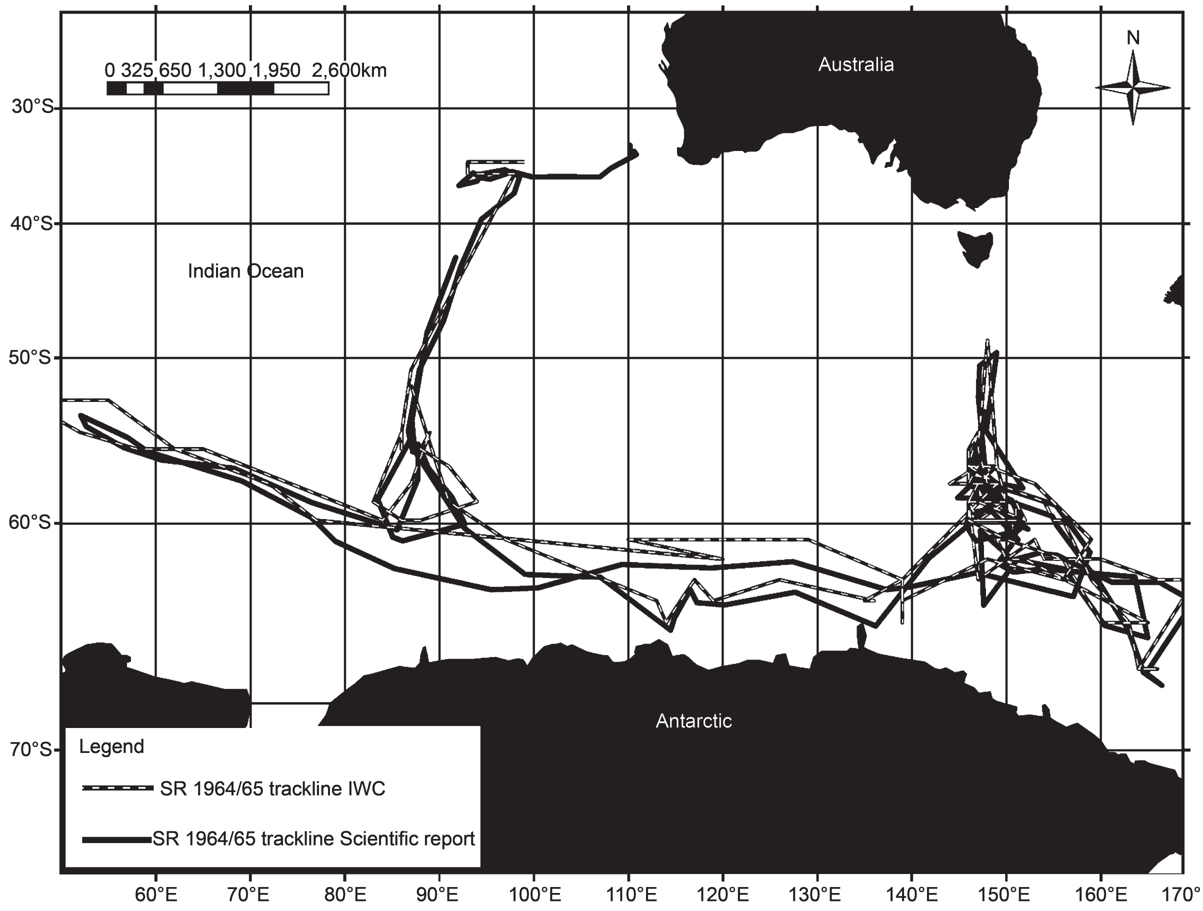

Fig. 5. Reported versus actual track from noon positions of *Sovetskaya Rossiya* (SR) in the Southern Hemisphere, 1964/65. The true track (solid line) was shown in the scientific report for the fleet's 1964/65 whaling season.

Movement of two humpback whales (*Megaptera novaeangliae*) satellite-radio tagged off Eden, NSW and matched by photo-identification with the Hervey Bay catalogue

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ABSTRACT

Photo-identification studies of humpback whales off eastern Australia show low levels of movement between eastern Australia and New Caledonia whales. Some eastern Australian humpback whales migrate through the southern waters of New Zealand on route to Antarctic feeding areas. Photo-identification studies have shown that the waters near the Balleny Islands, in Antarctic Area V, are a feeding area for some eastern Australian humpback whales. However, such studies provide no details of the routes taken between New Zealand and Australia and to and from Antarctic feeding areas. Sixteen humpback whales were satellite-linked radio tagged off Eden NSW in 2008. The number and duration of the tag positions reported revealed complete migratory transits from Eden to Antarctic Area V and IV feeding areas. Photographs of the Eden humpback whales were compared to the Hervey Bay photo-identification catalogue and yielded two matches, identified from lateral body marks and dorsal fins. This study provides the first evidence that during the southern migration some humpback whales stopover at Hervey Bay and also migrate past Eden on the NSW coast. The tracks of the two whales from Eden showed that a male sighted in Hervey Bay in the same season moved southeast from Eden towards southern New Zealand. A female with site-fidelity to Hervey Bay in previous seasons, accompanied by a calf when the tag was deployed, moved down and around the coast of Victoria, across Bass Strait and then southwest into the Antarctic Area IV feeding area. Eden may be a migratory hub for humpback whales departing from and approaching the east coast of Australia. This study suggests that eastern Australian humpback whales may exhibit a more diverse range of feeding destinations, after leaving Australian coastal waters, than previously reported.

KEYWORDS: HUMPBACK WHALE; PHOTO-IDENTIFICATION; SATELLITE TAGGING; MIGRATORY MOVEMENTS; ANTARCTIC; AFRICA; AUSTRALASIA; FEEDING AREAS; BREEDING GROUNDS

INTRODUCTION

A recent study of eastern Australian humpback whales and humpback whales across Oceania (South Pacific) documented four photo-identification matches between the nearby breeding grounds of New Caledonia and eastern Australia and three matches between New Zealand and eastern Australia (Garrigue *et al.,* 2011*).* Analyses of these matches showed that some eastern Australian whales migrate through Cook Strait and the southern waters of New Zealand, while travelling to and from Antarctic feeding areas (Franklin *et al.,* 2008b; Franklin *et al.,* 2014). Two of the New Zealand matches were whales photographed in Cook Strait in June 2004 and subsequently photographed in Hervey Bay in September the same year (Franklin *et al.,* 2014). These matches could not provide information about the routes taken by individual humpback whales between New Zealand and eastern Australia.

Dawbin and Falla (1949) and Dawbin (1956) noted that the Ross Sea, particularly around the Balleny Islands, 'almost certainly represents the summer concentration of humpback whales which pass the coasts of New Zealand, East Australia and other parts of the Pacific'. Dawbin (1956) developed the hypothesis that dispersal across the Antarctic Area V feeding area is a primary determinant of the routes taken by humpbacks as they approach New Zealand on their return to winter breeding grounds. Recent photo-identification evidence supports this view. Matches have been reported between the Antarctic Area V feeding area and breeding grounds to the north (Kaufman *et al*., 1990; Rock *et al*., 2006; Franklin *et al*., 2008a; Franklin *et al*., 2012; Constantine *et al.,* 2014). Most of these sightings were in close vicinity to the Balleny Islands (67°S, 163°E) (Rock *et al*., 2006; Franklin *et al*., 2008a; 2012; Constantine *et al.,* 2014), and one was near to the eastern border of the Antarctic Area V feeding area (69°S, 171°W) (Rock *et al*., 2006). The longitude of the most westerly sighting was 155°55'E, and the most easterly was at 170°52'W. The distance between these two sightings was approximately 817 n.miles (Rock *et al*., 2006; Franklin *et al.,* 2008a). All of these individuals are reported as having site fidelity to eastern Australian breeding grounds (Kaufman *et al*., 1990; Rock *et al*., 2006; Franklin *et al*., 2008a; 2012; Constantine *et al.,* 2014). Franklin *et al.* (2012) and Constantine *et al.* (2014) both concluded that some eastern Australian whales feed in and around the Balleny Islands in Antarctica Area V. Rock *et al.* (2006) also reported two individual humpback whales sighted in both Hervey Bay and Eden.

During late October 2008, 16 satellite-linked radio tags were attached to southbound humpback whales off Eden, NSW (Gales *et al*., 2009). The tags remained active from 3 to 156 days providing a full description of the transit tracks of some whales from Eden to Antarctic feeding areas (Fig. 1). All but one individual humpback whale travelled southward into the Antarctic Area V (130°E–170°W) feeding

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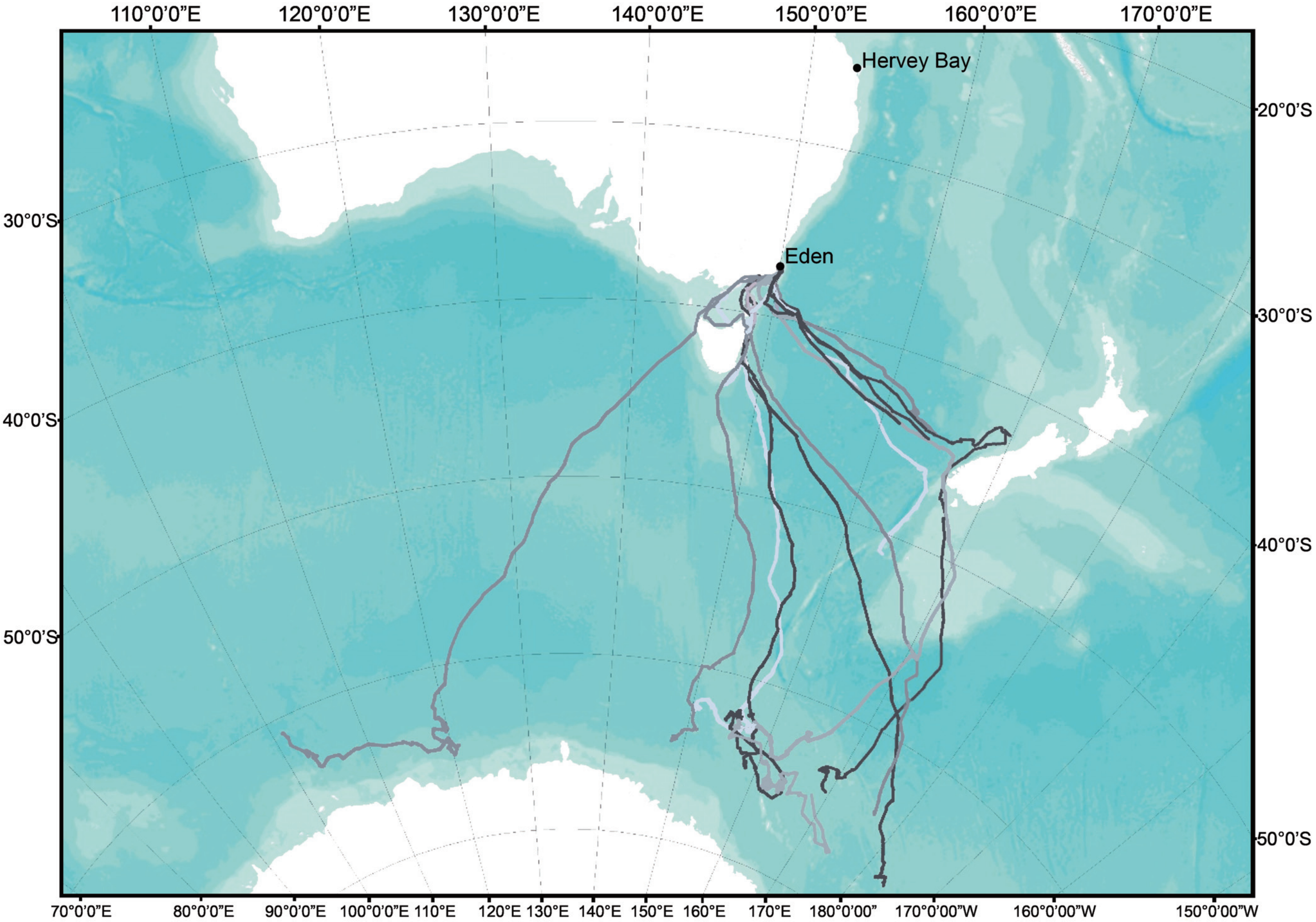

Fig. 1. Tracks of the 16 individual humpback whales satellite-linked radio tagged off Eden in October 2008 (from Gales *et al.,* 2009).

area. As predicted by Franklin *et al.* (2008b), several individual humpback whales travelled southeast from Eden passing to the southwest of southern New Zealand and then at least two of these whales continued south, well to the east of the Balleny Islands. Several other individual humpback whales moved down along the Victorian and Tasmanian coast and then migrated towards the Balleny Islands (approximately 67°S, 163°E), with some dispersing well to the west (approximately 148°E) and to the east (approximately 176°W) of the Balleny Islands. A single humpback whale, accompanied by a calf at the time of tag deployment, followed the Victorian coast westward, then travelled through Bass Strait to northwest Tasmania and from there southwest to the edge of the Antarctic ice shelf in Antarctic Area IV (Gales *et al.,* 2009; Fig. 1).

In this study photographs of the humpback whales tagged off Eden in 2008 are compared to the Hervey Bay humpback whale photo-identification catalogue for the period 1992–2009.

METHODS

Satellite-linked radio tags were deployed on 16 southbound humpback whales off the coast of Eden, NSW (37.15°S, 150.07°E) between 24 October and 1 November 2008 (Gales *et al.,* 2009). During deployment of the tags photo-identification images were taken of each of the 16 individual humpback whales. A total of 33 photographs was obtained. Of the 33 photographs, 24 were right lateral body and dorsal fin photographs, 7 were left lateral body and dorsal fin photographs and 2 were ventral tail fluke photographs.

Photo-identification of humpback whales in Hervey Bay, Queensland was undertaken for ten weeks each year between 1992 and 2009 as part of a long-term study of humpback whales in Hervey Bay (Franklin, 2012; 2014). Photographs of ventral tail flukes, and related left and right lateral body and dorsal fins were obtained wherever possible. The Hervey Bay fluke catalogue for the period 1992–2009 consists of *n*=2821 individual whales. A full description of the Hervey Bay study area, fieldwork, effort and data obtained is provided in Franklin *et al.* (2011).

To identify any matches between the humpback whales in the 2008 Eden catalogue and the humpback whales in the Hervey Bay catalogue, each ventral tail fluke, left and right lateral body and dorsal fin photograph in the Eden catalogue (*n*=16 whales) was compared to each ventral tail fluke, left and right lateral body and dorsal fin photograph in the Hervey Bay catalogue (*n*=2,821 whales).

RESULTS

The comparison of the Eden photography with the Hervey Bay photography yielded two matches. Both matches were based on right lateral body and dorsal fin photographs. The photo-identification images and the details of each individual whale matched are provided in Figs 2 and 3 below.

Fig. 2. Photographic match of a humpback whale photographed in Hervey Bay on 21 September 2008 (A) and subsequently photographed off Eden on 24 October 2008 (B) by Gales *et al.* (2009). The whale was coded as satellite-radio tagged whale 88746 off Eden and was identified in the field as a male. This male humpback whale was only sighted on one occasion in Hervey Bay during 2008, and was not identified in Hervey Bay during other years.

A satellite-linked radio tag was deployed on the male humpback whale 88746 on 24 October 2008 (Gales *et al.,* 2009). The whale was in a pod of two adults. The tag remained active for 20 days until 12 November 2008 and provided 138 position locations. The whale moved south from Eden and upon reaching open water in Bass Strait turned eastward and travelled in a steady south-easterly direction towards the southern coast of New Zealand until the tag ceased reporting (Gales *et al.,* 2009). The full track of whale 88746 is shown in Fig. 4, below.

A satellite-linked radio tag was deployed on the female humpback whale 88729 on 29 October 2008 (Gales *et al.,* 2009). A calf accompanied the female at the time the tag was deployed. The tag remained active for 98 days until 3 February 2009 and provided 1,160 position locations. The female followed the coastline from Eden moving westward around the Victorian coast until off Wilsons Promontory. Then the whale travelled southwest passing close to the northwest corner of Tasmania before continuing steadily southwest, moving out of Antarctic Area V (130°E–170°W) and into Antarctic Area IV (70°E–130°E) at approximately 55°S. It continued southwest until reaching approximately 60°S, 121°E on 4 December 2008. From there, female 88729 moved south towards the Antarctic ice edge and then turned west, tracking along the ice edge and slowly moving northwest until the tag ceased reporting on 3 February 2009. The full track of whale 88729 is shown below (Fig. 4).

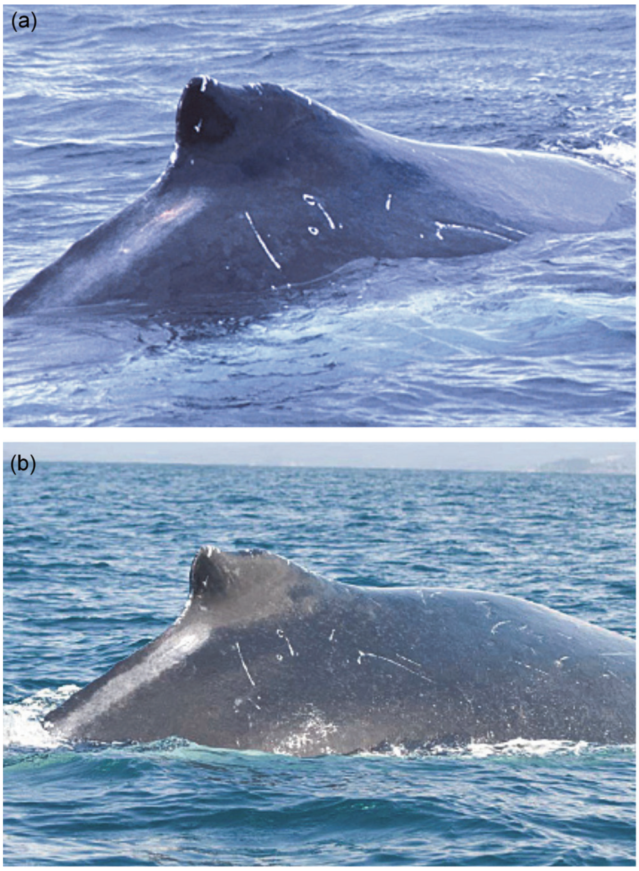

Fig. 3. Photographic match of a humpback whale photographed in Hervey Bay on 11 November 2002 (A) and then photographed off Eden 29 October 2008 (B) by Gales *et al.* (2009). The whale was coded as satellite-radio tagged whale 88729 off Eden and was inferred to be female as a calf accompanied the whale. This whale (mnemonic name 'Rama') was photographed in Hervey Bay in 1998 from 27 September to 1 October; in 1999 on 10 August; in 2000 from 6 to 25 September; in 2001 on 3 October; in 2002 on 11 October and in 2005 from 4 to 7 September. A calf accompanied the female 'Rama' in each year it was sighted in Hervey Bay, except 1999, providing further evidence that this whale is a female.

DISCUSSION

The photo-identification matches presented here, of two humpback whales satellite tagged off Eden, NSW and also sighted in Hervey Bay, provides further evidence that some humpback whales that use Hervey Bay as a stopover during the southern migration also migrate to and past Eden, off the southern NSW coast. Some eastern Australian humpback whales travel past southern New Zealand on route between eastern Australian breeding grounds and Antarctic Area V feeding area (Franklin *et al.,* 2008b; 2014). However, photo-identification provides no evidence of the routes taken between eastern Australia and New Zealand. Satellite-radio tagging has shown that some humpback whales passing Eden during the southern migration turn southwest directly towards southern New Zealand (Gales *et al.,* 2009).

It has been suggested that the coast off Eden, NSW is an important feeding area for some humpback whales during the southern migration (Paterson, 1987; Stamation *et al.,* 2007). The availability, early in the southern migration, of an accessible coastal feeding area may provide an incentive for southbound humpbacks, particularly immature males and females and females with this seasons calves, to travel close to the coast until they arrive in the feeding area off Eden. The

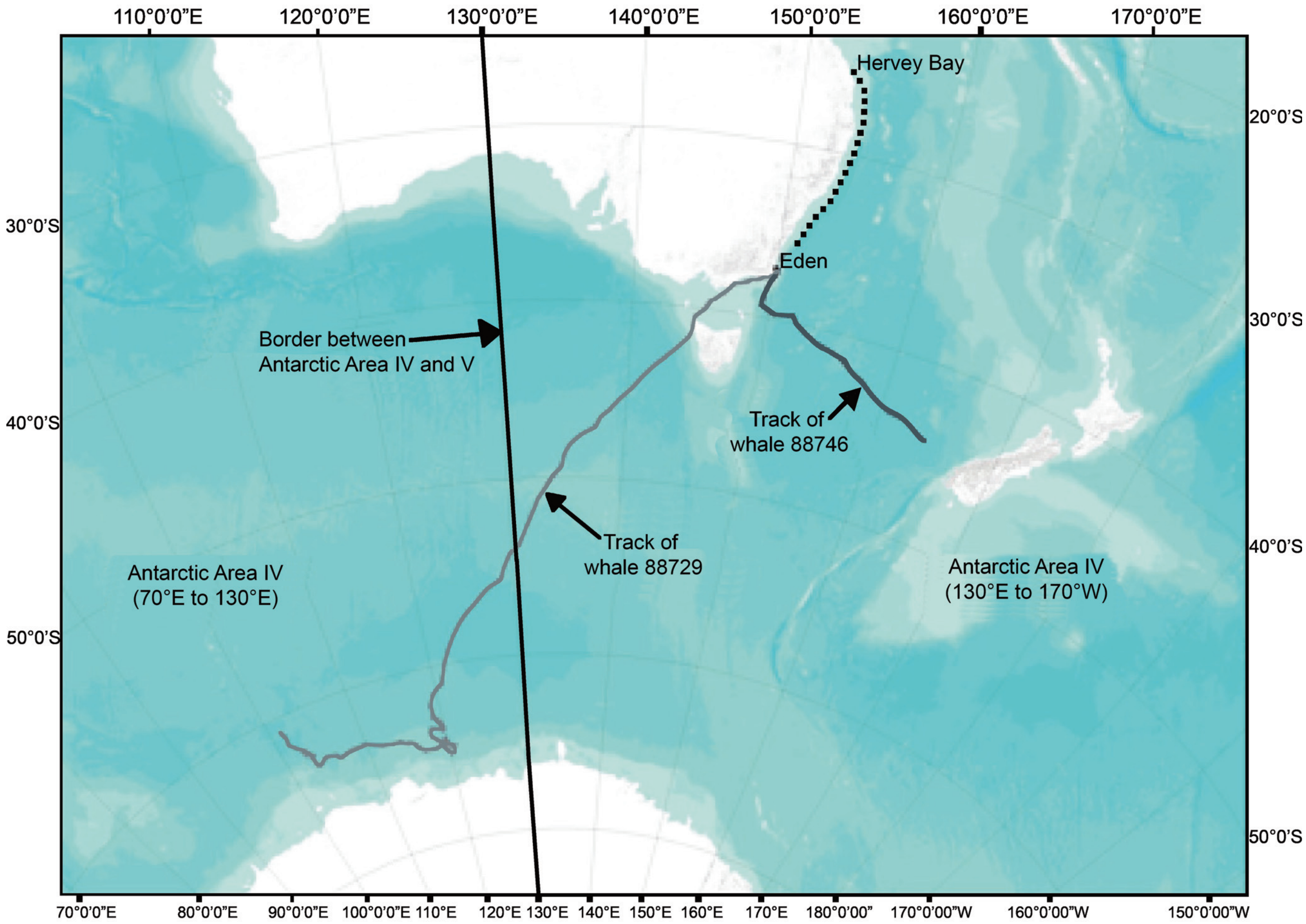

Fig. 4. Satellite-linked radio tag tracks of male humpback whale 88746 and female humpback whale 88729.

two matched whales reported here are likely to have travelled directly along the coast of Queensland and NSW from Hervey Bay to Eden off the south coast of NSW. Eden may be an important migratory hub for southbound humpback whales, and possibly northbound humpback whales. Comparison of any existing Eden fluke catalogues with eastern Australian, Victorian, Tasmanian, New Zealand, Oceania and Antarctic fluke catalogues may provide further insights into the migratory corridors and destinations of humpbacks passing through the waters off Eden, NSW.

Humpback whales leaving Eden travel in three primary migratory corridors prior to moving directly towards and dispersing across the Antarctic Area IV and V feeding areas (Gales *et al.,* 2009): southeast towards the southern coast of New Zealand; southward along the New South Wales, Victorian and Tasmanian east coast, and south past New South Wales, west along the Victorian coast then southwest through Bass Strait (Franklin *et al.,* 2008b; 2014; Gales *et al.,* 2009). This study confirms that some humpback whales using Hervey Bay as a stopover migrate past Eden, NSW before moving into primary migratory corridors towards Antarctic feeding areas.

Mitochondrial segregation of DNA haplotypes in the Northern Hemisphere has been interpreted as maternally directed fidelity to migratory destinations (Baker *et al.,* 1990). Long-term photo-identification studies of humpback whales in the Northern Hemisphere have also documented maternally directed fidelity to feeding destinations (Martin *et al*., 1984; Clapham and Mayo, 1987; Katona and Beard, 1990; Clapham *et al*., 1993; Palsboll *et al*., 1997). Female humpback whales with site-fidelity to eastern Australia, particularly Hervey Bay, have been found to feed in Antarctic Area V near and around the Balleny Islands (Kaufman *et al.,* 1990; Rock *et al.,* 2006; Franklin *et al*., 2008a; 2012; Constantine *et al.,* 2014). The female humpback whale 88729 reported herein had strong site-fidelity to Hervey Bay during previous breeding seasons, but travelled to the Antarctic Area IV feeding area in the 2008–09 feeding season. This result shows that at least one recent female humpback whale from eastern Australia does not always travel to Antarctic Area V to feed, and suggests that humpback whales may exhibit a diverse range of feeding destinations after leaving Australian coastal waters.

REFERENCES

Baker, C.S., Palumbi, S.R., Lambertsen, R.H., Weinrich, M.T., Calambokidis, J. and Brien, S.J.O. 1990. Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. *Nature* 344: 238–40.

Clapham, P.J. and Mayo C.A. 1987. Reproduction and recruitment of individually identified humpback whales, *Megaptera novaeangliae*, observed in Massachusetts Bay 1979–1985. *Can. J. Zool.* 65: 2,853–63.

Clapham, P.J., Baraff, L.S., Carlson, C.A., Christian, M.A., Mattila, D.K., Mayo, C.A., Murphy, M.A. and Pittman, S. 1993. Seasonal occurrence and annual return of humpback whales, *Megaptera novaeangliae*, in the Southern Gulf of Maine. *Can. J. Zool.* 71:440–3.

Constantine, R., Steel, D., Allen, J., Anderson, M., Andrews, O., Baker, C.S, Beeman, P., Burns, D., Charrassin, J.-B., Childerhouse, S., Double, M., Ensor, P., Franklin, T., Franklin, W., Gales, N., Garrigue, C., Gibbs, N., Harrison, P., Hauser, N., Hutsel, A., Jenner, C., Jenner, M.-N., Kaufman, G., Macie, A., Mattila, D., Olavarría, C., Oosterman, A., Paton, D., Poole, M., Robbins, J., Schmitt, N., Stevick, P., Tagarino, A., Thompson, K. and

Ward, J. 2014. Remote Antarctic feeding ground important for east Australian humpback whales. *Mar. Biol.* 161:1,087–93. [Available at: *http://dx.doi.org/10.1007/s00227-014-2401-2*].

Dawbin, W.H. 1956. The migrations of humpback whales which pass the New Zealand coast. *T. Roy. Soc. NZ*. 84:147–96.

Dawbin, W.H. and Falla, R.A. 1949. A contribution to the study of the humpback whale based on observations at New Zealand shore stations. *Proc. Seventh Pac. Sci. Congress* 4: 373–82.

Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M.M., Hauser, N., Donoghue, M., Russell, K., Mattila, D.K., Robbins, J., Oosterman, A., Leaper, R., Baker, C.S. and Clapham, P. 2008a. Migratory movements of humpback whales (*Megaptera novaeangliae*) between eastern Australia and the Balleny Islands, Antarctica, confirmed by photo-identification. Paper SC/60/SH2 presented to the IWC Scientific Committee June 2008, Santiago, Chile (unpublished). 12pp. [Paper available from the Office of this Journal]

Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M.M., Hauser, N., Donoghue, M., Russell, K., Mattila, D.K., Robbins, J., Oosterman, A., Leaper, R., Baker, C.S. and Clapham, P. 2008b. Eastern Australia (E1 breeding grounds) may be a wintering destination for Area V humpback whales (*Megaptera novaeangliae*) migrating through New Zealand waters. Paper SC/60/SH3 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 13pp. [Paper available from the Office of this Journal]. 14pp.

Franklin, T., Franklin, W., Brooks, L., Harrison, P., Baverstock, P. and Clapham, P. 2011. Seasonal changes in pod characteristics of eastern Australian humpback whales (*Megaptera novaeangliae*), Hervey Bay 1992–2005. *Mar. Mam. Sci.* 27(3): e134–e152 (July 2011) [DOI: 10.1111/j.1748-7692.2010.00430.x].

Franklin, T. 2012. The social and ecological significance of Hervey Bay Queensland for eastern Australian humpback whales (*Megaptera novaeangliae*). PhD thesis, Southern Cross University, Lismore, NSW. 245pp. [Available at: *http://epubs.scu.edu.au/theses/357/*].

Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M.M., Hauser, N., Donoghue, M., Russell, K., Mattila, D.K., Robbins, J., Oosterman, A., Leaper, R., Harrison, P., Baker, S.C. and Clapham, P. 2012. Antarctic waters (Area V) near the Balleny Islands are a summer feeding area for some Eastern Australian (E(i) breeding group) humpback whales (*Megaptera novaeangliae*). *J. Cetacean Res. Manage.* 12(3): 321–7.

Franklin, W., Franklin, T., Gibbs, N., Childerhouse, S., Garrigue, C., Constantine, R., Brooks, L., Burns, D., Paton, D., Poole, M.M., Hauser, N., Donoghue, M., Russell, K., Mattila, D.K., Robbins, J., Anderson, M., Olavarria, C., Jackson, J., Noad, M., Harrison, P., Baverstock, P., Leaper, R., Baker, S.C. and Clapham, P. 2014. Photo-identification confirms that Humpback whales (*Megaptera novaeangliae*) from eastern Australia migrate past New Zealand but indicates low levels of interchange with breeding grounds of Oceania. *J. Cetacean Res. Manage.* 14(1): 133–40.

Gales, N., Double, M., Robinson, S., Jenner, C., Jenner, M., Kink, E., Gedamke, J., Paton, D. and Raymond, B. 2009. Satellite tracking of southbound East Australian humpback whales (*Megaptera novaeangliae*): challenging the feast or famine model for migrating whales. Paper SC/61/SH17 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 11pp. [Paper available from the Office of this Journal].

Garrigue, C., Franklin, T., Constantine, R., Russell, K., Burns, D., Poole, M., Paton, D., Hauser, N., Oremus, M., Childerhouse, S., Mattila, D., Gibbs, N., Franklin, W., Robbins, J., Clapham, P. and Baker, C.S. 2011. First assessment of interchange of humpback whales between Oceania and the east coast of Australia. *J. Cetacean Res. Manage.* (*Special Issue 3*): 269–74.

Katona, S. K. and Beard J. A. 1990. Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the Western North Atlantic Ocean. *Rep. int. Whal. Commn* (*Special Issue 12*): 295–305.

Kaufman, G.D., Osmond, M.G., Ward, A.J. and Forestell, P.H. 1990. Photographic documentation of the migratory movement of a humpback whale (*Megaptera novaeangliae*) between East Australia and Antarctic Area V. *Rep. int. Whal. Commn* (*Special Issue 12*): 265–8.

Martin, A.R., Katona, S.K., Matilla, D., Hembree, D. and Waters, T.D. 1984. Migration of humpback whales between the Caribbean and Iceland. *J. Mammal.* 65:330–3.

Palsbøll, P.J., Allen, J., Berube, M., Clapham, P.J., Feddersen, T.P., Hammond, P.S., Hudson, R.R., Jorgensen, H., Katona, S., Larsen, A.H., Larsen, F., Lien, J., Mattila, D.K., Sigurjonsson, J., Sears, R., Smith, T., Sponer, R., Stevick, P. and Oien, N. 1997. Genetic tagging of humpback whales. *Nature* 388: 767–9.

Paterson, R. 1987. Recovery in the east Australian humpback whale stock. *Aust. Fish*. 46(8): 32–6.

Rock, J., Pastene, L.A., Kaufman, G., Forestell, P., Matsuoka, K. and Allen, J. 2006. A note on East Australia Group V Stock humpback whale movement between feeding and breeding areas based on photo-identification. *J. Cetacean Res. Manage*. 8(3): 301–5.

Stamation, K.A., Croft, D.B., Shaughnessy, P.D. and Waples, K.A. 2007. Observations of humpback whales (*Megaptera novaeangliae*) feeding during their southward migration along the coast of southeastern New South Wales, Australia: Identification of a possible supplemental feeding ground. *Aquat. Mam.* 33: 165–74.

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Review of contemporary cetacean stock assessment models

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ABSTRACT

Model-based methods of analysis are widely used to conduct cetacean stock assessments, and to provide the operating models on which management strategy evaluation is based. This paper reviews recent assessments and management strategy evaluations for cetacean populations, with a view towards establishing ‘best practice’ guidelines for such analyses. The models on which these analyses are based range from simple exponential trend models that ignore density-dependence to complex multi-stock age-sex- and stage-structured models that form the basis for management strategy evaluation. Most analyses assume that density-dependence is on calf survival (which implicitly includes maturity and pregnancy rate), but it could also impact the survival rate of adults or the age-at-maturity. Cetaceans seldom have more than one calf per female each year, which limits the variation in calf numbers, and places an upper limit on the effects of density-dependent calf survival. The models differ in terms of whether the population projections start when substantial catches first occurred or whether allowance is made for time-varying carrying capacity by starting the model in a more recent year. Most of the models are deterministic, but account needs to be taken of variation in cohort strength for analyses that include age-composition data or for species that are relatively short-lived. A limited number of analyses include process variability using a state-space-like modelling framework. For some stocks, abundance is so low that ideally both demographic and environmental variability should be included in models. The primary source of data for parameter estimation is a time-series of estimates of absolute abundance, although some approaches considered used a variety of data types, including relative abundance indices, mark-recapture data and minimum abundance estimates based on haplotype counts. In general, at least one estimate of absolute abundance is needed for parameter estimation; this is because there is a lack of catch-induced declines in abundance captured by indices of relative abundance that could be used to provide information on absolute abundance. Similarly, information on abundance from age- and length- composition data is limited. Most of the analyses quantify uncertainty using Bayesian methods to allow information on biological parameters, particularly the intrinsic rate of growth and the relative population at which maximum production occurs, to be included in the analyses, along with sensitivity testing. The future for the models on which assessments and management strategy evaluations are based will often involve multi-stock models that include age-, sex- and spatial-structure and are fitted as state-space formulations, although at present such models are often too computationally intensive to be feasible for implementation or there is insufficient information in the data to estimate the parameters representing all the processes, leading to simplifications, with the result that the performance of some of the methods of assessment used for cetacean stocks needs to be better understood, including through simulation testing.

KEYWORDS: ASSESSMENT; BAYESIAN; CETACEAN; MANAGEMENT STRATEGY

INTRODUCTION

Assessments of cetacean stocks[1] for use in management have, for several decades, been based on population dynamics models fitted to monitoring data. While conceptually similar to the approaches used to assess fish (Maunder and Punt, 2013) and invertebrate species (Punt *et al*., 2013), the assessment methods for cetacean stocks differ in some important ways. Specifically, catches (at least during the most recent three decades) have tended to be relatively low for most cetacean stocks – generally only bycatch, and in a few instances commercial, special permit or aboriginal subsistence catches. Therefore, information on absolute abundance provided by catch-induced declines in indices of relative abundance is not available. Consequently, most model-based assessments for cetacean stocks rely more on indices of absolute abundance than do assessments of fish and invertebrates. In addition, sample sizes for the age- and size-composition of removals are rarely high compared to those for commercially-important fish and invertebrate stocks.

Cetacean population assessments are used for a variety of purposes, often within specific contexts such as the conservation and management requirements of international bodies (such as the International Whaling Commission (IWC) or the North Atlantic Marine Mammal Commission (NAMMCO)) or national legislation (e.g. the US Marine Mammal Protection Act). In a conservation and management context, assessments can be used to provide:

(1) information on abundance in absolute terms and relative to the pre-exploitation size and to target and threshold levels;

(2) estimates of recent trends in abundance and/or mortality; and

(3) probabilities of rebuilding and extinction.

In addition, models are used to addresses questions of primarily scientific or ecological interest, such as which factors are driving population dynamics and distribution, and how might stocks or individuals respond to environmental change.

Particularly in the case of large whales in the context of the IWC, management advice is based on the application of ‘management strategies’[2]. However, in most of the cases where catch limits (or ‘strike’ limits as they are called in the case of aboriginal subsistence whaling) are set for cetacean stocks, these are based on management strategies that use survey-based estimates of abundance, empirical rules that

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[1] Stocks for the purposes of this review are generally taken to be management units. However, there is usually an attempt to use various sources of data to identify demographically independent units within a species or ocean basin e.g. see discussion in Donovan (1991).

[2] Combinations of data collection schemes, analysis methods and harvest control rules that have been selected using simulations that have evaluated their ability to achieve the management goals (Punt *et al*., 2016). Pioneered to a great extent by the IWC Scientific Committee, they are called ‘management procedures’ in the IWC and other cetacean literature e.g. the IWC’s Revised Management Procedure (RMP) used to specify catch limits for baleen whales that are caught on their feeding grounds by commercial whalers and its Aboriginal Whaling Management Procedure (AWMP), which incorporates several stock-specific *Strike Limit Algorithms* to specify strike limits for subsistence hunts.

use survey estimates of abundance, or (in rare cases) simple model-based assessment methods combined with a harvest control rule. The selection of a management strategy should be based on simulation testing; a core element of simulation testing is the population dynamics model that represents the truth for the simulations (called the 'operating model'). The operating model is not an assessment model *per se*, but has many of the features of an assessment model and can be used to provide many of the types of outputs typically produced by an assessment. Thus, this review includes population models that have formed the basis for operating models, as well as those used to provide traditional outputs from stock assessments. For this reason, the term 'analysis' is used for the process of analysing monitoring data using methods that rely on some form of population dynamics model. However, and where appropriate, the term 'assessment' will be used to refer to a conventional stock assessment and 'MSE' to management strategy evaluation.

The aim of this paper is first to provide a summary of the stocks for which analyses have been undertaken and the analysis methods used most recently for those stocks. The analyses primarily concern large baleen whales in the context of the IWC and NAMMCO, which aim to conduct population model-based assessments, but some analyses exist for other stocks of cetaceans. The focus is on methods rather than results or whether those results were considered useful for management purposes (although in most cases, the assessments were approved by the relevant management bodies following a peer-review process). The results of this review are then used to identify (a) key issues that need to be addressed when deciding on the specifications for an analysis, (b) the choices made in current analyses and (c) the advantages and disadvantages associated with the different choices. Finally, the paper develops a set of 'best' practices for conducting cetacean stock assessments, with a focus on analyses for baleen whales (the subject of most analyses and for which most data are available).

STOCKS AND ANALYSES

The review focuses on recent (generally since 1995) analysis methods that involve population dynamics models that were applied to cetacean stocks. It does not cover the models used to analyse the monitoring data that provide the estimates of abundance for the assessments (e.g. Gerrodotte and Forcada, 2005; Cañadas *et al*., 2006), the models used to standardise catch-per-unit effort data (e.g. Cooke, 1993) or the models used to analyse mark-recapture data (e.g. Cooch and White, 2007)[3]. This review is restricted to analyses in which at least some of the parameters of the population dynamics model were estimated by fitting it to available data. Thus, model-based analyses in which all of the parameters are based on literature values/or 'guesstimated' by experts (e.g. Alvarez-Flores, 2006; Dueck and Richard, 2008; Reeves and Brownell, 2009; Slooten, 2015) are not covered in this review. Similarly, models that were based on back-calculation (e.g. Smith and Polacheck, 1979; Smith, 1983; Wade, 1993) where the only estimable parameter is carrying capacity and it is selected so that an estimate of current abundance is 'hit' are not the focus on this paper, nor are models that were developed primarily to estimate life history parameters (e.g. Fifas *et al*., 1998; Stolen and Barlow, 2003).

The stocks and hence the analysis methods summarised in this review were identified through: a literature search (Web of Science/Google Scholar); contacts with representatives of key management bodies; and contacts with individual analysts. Many of the reports describing analyses are found in the literature of management bodies (either the reports of the Scientific Committees of those bodies or papers presented to them) and are not necessarily searchable in databases such as Web of Science.

The results for 'large whales' (i.e. baleen whales and the sperm whale) are presented separately from those for other cetacean species, primarily because the peer-review process for analyses for baleen and sperm whales takes place through the IWC Scientific Committee, while that for the other species occurs as part of national (or in the case of some of the species harvested off West Greenland, the NAMMCO) review processes. The information is summarised by ocean basin or by stock, depending on the unit of analysis. In some cases, a stock has been assessed both as a single unit and as part of a regional analysis. In such cases, results are presented separately for the single unit and the regional analyses.

Tables 1 and 2 lists the stocks/species considered in this review, their major purpose (to form the basis of an assessment or to be the operating model for an MSE), the basic structure and some key (usually the most recent) references. However, in many cases the assessments were developed over several years. For example, Butterworth *et al*. (1999) outline an approach based on ADAPT-VPA for assessing Antarctic minke whales that was superseded by the integrated catch-at-age analysis method of Punt *et al.* (2014). Tables 3 and 4 outline the data types that were used in each analysis, while Tables 5 and 6 summarise how the analyses treated density-dependence, natural mortality and selectivity, three of the key processes that need to be included in any model-based analysis of a cetacean population. Finally, Tables 7 and 8 outline the types of outputs provided for each application and how uncertainty was quantified.

MODEL STRUCTURE ASSUMPTIONS

Population dynamics models

The assessments in Tables 1 and 2 are based on several types of population dynamics model. At the simplest level, are the analyses that aim only to estimate trends in abundance by fitting exponential models, perhaps using state-space formulations, to time-series of estimates of absolute abundance (e.g. those for eastern tropical Pacific spinner dolphins, and spotted dolphins). Such analyses provide no information about the status of stocks relative to reference points such as carrying capacity, but may provide information as to whether populations are increasing or not.

Most of the analyses in Tables 1 and 2 are based on age-structured models (often age- and sex-structured models) or production models. In general, the production models are based on the Pella-Tomlinson production function so that the point at which maximum surplus production occurs (MSYL, the Maximum Sustainable Yield Level) can be set to a value other than 0.5, with many assessments assuming that MSYL = 0.6. A small fraction of the population dynamics models also include stage structure. For example, Hoyle and

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[3] Except where such data are integrated into an assessment model (e.g. Müller *et al*., 2011; Cooke *et al*., 2003, 2016).

Table 1

Assessments for baleen and sperm whales. '(a, b, etc.)' are used to distinguish among multiple analyses for the same species in this and all subsequent tables.

Species; stock	Purpose	Model types	Stock/spatial structure	Key references
BALAENOIDEA				
Bowhead whale				
Bering-Chukchi-Beaufort	Assessment (a, b); MSE (c, d)	Sex- and age-structured (a, b, c) Production model (d)	1 stock (a, b, c); 2 stocks (d)	Brandon and Wade (2006) (a); Punt (2006) (b); IWC (2003; 2008a) (c, d)
West Greenland	MSE	Sex- and age-structured	1 stock	IWC (2014a)
Southern right whale				
Southeast Atlantic	Assessment	Sex- and- and stage-structured	1 stock	Brandão *et al*. (2013)
Southwest Atlantic	Assessment	Sex- and- and stage-structured	1 stock	Cooke *et al*. (2003)
New Zealand	Assessment	Production model	1 stock	Jackson *et al*. (2016)
BALAENOPTERIDAE				
Common minke whale				
North Atlantic				
Eastern North Atlantic	Assessment	Sex- and age-structured	1 stock	Cooke (1993)
All	MSE	Sex- and age-structured	1, 2 or 3 stocks; 11 sub-areas	IWC (2017)
Western North Pacific	MSE	Sex- and age-structured	2, 3 or 5 stocks; 22 sub-areas	IWC (2014b)
Antarctic minke whales				
Indian and Pacific	Assessment	Sex- and age-structured	2 stocks (5 areas)	Punt *et al*. (2014)
Sei whale				
North Pacific	Assessment*			Tillman (1977)
Southern Hemisphere	Assessment*			Horwood (1980); Jones (1980)
Bryde's whale				
Western North Pacific	MSE	Sex- and age-structured	1 or 2 stocks (some with sub-stocks); two sub-areas	IWC (2008b)
Blue whale				
Eastern North Pacific	Assessment	Production model	1 stock	Monnahan *et al*. (2015)
Fin whale				
North Atlantic				
East Greenland-Iceland	Assessment	Sex- and age-structured	1 stock; sensitivity explored to alternative spatial definitions of the stock	Butterworth and Punt (1992)
All	MSE	Sex- and age-structured	3 or 4 stocks (some with sub-stocks); seven sub-areas	IWC (2017)
Southern Hemisphere	Assessment*			Breiwick (1977)
Humpback whale				
North Atlantic				
West Greenland	MSE	Sex- and age-structured	1 stock	IWC (2014a)
All	Assessment	Sex- and age-structured	2 stocks; 7 sub-areas	Punt *et al*. (2006)
Southern Hemisphere				
BSA (Brazil)	Assessment	Production model	1 stock	Zerbini *et al*. (2011)
BSB (West Africa)	Assessment	Production model	2–3 stocks off west Africa	Muller *et al*. (2011)
BSC (East Africa)	Assessment	Production model	2 stocks off east Africa	Johnston and Butterworth (2010)
BSD (W Australia) + BSE (E Australia) + BSF (Oceania)	Assessment	Production model	3 stock model	Ross Gillespie *et al*. (2014; 2015); Jackson *et al*. (2016)
BSG (West South America)	Assessment	Production model	1 stock	Johnston *et al*. (2011)

Cont.

Table 1 (*continued*).

Species; stock	Purpose	Model types	Stock/spatial structure	Key references
Gray whale				
North Pacific				
Western gray whale	Assessment	Individual-based stage-structured (26 stages) model	1 stock	Cooke *et al*. (2016)
Eastern gray whale	Assessment (a, b, c); MSE (d)	Production model (a); sex- and age-structured (b, d); sex-, age- and stage-structured (c)	1 stock	Wade (2002) (a); Punt and Wade (2012) (b); Brandon and Punt (2013) (c); IWC (2005) (d)
PCFG	MSE		2 stocks; no explicit spatial structure	IWC (2013)
All	Assessment	Sex- and age-structured	1 or 2 stocks (some with sub-stocks); 13 sub-areas	Punt (2016)
Sperm				
Western North Pacific	Assessment	Sex- and age-structured	1 stock; 12 fleets accounted for	Beddington and Cooke (1981)
		Sex-, age- and size-structured	1 stock; 12 fleets accounted for	Beddington and Cooke (1981); Cooke *et al*. (1983); Shirakihara, and Tanaka (1983); de la Mare and Cooke (1984)

*Out of date; not considered further.

Table 2

Assessments for other cetacean stocks. '(a)', '(b)', etc. are used to distinguish among multiple analyses for the same species in this and all subsequent tables.

Species; stock	Purpose	Model types	Stock/spatial structure	Key references
DELPHINOIDEA				
Hector's dolphin				
Banks Peninsula	Assessment	Age- and area-structured	1 stock; four areas	Davies *et al*. (2008)
Spotted dolphin				
Eastern	Assessment	Exponential model (a); production model (a, b, d, e); age-sex-, and stage-structured (c)	1 stock	Wade *et al*. (2002) (a); Wade *et al*. (2007) (b); Hoyle and Maunder (2004) (c); Lennert-Cody *et al*. (2012) (d); Anon (2009) (e)
Southern/western	Assessment	Production model	1 stock	Anon (2009)
Spinner dolphin				
Eastern	Assessment	Exponential model (a); production model (a, b, c, d); age-structured model (a)	1 stock	Wade *et al*. (2002) (a); Wade *et al*. (2007) (b); Lennert-Cody *et al*. (2012) (c); Anon (2009) (d)
Whitebelly		Production model	1 stock	Anon (2009)
Common bottlenose dolphin				
Northern Adriatic	Assessment	Stochastic production model	1 stock	Simeoni (2014)
White whales				
Eastern Hudson Bay	Assessment	Exponential model	1 stock	Hammill *et al*. (2009)
Cook Inlet	Assessment	Stochastic sex- and age-structured	1 stock	Hobbs and Sheldon (2008); Hobbs *et al*. (2016)
West Greenland	Assessment	Sex- and age-structured	1 stock	Witting and Heide-Jørgensen (2015a)
Narwhal				
Northern Hudson Bay	Assessment	Production model	1 stock	Kingsley *et al*. (2012)
East Canada – West Greenland	Assessment	Sex- and age-structured	Eight areas (separately)	Witting (2015)
East Greenland	Assessment	Sex- and age-structured	Two areas (separately)	Witting and Heide-Jørgensen (2015a)
Harbour porpoise				
West Greenland	Assessment	Sex- and age-structured	1 stock	Witting (2013)
False killer whales				
Hawaii	Assessment	Production model	1 stock	Oleson *et al*. (2010)

Table 3
Summary of the data used in assessments of baleen whale stock assessments.

Species; stock	Catch	Absolute abundance	Relative abundance	Age/size structure	Other
Bowhead whale					
Bering-Chukchi-Beaufort	Yes	Yes	No	Age- and size-composition (b)	Proportion of calves and mature animals (a, b, c); assumptions about stock mixing rates (d)
West Greenland	Yes	Yes	No	No	
Southern right whale					
Southeast Atlantic	No	No	No	No	Yes
Southwest Atlantic	No	No	No	No	Yes
New Zealand	Yes	No	No	No	Yes
Common minke whale					
North Atlantic					
Eastern North Atlantic	Yes	Yes	CPUE	No	
All	Yes	Yes	No	No	Sex-ratio data (pre-fishery and current)
Western North Pacific	Yes	Yes	No	No	Bycatch estimates; mixing proportions; minimum and maximum abundance estimates
Antarctic minke whale					
Indian and Pacific	Yes	Yes	Yes	Age- and size-structure data from Japan	
Bryde's whale					
Western North Pacific	Yes	Yes	No	No	Mark-recapture
Blue whale					
Eastern North Pacific	Yes	Yes	No	No	Data on ship strikes
Fin whales					
North Atlantic					
East Greenland-Iceland	Yes	Yes	Yes (CPUE; account taken of correlations between CPUE indices for different years)	No	
All	Yes	Yes	Yes (CPUE account taken of correlations between CPUE indices for different years*)	Age-composition data for catches off Iceland	Mark-recapture
Humpback whale					
North Atlantic					
West Greenland	Yes	Yes	No	No	
All	Yes	Yes	Yes	No	
Southern Hemisphere					
BSA	Yes	Yes	Yes	No	Minimum abundance estimate based on haplotype counts
BSB	Yes	Yes	No	No	Mark-recapture data, minimum abundance estimate based on haplotype counts
BSC	Yes	Yes	Yes	No	Mark-recapture data
BSD + BSE + BSF	Yes	Yes	No	No	Mark-recapture data, minimum abundance estimate based on haplotype counts
BSG	Yes	Yes	Yes	No	Minimum abundance estimate based on haplotype counts
Gray whale					
North Pacific					
Western gray whale	No	No	No	Indirectly through individual hetero-geneity/ annual variation of pregnancy rates	Photo-ID; genetic sex determination
Eastern gray whale	Yes	Yes	No	No	Calf counts (b, c); Strandings and ice-cover (c)
PCFG	Yes	Yes	No		
All	Yes	Yes	No	No	Mixing proportions; bycatch numbers
Sperm					
Western North Pacific	Yes	No	No	Male length-frequency	Account is taken of male limitation on pregnancy rate

*Sensitivity test only

Table 4

Summary of the data used in assessments of other cetacean stocks.

Species; stock	Catch	Absolute abundance	Relative abundance	Age/size structure	Other
DELPHINOIDEA					
Hector's dolphin					
Banks Peninsula	Yes	Yes	Yes	Yes	Total survival (from mark-recapture); bycatch (assumed Poisson distributed); ages at first reproduction
Spotted dolphin					
Eastern	Yes	Yes	Yes (a) No (b,c,d,e)	No (a,b,d,e) Yes (c)	No
Southern/western	Yes	Yes	No	No	No
Spinner dolphin					
Eastern	Yes	Yes	Yes (a) No (b,c,d)	No	No
Whitebelly	Yes	Yes	No	No	No
Common bottlenose dolphin					
Northern Adriatic	Yes	Yes	No	No	No
Beluga whales					
Eastern Hudson Bay	Yes	Yes	No	No	No
Cook Inlet	Yes	Yes	No	Yes (by stage)	No
West Greenland	Yes	Yes	Yes	No	No
Narwhal					
Northern Hudson Bay	Yes	Yes	No	No	No
East Canada – West Greenland	Yes	Yes	No	No	No
East Greenland	Yes	Yes	No	Yes	No
Harbour porpoise	Yes	Yes	Yes	No	No
West Greenland	Yes	Yes	No	Yes	No
False killer whales					
Hawaii	No	Yes	Yes	No	No

Maunder (2004) represented the population of eastern tropical Pacific spotted dolphins using a model that kept track of age, sex and colour pattern. The more common use of stages in cetacean assessment models is to account for calving intervals that exceed a year. For example, the models developed by Brandon and Punt (2013) and Cooke *et al.* (2016) for gray whales and by Cooke *et al.* (2003) and Brandão *et al.* (2013) for right whales were stage-structured. Some of the assessments of sperm whales conducted by the Scientific Committee of the IWC were based on population dynamics models that tracked numbers of animals by sex and size-class.

The assessments of right whales in the southwest and southeast Atlantic (Cooke *et al.*, 2003; Brandão *et al.*, 2013) and of gray whales off Sakhalin Island (Cooke *et al.*, 2016) are examples of integrated mark-recapture-population dynamics models. The values for the parameters of the models on which these analyses were based were estimated by fitting the population model to the recapture histories for naturally marked animals. A key feature of these analyses is that data on newly-identified calves were used to provide information on calving rates and calving intervals. Unlike most of the models on which the analyses considered in this review are based (with the exception of the assessment of eastern North Pacific gray whales by Brandon and Punt, 2013), the models on which the assessments for southeast and southwest Atlantic right whales and gray whales off Sakhalin Island are based on dividing females into 'receptive', 'resting' and 'calving' classes to better mimic calving intervals. These analysis methods can be computationally intensive, especially if the aim is to quantify uncertainty using bootstrap and/or Bayesian methods, so their application has been limited to small populations (<1,000 animals in total) for which resighting probabilities are at least 10%.

Most of the analyses considered are for a single stock in a single area. However, there is an increasing trend towards accounting for spatial structure explicitly and including multiple stocks that mix and (in a limited number of cases) between which dispersal occurs. Many of these models were developed to form the basis for MSEs given the well-known sensitivity of the performance of management strategies for cetaceans to stock structure uncertainty (Punt and Donovan, 2007). Spatial and multi-stock models have been developed for bowhead, gray, common minke and humpback whales to account for the situation of feeding grounds where it is likely that animals from multiple stocks mix and for which there is no objective way to assign either catches or estimates of abundance to individual stocks. Another reason for including multiple stocks in analyses is when there are discrete feeding grounds, but the relationships among the animals on these grounds is unknown (e.g. Müller *et al.*, 2011, who identified ten alternative models/stock structure hypotheses for humpback whales off the west coast of Africa).

Many of the models on which cetacean assessments are based assume that stocks were at carrying capacity prior to exploitation and that carrying capacity has not changed over time. However, evidence for stocks such as the eastern North Pacific gray whales (Reilly, 1981, 1992; Cooke, 1986; Butterworth *et al.*, 2002) and humpback whales in the North Atlantic (Punt *et al.*, 2006) is that either carrying capacity has changed over time or some other assumptions of the model are badly violated (e.g. catches are greatly under-estimated for example if struck and lost rates are markedly

Table 5

Technical aspects of the assessments of baleen and sperm whales.

Species; stock	Density-dependent component	Natural mortality	Selectivity (time-varying; estimated)	Other key features/notes
Bowhead whale				
Bering-Chukchi-Beaufort	None (a); births (Pella-Tomlinson form) (a, b, c); estimated MSYR (a, b); stochastic recruitment (c)[&]	Age-specific[$] (estimated) (a, b, c); episodic mortality events (c)[&]	Pre-specified (a, c, d); estimated (b)	Brandon and Wade (2006) examined several alternative models
West Greenland	Births (Pella-Tomlinson form); pre-specified MSYR (stochastic recruitment[&])	Pre-specified/episodic mortality events[&]	Pre-specified	
Southern right whale				
Southeast Atlantic	No	Age-specific[$] (estimated)	N/A	Time-variation variation in calving probabilities
Southwest Atlantic	No	Age-specific[$] (estimated)	N/A	Time-variation variation in calving probabilities
New Zealand	Pella-Tomlinson form (MSYR estimated with prior)	N/A	Implicitly assumed to be same as maturation	
Common minke whale				
North Atlantic				
Eastern North Atlantic	Births (Pella-Tomlinson form); estimated MSYR	Pre-specified (age-specific)	Pre-specified	
All	Births (Pella-Tomlinson form); pre-specified MSYR	Pre-specified (age-specific)	Pre-specified	
Western North Pacific	Births (Pella-Tomlinson form); pre-specified MSYR	Pre-specified (age-specific)	Pre-specified	Diffusion between sub-stocks (estimated); mixing rates (estimated); structured by season as well as space
Antarctic minke whale				
Indian & Pacific	Births (Ricker form); estimated MSYR, carrying capacity and recruitment deviates	Estimated (age-specific)	Logistic or dome-shaped by fleet; commercial selectivity time-varying	Random deviations in recruitment, mixing proportions; carrying capacity; growth
Bryde's whale				
Western North Pacific	Births (Pella-Tomlinson form); pre-specified MSYR	Pre-specified (age-specific)*	Pre-specified	Mixing rates (age-specific[&]) estimated
Blue whale				
Eastern North Pacific	Pella-Tomlinson form; estimated MSYR	N/A (production models)	Implicitly assumed to be same as maturation	Ship 'effort' predicted from model of shipping numbers
Fin whales				
North Atlantic				
East Greenland-Iceland	Births (Pella-Tomlinson form); estimated MSYR	Pre-specified*	Pre-specified*	
All	Births (Pella-Tomlinson form); pre-specified MSYR	Pre-specified	Estimated (logistic and time-invariant; logistic and time-dependent[&])	Diffusion between sub-stocks (estimated); mixing rates (estimated)
Humpback whale				
North Atlantic				
All	Births (Pella-Tomlinson/ Ricker form); estimated MSYR	Pre-specified	Pre-specified	Allowance is made for changing carrying capacity
West Greenland	Births (Pella-Tomlinson form); pre-specified MSYR (stochastic recruitment[&])	Pre-specified/episodic mortality events[&]	Pre-specified	
Southern Hemisphere				
BSA	Pella-Tomlinson form (MSYR estimated with prior)	N/A	Implicitly assumed to be same as maturation	
BSB	Pella-Tomlinson form (MSYR estimated with prior)	N/A	Implicitly assumed to be same as maturation	
BSC	Pella-Tomlinson form (MSYR estimated with prior)	N/A	Implicitly assumed to be same as maturation	Based on the 'sabbatical model'
BSD + BSE + BSF	Pella-Tomlinson form (MSYR estimated with prior)	N/A	Implicitly assumed to be same as maturation	
BSG	Pella-Tomlinson form (MSYR estimated with prior)	N/A	Implicitly assumed to be same as maturation	
Gray whale				
North Pacific				
Western gray whale	Individual heterogeneity / annual variation in pregnancy rate	Estimated		Accounts for the possibility of immigration; individual variation in sampling probability
Eastern gray whale	Births (Pella-Tomlinson form); estimated MSYR (a, b); estimated MSYR with stochastic recruitment (c); pre-specified MSYR (stochastic recruitment[&] (d)	Pre-specified/episodic mortality events[&]	Pre-specified	Effect of mass mortality event (estimated) (b, c); recruitment and natural mortality deviations linked to ice-cover (c)
PCFG	Births (Pella-Tomlinson form); pre-specified MSYR (stochastic recruitment[&])	Pre-specified/episodic mortality events[&]	Pre-specified	Diffusion (estimated); Effect of mass mortality event (estimated)
All	Births (Pella-Tomlinson form) pre-specified MSYR	Pre-specified	Pre-specified	Effect of mass mortality event (estimated); mixing rates (estimated)
Sperm				
Western North Pacific	Births (Pella-Tomlinson form); estimates MSYR and MSYL	Estimated; female linked to male	Tuned	

[$] Separately for calves and non-calves. *Sensitivity explored to alternative assumptions. [&] Sensitivity test only.

Table 6

Technical aspects of the assessments of other stocks.

Species; stock	Density-dependent component	Natural mortality	Selectivity (time-varying; estimated)	Other key features/notes
DELPHINOIDEA				
Hector's dolphin				
Banks Peninsula	Linear, with stochastic variation	Estimated (age-dependent; 5-parameter models)	Double-normal (estimated)	The model tracks abundance spatially, but the model itself is spatially-aggregated
Spotted dolphin				
Eastern	Pella-Tomlinson form (MSYR estimated) (a ,b, d, e); none (a); Pella-Tomlinson form with stochastic recruitment (MSYR estimated) (c)	Estimated (a, b, c, d, e); N/A (a)	Logistic (estimated) (c); implicitly assumed to be same as maturation (a, b, d, e)	Models in which *r* and *K* changed, with the year of change estimated were considered (a, b, e); Probability of moving between stages was assumed to logistic (c)
Southern/western	Pella-Tomlinson form (MSYR estimated)	N/A (production models)	Implicitly assumed to be same as maturation	Models in which *r* and *K* changed, with the year of change estimated were considered
Spinner dolphin				
Eastern	Pella-Tomlinson form (MSYR estimated) (a, b, c); None (a)	Estimated (a, b, c, d); N/A (a)	Implicitly assumed to be same as maturation (c)	Models in which *r* and *K* changed, with the year of change estimated were considered (a, b)
Whitebelly	Pella-Tomlinson form (MSYR estimated)	N/A (production models)	Implicitly assumed to be same as maturation	Models in which *r* and *K* changed, with the year of change estimated were considered
Common bottlenose dolphin				
Northern Adriatic	Schaefer model (MSYR estimated)	N/A (production model)	Implicitly assumed to be same as maturation	Carrying capacity allowed to change with prey abundance
White whales				
Eastern Hudson Bay	None	Included in intrinsic rate of growth	Pre-specified (uniform on 1+ animals)	State-space model; extent of struck and lost estimated; process variance pre-specified
Cook Inlet	Births and survival (Pella-Tomlinson form) (parameterised as growth rate); stochastic birth-death processes	Calculated from the growth rate	Pre-specified (uniform on mature animals)	Several stochastic processes; allowance is made for catastrophic mortality and Allee effects; *K* specified
West Greenland	Births (Pella-Tomlinson form) (MSYR estimated)	Estimated (age-specific)	Pre-specified (uniform on 1+ animals)	
Narwhal				
Northern Hudson Bay	None	Included in intrinsic rate of growth	Included in intrinsic rate of growth	State-space model; extent of struck and lost estimated; process variance pre-specified; includes killer whale predation
East Canada-West Greenland	Births (Pella-Tomlinson form) (MSYR estimated)	Estimated (age-specific)	Pre-specified (uniform on 1+ animals)	
East Greenland	Exponential growth (productivity estimated)	Estimated (age-specific)	Estimated	
Harbour porpoise				
West Greenland	Births (Pella-Tomlinson form) and exponential growth (productivity estimated)	Estimated (age-specific)	Estimated	Assessment not used for management
False killer whales	None	Implicit in the rate of growth	Not applicable	Scenarios explored two rates of change; Allee effects; catastrophic mortality event
Hawaii				

Table 7

Projection options, output statistics, and quantification of uncertainty for the assessments of baleen and sperm whales. Unless otherwise stated, the assessment examined uncertainty using sensitivity testing.

Species; stock	Projection ability	Reference points	Model output	Quantification of uncertainty
Bowhead whale				
Bering-Chukchi-Beaufort	No (a); Yes (b, c, d)	K, MSY, MSYR (a, b); K, MSYL (c, d)	RY, N^{tot} N^{tot}, need satisfaction, recovery rate, catch variation (b, c, d)	Bayesian
Southern right whale				
Southeast Atlantic	No	No	N^{mat}	Sensitivity analysis
Southwest Atlantic	No	No	N^{mat}	Sensitivity analysis
New Zealand	Yes	K	N, N/K	Bayesian
Common minke whale				
North Atlantic				
Eastern North Atlantic	No	None	N^{tot}, N^{exp}, N^{ma}	Asymptotic
All	MSE	K	N^{mat}/K^{mat}; predicted catches	Bootstrap
Western North Pacific	MSE	K	N^{mat}/K^{mat}; predicted catches	Bootstrap
Antarctic minke whale				
Indian and Pacific	Government of Japan (2016)	K, MSYR	Recruitment, N^{tot}, N^{tot}/K^{tot}	Asymptotic; likelihood profile*
Bryde's whale				
Western North Pacific	MSE	K	N^{mat}/K^{mat}; predicted catches	Bootstrap
Blue whale				
Eastern North Pacific	Yes	K	N, N/K	Bayesian
Fin whale				
North Atlantic				
East Greenland-Iceland	None	MSY, MSYR	RY, N^{tot}, N^{exp}, N^{tot}/K^{tot}, N^{exp}/K^{exp}	Bootstrap
All	MSE	K	N^{mat}/K^{mat}; predicted catches	Bootstrap
Humpback whale				
North Atlantic				
West Greenland	MSE	K	N^{tot}/K^{tot}; recovery rate, need satisfaction; catch variation	Bayesian
All	No	K, change in K		
Southern Hemisphere				
BSA	Yes	K	N, N/K	Bayesian
BSB	Yes	K	N, N/K	Bayesian
BSC	Yes	K	N, N/K	Bayesian
BSD + BSE + BSF	Yes	K	N, N/K	Bayesian
BSG	Yes	K	N, N/K	Bayesian
Gray whale				
North Pacific				
Western gray whale	Yes		N^{tot}, N^{mat}, Immigrants	Bayesian
Eastern gray whale	Yes (a, c, d)	MSY,RY (a); K (b, c, d)	N^{tot} (a,b); N^{tot}, need satisfaction (c); N^{tot}/K^{tot}; recovery rate, need satisfaction; catch variation (d)	Bayesian
PCFG	Yes	K	N^{tot}/K^{tot}; recovery rate, need satisfaction; catch variation	Bayesian
All	Yes	K	N^{tot}/K^{tot}; recovery rate, need satisfaction; catch variation	Bootstrap
Sperm				
Western North Pacific	No	K	N^{exp}/K^{exp}, N^{exp}	Sum of squares; likelihood profile

*Sensitivity test only.

Table 8

Projection options, output statistics, and quantification of uncertainty for other stocks.

Species; stock	Projection ability	Reference points	Model output	Quantification of uncertainty
DELPHINOIDEA				
Hector's dolphin				
Banks Peninsula	Yes	K	N^{ot}	Bayesian
Spotted dolphin				
Eastern	Yes (c); No (a, b, d, e)	K	N^{ot}	Bayesian (a, b, e); none (c)
Southern/western	No	K	N^{ot}	Bayesian
Spinner dolphin				
Eastern	No	K	N^{ot}	Bayesian
Whitebelly	No	K	N^{ot}	Bayesian
Common bottlenose dolphin				
Northern Adriatic	No	K	N^{ot}	Bayesian
White whales				
Eastern Hudson Bay	Yes (catches)	None	N^{tot}	Bayesian
Cook Inlet	Yes	Extinction	N^{tot}	Bayesian
West Greenland	Yes (catches)	RY, K	N^{tot}	Bayesian
Narwhal				
Northern Hudson Bay	Yes (catches)	None	N^{tot}	Bayesian
East Canada-West Greenland	Yes (catches)	K	N^{tot}	Bayesian
East Greenland	Yes (catches)	K	N^{tot}	Bayesian
Harbour porpoise				
West Greenland	Yes (catches)	RY, K	N^{tot}	Bayesian
False killer whales				
Hawaii	Yes	Near extinction	N^{tot}	Bayesian

higher than believed). In this respect, the Bering-Chukchi-Beaufort Seas stock of bowhead provides an illuminating example. Earlier assessments of this stock (e.g. Givens *et al*., 2005) were able to fit the available data under the assumption of time-invariant carrying capacity. However, the most recent data indicate that the rate of increase has not slowed down as would be expected for a population that is approaching its carrying capacity. Consequently, the most recent models for this stock of bowhead whales (e.g. Punt, 2015a) do not assume that carrying capacity has been constant for 150 years and instead, following Wade (2002), start the population projections in 1940, with the age-structure at that time assumed to be stable. Punt and Butterworth (2002) started population projections for the Bering-Chukchi-Beaufort Seas stock of bowhead whales from various years and assumed that the age-structure at that time corresponded to a population increasing an estimated rate.

In general, there is little need to include multiple fleets in model-based analyses for cetaceans, unlike the case for fish and invertebrates where differences in catch age- or size-compositions among areas or groups of vessels are often addressed by assuming that fishery selectivity differs spatially or seasonally. This is because it is difficult for whalers to select for animals of particular ages and even sizes. In addition, catch data are usually available by sex. However, spatial variation in age structure may interact with the spatial distribution of the whaling operations to produce apparent spatial and temporal differences in selectivity. There are some analyses with multiple fleets e.g. for the eastern North Pacific stock of gray whales and common minke whales off West Greenland, owing to differences in selectivity patterns between commercial and aboriginal whalers. Multiple fleets were also considered in the assessments for sperm whales in the North Pacific as a proxy for spatial structuring of the population, and in the assessments of Antarctic minke whales. The latter assessment allows for time-varying commercial selectivity given among-year changes in where the various fisheries operated.

Density-dependence

Density-dependence may operate on a variety of population processes including maturation, growth, calving rate, juvenile survival, adult survival and even movement rates. However, it is seldom the case that sufficient data are available to estimate the parameters governing even one of these processes.

The models that assume that population size has been increasing exponentially have no explicit representation of density-dependence. Brandon and Wade (2006) compared several models for the Bering-Chukchi-Beaufort Seas stock of bowhead whales and found that the highest posterior probability was assigned to the model that did not start the population projections when catches were first recorded and ignored density-dependence[4]. The analyses based on mark recapture data only (i.e. those for gray whales off Sakhalin Island and right whales in the southwest and southeast Atlantic) also do not account for density-dependence. These populations are all assessed to be increasing exponentially so any estimates of density-dependence parameters (and carrying capacity) would be very uncertain anyway.

With one exception, assessments that allow for density-dependence assume that it operates on births, generally assuming the Pella-Tomlinson density-dependence form i.e. the expected number of calves during year y, C_y, is given by:

$$C_y = N_y^m f_0(1 + A(1 - (N_y^d/K^d)^z)) \qquad (1)$$

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[4] This conclusion was strengthened once additional abundance data were collected (Punt, 2015a).

where N_y^m is the number of females capable of calving during year y, f_0 is the pregnancy rate at carrying capacity, A is the resilience parameter, z is the degree of compensation, N_y^d is the magnitude of the density-dependence component of the population during year y, and K^d is the magnitude of the density-dependence component of the population at carrying capacity. The parameter z is related to the value of MSYL, while the value of A is related to both the maximum pregnancy rate and the Maximum Sustainable Yield Rate[5]. Punt (1999) provides the relationships among A, z, MSYL and MSYR for the case of an age- and sex-structured population dynamics model. Equation 1 can lead to negative numbers of calves when the population is larger than K, which is clearly unrealistic so the constraint is usually imposed that the number of calves cannot be less than zero. Such a constraint can lead to convergence problems when minimisation is based on software that requires a differentiable objective function (such as AD Model Builder, Fournier *et al*., 2012). Consequently, the assessment of Antarctic minke whales by Punt *et al*. (2014) assumed a Ricker-like formation of equation 1, which implies that the number of calves tends to zero for $N_y^d/K^d \gg 1$.

It is possible to assume that density-dependence acts on births (equivalent in most cases to density-dependence on fecundity or calf mortality) and/or non-calf survival (Punt, 2015b). However, only one of the analyses (that for Cook Inlet white whales[6], Hobbs and Sheldon, 2008; Hobbs *et al*., 2016) included density-dependent natural mortality.

Other population dynamic assumptions

The base versions of the analyses are generally similar, but there are often many differences in the alternative models examined to explore uncertainty. The focus in this paper is on the assumptions for the base versions of the models. The key differences among the models are discussed below.

Is the population dynamics model deterministic or is some aspect of the dynamics stochastic?

The most general model in this respect is that developed for Antarctic minke whales that allows for deviations in (a) recruitment about the density-dependence function (i.e. about expected calf numbers), (b) the proportion of the population in each area in which two stocks are found, (c) selectivity spatially and over time and (d) in carrying capacity. Several other assessments (generally of shorter-lived species) consider stochastic recruitment, including the model developed Hoyle and Maunder (2004) for eastern tropical Pacific spotted dolphins, that for false killer whales, that for Cook Inlet (Alaska) white whales and that for Hector's dolphins off Banks Peninsula, New Zealand. Several of the analyses consider the possibility of episodic events in the future, but only the analyses for the eastern North Pacific gray whales estimate an episodic event (or catastrophe) in the past (for which direct evidence exists). Some stocks are 'very small', necessitating modelling of both demographic and environmental variation (e.g. Breiwick and Punt, 2002).

Is natural mortality (M) age-, sex- or stage-structured?

In general, the values for the parameters related to natural mortality or survival for cetaceans are pre-specified (Tables 5 and 6) and in some cases, natural mortality depends on age (e.g. for fin and common minke whales in the North Atlantic and North Pacific). Some of the analyses estimate natural mortality (and in the case of Antarctic minke whales how natural mortality depends on age). Hoyle and Maunder (2004) assumed there was an age-at-senescence, an assumption that was not made in other analyses (the limited evidence available suggests that senescence does not occur in baleen whales). Survival is, however, poorly estimated unless age data are available for which selectivity can either be estimated precisely of for which selectivity can reasonably be assumed to be uniform. Obtaining data to estimate juvenile and calf natural mortality is more challenging than for estimating adult natural mortality (if it is assumed that mortality is constant for all adult ages).

What is the first year of the modelled period?

Conventionally, analyses for cetacean stocks started in the first year for which (non-trivial) catches were recorded and it was assumed that the stock was at carrying capacity at that time. However, increasingly analyses are being conducted in which the model projections start after the stock has been subject to high previous catches. This is either because the earlier catches are considered to be very uncertain (or simply unknown) or because the assumption that the stock was at carrying capacity when catches were first recorded is incompatible with recent trends in estimates of abundance. In general, however, the estimates of carrying capacity from analyses in which the projections start fairly recently are imprecise. The exception is for stocks such as the eastern North Pacific stock of gray whales for which the rate of increase in abundance has declined, suggesting that the population is now approaching its (new) carrying capacity.

Has carrying capacity or productivity changed over time?

Most of the assessments assume that K and MSYR have remained constant over time. The assessments that start the population projections in a year more recently than when the first catches were recorded (e.g. Brandon and Wade, 2006), implicitly assume that carrying capacity may have changed over time (and, for the eastern North Pacific gray whales, models that assume time-invariant K are unable to mimic the trend in abundance inferred from the survey data) and some of the analyses for dolphins in the eastern tropical Pacific considered models in which K changed at some point in the past (with the year in which the change occurred treated as an estimable parameter). Thus, these analyses implicitly postulate that a regime shift in K occurred (without specifying the cause). The Antarctic minke whale assessment estimates changes over time in K as a random walk, thereby avoiding having to specify (or estimate) when it changed. Estimation of MSYR is challenging (e.g. IWC, 2014c) even when it is assumed to be time-invariant and thus consideration of time-varying productivity is unusual[7]. However, the analyses of dolphin populations in the eastern tropical Pacific considered model variants that estimated two

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[5] MSYR, the ratio of MSY to the equilibrium number of recruited animals when the population is producing MSY.

[6] 'White whales' are also commonly known as 'beluga' or 'beluga whales'; the common name is white whale as agreed by the IWC Scientific Committee is used throughout this paper.

[7] Scenarios in which productivity is assumed to change over time are, however, commonly included in MSEs.

levels for MSYR (modelled as the intrinsic rate of growth), i.e. implicitly assuming that a regime change in productivity occurred.

How is selectivity modelled?

The choice of the fishery selectivity pattern is probably inconsequential when the catch is small relative to the population size and there are no data on the age- or size-composition of the catch. Consequently, many analyses based on age-structured models make simple assumptions regarding fishery selectivity, such as that selectivity is uniform above age 1 or selectivity is pre-specified based on historical assumptions (e.g. for common North Atlantic minke whales). However, the availability of age-composition data has allowed selectivity to be estimated for some stocks (Antarctic minke whales, North Atlantic fin whales, the Bering-Chukchi-Beaufort Seas stock of bowhead whales, sperm whales in the western North Pacific, spotted dolphins in the eastern tropical Pacific, and narwhals and harbour porpoise off West Greenland). The assessment of Antarctic minke whales in the southern Pacific and Indian Ocean appears to be the only assessment that explored alternative functional forms for selectivity (dome-shaped vs asymptotic). This exploration supported the use of sex-specific dome-shaped selectivity that changed over time and differed spatially. Dome-shaped and spatial differences in selectivity are probably a consequence of the spatial distribution of the population (larger animals tend to be closer to or in the ice and hence less available to the fleet), while selectivity would differ over time as a function of where in the large areas on which the model is based the fishery operated in. Correct specification of selectivity is particularly important when catch age- or length-composition data are used for parameter estimation because these data can have a large influence on estimates of absolute abundance unless they are highly down weighted. Misspecification of selectivity can lead to biased estimates of exploitation rate and hence abundance.

How are the values of biological parameters linked to environmental factors?

In principle, environmental drivers of the population dynamics can be represented implicitly by estimating parameters such as the annual deviations in calf numbers about those expected given the deterministic relationship between abundance and pregnancy rate. Only one assessment (Brandon and Punt, 2013) attempted to explicitly link an environmental variable (ice-cover) to the deviations in calf numbers. Cooke (2007) outlined a modelling framework that does not explicitly model environmental drivers of productivity, but that allows a distinction to be made between the maximum growth rate a species can achieve in ideal habitat and the average growth rate that a population at low level will achieve in a given habitat. This model leads to the conclusion that the rate of population growth will be closer to deterministic at low stock size than close to carrying capacity. Cooke (2016) outlined how reference points such as MSYL can be defined when carrying capacity is varying over time.

The models that consider spatial structure rarely represent spatial structure explicitly, i.e. no attempt is made to define the probability that whales in one area move to another area. Rather, the models that consider spatial structure estimate (or pre-specify) the proportion of each stock in each area. The estimates of the mixing proportions are based primarily on data on the proportion of each stock in each area (e.g. using genetic information). In general, the models that include multiple stocks assume that there is no permanent transfer of animals between stocks (known as ‘diffusion’); exceptions include the models developed to test management strategies for common minke whales in the western North Pacific, fin whales in the North Atlantic and gray whales off the west coast of North America.

All but one of the analyses considered are based on models with an annual time-step. The exception is the model on which the MSE for the western North Pacific common minke whales is based, which operated on a monthly time-step to capture the impact of catching animals during their migration.

DATA USED FOR ASSESSMENT PURPOSES

The key data inputs to a stock assessment/MSE are a time-series of catches (ideally by fleet and sex), along with an index of relative or absolute abundance. The primary source on trends in abundance are estimates of abundance from surveys (Tables 3 and 4). Some earlier assessments (e.g. Cooke, 1993; Butterworth and Punt, 1992) were based on analyses of commercial catch and effort data. However, catch-rate-based indices of abundance are now considered to insufficiently reliable for use in cetacean assessments without a level of detail of knowledge of the operations that rarely, if ever, exists (IWC, 1989).

Catches were included in most of the analyses (Tables 3 and 4). However, catches, particularly those for the earliest years of exploitation (in some cases as early as the 16th century), often need to be adjusted by struck and lost rates (e.g. Smith and Reeves, 2003). Most analyses for baleen and sperm whales only considered removals due to modern (*ca*. post-1865) commercial and aboriginal harvesting, although more recently other direct removals such as bycatches in fishing gear and deaths due to ship strikes are being considered. For example, the model used for the rangewide assessment of Pacific gray whales (Punt, 2016) also included bycatch data, while that on which the assessment of eastern North Pacific blue whales was based included the impact of shipstrikes. In contrast to large whales, most of the anthropogenic removals of dolphins and porpoises are due to bycatch; estimating robust bycatch estimates is difficult and such estimates are usually much more uncertain than catches by commercial whaling (e.g. Lewison *et al.,* 2004).

All but one of the analyses considered made use of estimates of absolute abundance for parameter estimation purposes. A noteworthy exception is the models developed for sperm whales in the western North Pacific, which were fitted to the catch length-frequency data for males (although these data were subsequently found to be unreliable). Those models were developed in the early 1980s, prior to the start of most of the major abundance survey programmes. Consequently, should new assessments of western North Pacific sperm whales be undertaken, they would probably use survey estimates of abundance (perhaps as relative indices of abundance given difficulties estimating the number of animals missed for long-diving species such as sperm whales). In general, analyses that fit to data on trends in absolute abundance involve analysing data from sighting surveys to provide estimates of abundance that are then treated as data in a second analysis that estimates parameters such as productivity and carrying capacity. This is appropriate when the estimates of abundance are independent. However, this is not the case when sample sizes are small such that some parameters are assumed to be same among years. Moore and Barlow (2013) analyse survey data for beaked whales off the west coast of North America in which trend estimation is conducted simultaneously with abundance estimation and model changes in abundance using a deterministic exponential model – in principle changes in abundance could have been represented using a model in which annual changes in abundance were stochastic, i.e. using a full state-space model.

Several of the analyses also made use of data on relative abundance. These are usually estimates of abundance from surveys, but when it has not proven possible to estimate the constant of proportionality for the surveys, often because $g(0)$, the probability of detecting a school on the trackline, is not equal to 1 and cannot be estimated, or surveys only cover only a proportion of the area in which the stock being assessed is found. In the latter case, the estimates of relative abundance may be biased due to temporal variation of the proportion of the stock inside the survey area.

There was generally only a single estimate of absolute abundance for the earliest assessments that used such data for parameter estimation (e.g. Butterworth and Punt, 1992) and assessments selected the value for K such that the model 'hit' that abundance estimate (e.g. Smith and Polacheck, 1979; Smith, 1983; de la Mare, 1989). However, as additional surveys were conducted, it was possible to include the abundance data in the likelihood function maximised to estimate the values for the parameters. Increasing numbers of surveys led to the observation (e.g. Wade, 2002) that the sampling standard deviations for the survey estimates were too small given the demographics of cetaceans, i.e. the estimates varied more among years than was possible for a long-lived animal. This has led to now common practice of estimating an 'additional variance' parameter in analyses in which there are multiple estimates of absolute or relative abundance. This additional variation may represent sampling error, temporal variation in the constant of proportionality between survey estimates of abundance and actual abundance, unmodelled stochastic population dynamics or model misspecification.

Some methods for estimating abundance share parameters among years (e.g. Zeh and Punt, 2005; Laake *et al*., 2010), while other methods analyse sightings data pooled over several years (e.g. Bøthun and Øien, 2011). This leads to the error in the estimates of abundance being correlated, which must be accounted for in the likelihood function assumed for the estimates of abundance (e.g. Givens *et al*., 1995). The analyses for the eastern North Pacific gray whales and the Bering-Chukchi-Beaufort Seas stock of bowhead whales include a variance-covariance matrix for the estimates of absolute abundance.

Mark-recapture data are available for several stocks. These data have been used to estimate (a) mixing rates for North Atlantic fin whales and western North Pacific Bryde's whales (b) abundance for southwest and southeast Atlantic right whales, gray whales off Sakhalin Island and several Southern Hemisphere humpback whales and (c) survival for Hector's dolphins off Bank's Peninsula. Mark-recapture data are commonly used to estimate abundance, but several of the analyses for Southern Hemisphere humpback whales have instead integrated the mark-recapture data directly into the analysis (Table 3). Reasons for this include being able to account for losses in numbers due to natural mortality directly, as well as to let the data on trend from the mark-recapture data enter the analyses. In principle, mark-recapture data may imply a non-significant trend in abundance, but a statistically significant trend may be detected when all of the information for the stock is taken into account. Caution needs to be taken to ensure that the data are appropriately weighted when multiple sources of data are included in an analysis.

Several of the assessments of Southern Hemisphere humpback whale stocks included a constraint on the lower bound for the total number of animals in the population based on counts of mtDNA haplotypes[8]. To be included in an assessment in the form of a lower bound for the minimum total number of animals (N_{min}), the observed number of haplotypes needs to be corrected for sampling probability, for the number of males and the number of immature animals and for the number of haplotypes that might have been lost subsequent to the population being at its lowest level. In general, the impact of imposing an N_{min} is greatest when it is large because N_{min} places an implicit constraint on the maximum rate of increase (and hence MSYR).

Age- and size-composition data are only available for a small number of cetaceans and these are the species/stocks for which selectivity and deviations in calf numbers from expectation have been estimated. The data tend to be downweighted given a lack of independence in the sampling process, particular for commercial catches (e.g. Punt *et al*., 2014); such downweighting is common in assessments of fish and invertebrate stocks (e.g. McAllister and Ianelli, 1997; Francis, 2011; Punt, 2017). Care needs to be taken when including age- and length-composition data in analyses because while these data can provide information on absolute abundance, the information is sensitive to model misspecification, particularly misspecification of the selectivity function. Hobbs *et al.* (2016) fit their model to data on the proportion of the catch that consists of immature animals, mature females and mature males. Other data sources included in population analyses for cetaceans include the proportion of calves and mature animals from aerial surveys (Bering-Chukchi-Beaufort Seas bowhead whales), the sex-ratio of catches (North Atlantic minke whales), mixing proportions based on genetics data (eastern North Pacific gray whales, western North Pacific minke whales), and calf counts (eastern North Pacific gray whales).

MODEL FITTING AND QUANTIFICATION OF UNCERTAINTY

The models on which the analyses are based were, with a few (historical) exceptions, fitted using maximum likelihood or Bayesian methods.

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[8] The observed number of haplotypes in a population provides an absolute minimum of the number of females when the population was at its lowest level (Jackson *et al*., 2006).

Measures of statistical uncertainty

Most of the analyses have attempted to quantify parameter uncertainty using Bayesian, bootstrap, or asymptotic methods (e.g. Wade, 1999; Tables 7 and 8), although other methods such as Monte Carlo methods and likelihood profiling have also been applied. The bootstrap approach has been used most extensively to quantify the uncertainty associated with values for the parameters of the operating models on which MSEs have been based. These operating models are usually based on pre-specifying the parameter that determines productivity (normally expressed as MSYR), which is usually poorly determined even in data rich situations (e.g. Punt *et al*., 2014; de la Mare, 2016). The bootstraps tend to be parametric, where data are generated from their sampling distributions, and the model fitted to each such bootstrap data set.

Most of the analyses in Tables 1 and 2 quantified uncertainty using Bayesian methods (Tables 7 and 8). There are a variety of reasons for this. One is simply historical precedence – some of the first uses of Bayesian methods in assessments of harvested marine populations were for cetaceans (e.g. Givens *et al*., 1995). In addition, production of posterior distributions is computationally feasible for many cetacean stocks given the relatively limited amount of data available. More importantly, given the limited amount of information contained in the data for most stocks (e.g. for MSYL), Bayesian methods provide a way to include prior information in analyses. Whilst priors can be assumed to be uniform (e.g. Wade *et al*. 2002, 2007), it is preferable to base a Bayesian analyses on 'data-based' priors that are informative and represent a synthesis of parameter estimates among species and stocks. Most of the analyses in Tables 1 and 2 based on Bayesian methods imposed priors on biological parameters such as age-at-maturity, maximum pregnancy rate and the survival rates for calves and non-calves (with the constraint imposed that the calf survival rate cannot exceed that of non-calves). Placing a prior on the maximum pregnancy rate is equivalent to imposing a prior on MSYR or the maximum growth rate. However, there is often little information to update the priors (e.g. the eastern North Pacific blue whales), and in some cases, priors are updated to biologically unrealistic or implausible values. Zerbini *et al*. (2010) used information about biological parameters, in conjunction with an age-structured model, to develop a probability distribution for the maximum rate of increase for humpback whales. Furthermore, IWC (2014b) used a Bayesian approach to construct a probability distribution for the rate of increase for whale stocks that were severely depleted when data collection started, and this distribution was used to select a minimum plausible bound for MSYR expressed in terms of the 1+ component for the population for use in MSEs for baleen whales. It is difficult to impose upper bounds on biological parameters such as survival rate, age-at-maturity and maximum pregnancy rate because these parameters tend to be highly correlated (Brandon *et al*., 2007).

The difficulties of specifying priors are well known. In the context of assessments of cetaceans, the key discussions have related to (a) whether it is reasonable to impose independent priors on each of age-at-maturity, survival rate and maximum pregnancy rate given observed correlations between the values for these parameters when estimates can be made, (b) which parameters to impose priors on, specifically because priors for parameters for which information is lacking are often assumed to be uniform (e.g. should a prior be imposed on MSYL or *z*, both of which relate to the shape of the production function), and (c) should a prior be imposed on *K* or abundance in a recent year[9]. In general, while data can update the prior for *K* (or current abundance) and perhaps productivity, parameters such as the age-at-maturity and MSYL are seldom updated much.

An important difference between assessments for fish and invertebrate populations and those for cetaceans is that for cetaceans, catches tend to be low compared to productivity, particularly during recent years when most of the monitoring data are available i.e. there is no information on absolute abundance from catch-induced changes in relative abundance. However, parameters related to the density-dependence function can be estimated when stocks were depleted prior to the collection of indices of relative and absolute abundance and the monitoring data cover a period during which the population was increasing at close to the maximum possible rate (IWC, 2015; Tables 3 and 4).

Sensitivity analyses

All but one of the analyses considered examined sensitivity to assumptions by changing some of the assumptions of the base model (or a set of base models). The exploration of sensitivity tends to be most extensive for MSEs since one of the primary aims is to identify a management strategy that is robust to uncertainty; in designing an MSE, the aim should be for the set of operating models to be reduced with additional research (Punt *et al*., 2016). The set of operating models must be reasonable so that selection of the management strategy is not dictated by unrealistic assumptions and thus it rare that even MSEs will explore *all* 'plausible' hypotheses and assumptions[10]. Nevertheless, the number of sensitivity tests can be substantial for some MSEs. Table 9 provides an example for a single stock situation and the number can be considerably greater where there is uncertainty regarding stock structure, which can involve changing the number of stocks in the region being managed and where they are located (e.g. fin and common minke whales in the North Atlantic and common minke whales in the western North Pacific).

Most of the sensitivity tests for assessments involve changing the values for pre-specified parameters, changing the priors imposed on the parameters as part of Bayesian analyses, and (much less often) considering different structural models and different functional forms for natural mortality and selectivity.

Simulation evaluation

It is now considered essential in resource management to evaluate the performance of assessment methods before they are used to provide management advice. The IWC Scientific

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[9] Most Bayesian cetacean assessments now place a prior on current abundance to avoid the prior for carrying capacity being updated prior to inclusion of data simply because some combinations of productivity and carrying capacity are inconsistent with the population being currently extant given the model and historical catches.

[10] Assigning 'plausibility' remains one of the greatest challenges in developing and implementing management procedures within the IWC (Punt and Donovan, 2007).

Table 9

The *Robustness Trials* (sensitivity tests) for the MSE for the Bering-Chukchi-Beaufort Seas bowhead whales (from IWC, 2003).

Trial	Factor	Basic trials	Factor level
BR01	A: Density-dependence	1, 1^{S}, 9, 9^{S}	Density-dependence on mature (BE trials use 1+)
BR02	B1: Stochastic dynamics	8^{S}, 13^{S}	Stochastic dynamics (with serially-correlated environmental variation)
BR04	E: Survey frequency	9, 13, 14, 16, 20	(a) 15 yrs
		16, 20	(b) 5 yrs
BR05	F: Strategic surveys	9	(a) Yes + CV = (0.25, 0.25)
		9	(b) Yes + CV = (0.34, 0.25)
BR06	G: Survey bias time dependence	1	(a) Historic bias (1978–2002): 1.5 constant; Future bias: decreasing (1.5 → 1)
		1	(b) Historic bias (1978–2002): 0.67 constant; Future bias: increasing (0.67 → 1)
		9, 9^{S}	(c) Future bias: sinusoidal from base value in yr 0 to maximum of 150% in yr 40
		12, 12^{S}	(d) Future bias: decreasing (1.5 → 1) from year 0 to 100
		14	(e) Future bias: increasing from 1 → 1.5 in year 25 and constant thereafter (former BE15)
BR07	H: Future survey *CV*	1	(a) CV = (0.1, 0.1)
		1^{S}	(b) CV = (0.34, 0.25)
		9	(c) (0.1, 0.1) + sinusoidal survey bias
BR08	I: Historic catch bias	14, 16^{S}	(a) 0.5 bias from 1848–1914
		14, 16, 16^{S}	(b) 1.5 bias from 1848–1914
BR09	K: Time dependence in *K*	1, 9, 10	(a) *K* halves linearly over 100 years
		1, 9, 10	(b) *K* doubles linearly over 100 years
		1	(c) *K* sinusoidal from base value in year 0 to maximum of 150% in year 40
		1, 21	(d) Tent *K: K* doubles linearly from years-50 to 0 and halves from years 0 to 50
		1, 9	(e) *K* halves linearly over 100 years + strategic surveys
BR10	L: Time dependence in *MSYR*	10	(a) Resilience (*A*) halves linearly over 100 years,
		9	(b) Resilience (*A*) doubles linearly over 100 years
		1, 8	(c) Resilience steps 2½% → 1% → 2½% every 33 yrs over 100 years
		1, 8	(d) Resilience steps 2½% → 1% → 2½% every 33 yrs over 100 years in sync with *M* (compute MSYR first) – if it is practical halve *M* for each age class
		1	(e) *K* and *A* halve linearly over 100 years
		1, 21	(f) *K* and *A* vary as tent (see BR09)
BR11	M: Time dependence in *M*	1, 9, 10	(a) Natural mortality *M* halves linearly over 100 years (and calculate resulting MSYR)
		1, 9, 10	(b) *M* doubles linearly over 100 years
BR12	N: Episodic events	1, 1^{S}, 9, 9^{S}	2 events occur, between years 1–50, in which 20% of animals die
BR13	O: Integrated	1, 11, 14	(a) $MSYR_{1+} \sim U[0.01, 0.04]$; fixed $MSYL_{1+} = 0.6$
		11, 14	(b) $MSYR_{1+} \sim U[0.01, 0.04]$; $MSYL_{1+} \sim U[0.4, 0.8]$
		1, 1^{S}, 11, 11^{S}, 14	(c) $MSYR_{1+} \sim U[0.01, 0.04]$; $MSYL_{1+} \sim U[0.4, 0.8]$; historical catch bias ~ U[0.5, 1.5]; Serial correlation ~ U[0.47, 0.95]
		1^{S}, 11^{S}	(d) $MSYR_{1+} \sim U[0.01, 0.04]$; $MSYL_{1+} \sim U[0.4, 0.8]$; historical catch bias ~ U[0.5, 1.5]; Serial correlation $\rho \sim U[0.47, 0.95]$, time delay in density-dependence ~ U[0, 30]
BR14	P: 1st year of population projection	1, 9	1940 (reference or base case level is 1848 or 1748 for stochastic trials)
BR15	$MSYL_{1+} = 0.9$	1, 9, 10	
BR16	B2: Different stochastic parameter	1^{S}	(a) Negative correlation in recruitment $\rho = -0.75$
		1^{S}	(b) High correlation in recruitment $\rho = 0.9$
		1^{S}, 9^{S}, 10^{S}	(c) High correlation in recruitment $\rho = 0.9$; + Episodic events
		1^{S}	(d) Change σ_{ε}^{2} to give 3* variation in population size at equilibrium
		9^{S}	(e) $\rho = 0.9$ + change σ_{ε}^{2} to give 3*equilibrium variation + episodic events

^{s}Stochastic.

Committee pioneered the testing of stock assessment methods using simulation (e.g. Kirkwood, 1981; de la Mare, 1986). For example, the estimation performance of the length-structured models used for assessment of sperm whale stocks in the western North Pacific was explored in several simulation studies (e.g. Cooke and de la Mare, 1983; Shirakihara and Tanaka 1984; Shirakihara *et al*., 1985; de la Mare, 1988).

In contrast to the situation for fisheries assessments (see the summary in Table 6 of Dichmont *et al.,* 2016), only a relatively small proportion of the methods on which the analyses in Table 1 and 2 are based have been subject to simulation evaluation. This is due in part to several of these methods being computationally extensive. However, there are some examples of recent assessment methods (including Bayesian methods) having been evaluated using (often limited) simulation including: (a) the Bering-Chukchi-Beaufort Seas stock of bowhead whales (Punt and Butterworth, 1997); (b) Antarctic minke whales in the Indian and Pacific Oceans (Punt and Polacheck, 2008; de la Mare, 2016); and humpback whales off the east and west coasts of Australia (Leaper *et al*., 2011).

PROJECTIONS AND MANAGEMENT OUTPUTS

Most, but not all, of the methods on which the analyses considered are based have the capability to project into the future (Tables 7 and 8). The models developed as the basis for operating models for MSEs and those that have formed the basis for Population Viability Analysis (PVA) are the most general in this respect. The assessments tend to be used to evaluate the implications of future series of catches, or simply to project the population ahead in the absence of exploitation to estimate the time for the population to reach some proportion of *K* or other target level. Perhaps the most extensive evaluation of the future state of a cetacean population was that of Hobbs *et al*. (2016) for white whales in Cook Inlet, Alaska. In addition to removals due to hunts, they considered the impact of predation by killer whales (in the past and in the future), catastrophic events in the future, as well as mass mortality events. They did not estimate posterior distributions for these processes, but rather examined sensitivity to alternative plausible values for the parameters governing them. The assessment of Antarctic minke whales reported time-trends in calf numbers, as well as growth rates and carrying capacity (this can only be done for the few assessments that estimate changes over time in recruitment, growth and carrying capacity).

In contrast to the assessments, the MSEs evaluate full-feedback management strategies. They thus include a component that generates the types of future data (usually absolute abundance data[11]) that will form the basis for new assessments. This contrasts with fisheries MSEs where it is common to generate several types of data including catch rate indices of relative abundance, catch age-and size-composition data, survey indices of abundance, along with the associated survey age- and size-composition data (Punt *et al*., 2016). The relative lack of data generated by cetacean MSEs reflects the data available for most species (Tables 3 and 4), and the fact that management strategies, even those based on population models (such as the IWC's RMP and AWMP) use relatively few data types. The MSEs generally assume that all of the removals are managed using the management strategy under evaluation, but there are some exceptions to this, including the IWC's strategy for the Greenlandic hunt for bowhead whales where account is taken of catches by Canada (which is not a member of the IWC). The evaluation of recent implementations of the IWC's RMP for commercial catches of fin and common minke whales in the central and western North Atlantic was based on MSEs that pre-specified the catches in aboriginal hunts from the same stocks (IWC, 2017).

The common outputs from analyses (and their projections) are time-trajectories of numbers of animals in absolute terms or relative to reference points such as K or MSYL. The population numbers are usually summarised as the total population size, although some assessments also report numbers of all females (e.g. Cooke *et al*., 2016) or mature females. Some of the earlier assessments for the eastern North Pacific stock of gray whales (e.g. Wade, 2002) and for the Bering-Chukchi-Beaufort Seas stock of bowhead whales (e.g. Givens *et al*., 1995; Brandon and Wade, 2006) reported estimates of current replacement yield (the catch so that the population size in the next year equals that at the start of the present year), as this quantity formed the basis for management advice before IWC *Strike Limit Algorithms* were developed for these stocks in 2005 and 2003 respectively.

The MSEs are capable of producing a large number of outputs. The most common outputs include the final depletion (the ratio of the mature population size at the end of the projection period to carrying capacity or the mature population size at the end of the projection period in the absence of exploitation had there been no catches – when carrying capacity is changing over time), the lowest depletion (or the ratio of the mature population size to that which would have arisen had there been no catches) over the projection period, and the recovery rate for depleted populations. The MSEs that have evaluated management strategies for commercial whaling have reported average catches as well as catch variation, and those that have evaluated management strategies for aboriginal subsistence whaling have reported what fraction of the need of aboriginal communities can be satisfied.

DISCUSSION

'Best' practices for modelling cetacean stocks

Table 10 lists a set of 'best practice' guidelines for conducting analyses for cetacean stocks. The words 'best practice' here are used in the way that has become common parlance but it should be recognised that what is important is that analyses *are adequate for the purpose they are intended* – 'best' in the sense of the 'best available at present' may not necessarily be adequate depending on what they are to be used for and 'adequate' analyses may not always need to be the best available That being said, the best practices suggested here represent (a) a synthesis of recent modelling decisions for cetacean stocks; (b) best practices in the field of fisheries assessment and wildlife modelling; and (c) highlight those factors that are likely to be consequential for the provision of management advice and should at least be considered in analyses. They are based primarily on the experience of the author – in principle, they could be tested using simulation studies, but this is beyond the scope of the present paper.

Choice of modelling structure

The type of model on which the analyses are based is determined in part by the sizes of the populations. The analyses that rely on mark-recapture data (e.g. those for gray whales off Sakhalin Island, and those for right whales in the Atlantic) are tailored to populations that are in the low 100s of animals. Nevertheless, some of the analyses based on age- and sex-structured population dynamics models, and population dynamics models that are sex- and age-aggregated have been applied to populations that are relatively small (e.g. low 100s Cook Inlet white whales and Banks Peninsula Hector's dolphins) as well as to populations consisting of thousands to hundreds of thousands of individuals (e.g. Antarctic minke whales, dolphin stocks off the west coast of North America).

The state of the art in terms of population projections for marine renewable resources is to allow for parameter uncertainty, and stochastic dynamics (demographic uncertainty as well as environmental stochasticity) in the future. Analyses of stocks in the low 100s of animals should ideally account for both demographic and environmental stochasticity. In contrast, analyses for large populations can safely ignore the effects of demographic uncertainty, but should still consider the impact of environmental stochasticity, particularly for birth rates and survival. The estimates of parameters related to environmental stochasticity may be very imprecise unless data on, for example, catch age-composition are available, which is uncommon for many cetacean stocks. Unlike fish and invertebrates, the number of calves-per-female is constrained for a cetacean. Consequently, there are limits to the amount

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[11] Other data could include the proportion of the population that are calves, juveniles or adults (e.g. for the Bering-Chukchi-Beaufort Seas stock of bowhead whales; IWC, 2003).

Table 10

Tentative best practice guidelines for cetacean stock assessments.

Issue	Guidelines
Model structure assumptions	
Spatial and stock structure	Required if evidence suggests population structuring within the area being assessed or perhaps if there is limited information to assess possible stock structuring (the absence of information is not information on absence).
Age- and sex-structure	Should be the default (sex-structure can be ignored if demographic parameters do not differ between the sexes and the sex ratio of the historical removals is close to 1–1).
Stage-structure	Often unnecessary, but can be used to impose assumptions regarding calving intervals or where the data suggest it might be important.
First year of the model	Ideally, the first year for which catches are available so that population can be assumed to have been at carrying capacity at the start of the first year with removals. However, a later year may be appropriate if the historical removals are very uncertain, or carrying capacity is likely to have changed over time.
Demographic stochasticity	Not needed for populations of 1,000 or more animals.
Environmental stochasticity	Worth including in base-case models when there is evidence for catastrophic events or simply for stocks for which there is likely to be among-year variation in pregnancy rate and or calf survival. Should be considered routinely if data on age- or size-composition are available.
Key biological and fishery processes	
Density-dependent processes	Models should consider density-dependence in birth rate and adult natural mortality.
Natural mortality	Should be age- or stage-specific (minimally calf, non-calf; but alternative forms such as the Siler form should be considered).
Selectivity	Usually only required to be estimated if removals are a substantial proportion of the population or if age- or size-composition data are included in the likelihood function. In principle, selectivity should depend on fleet, and consideration should be given to domed-shaped and time-varying selectivity.
Time-varying parameters	These pertain to selectivity, growth, distribution, and calf mortality, and should be treated as random effects (with the extent of variation estimated).
Model fitting	
Additional variation	The presence of additional variance should be tested for and accounted for. Similarly, the extent of overdispersion should be estimated for age- and size-composition data to avoid overfitting these data.
Prior distributions	Consider, to the extent possible, the use of data-based priors, and place priors on current abundance rather than carrying capacity.
Fit to raw data rather than summarised data	Where possible, models should be fit to the data in their rawest form (e.g., recapture histories instead of estimates of abundance from program MARK) to avoid the methods for analysing the raw data and those underlying the population making different sets of assumptions.
Use a state-space formulation	Inclusion of time-varying parameters requires the specification of parameters that constrain the extent to which such parameters can vary over time. Sensitivity can be explored to the values for these parameters if they have to be pre-specified rather than being estimated (e.g. Punt *et al*., 2014).
Uncertainty quantification	
Primary basis for quantify uncertainty	Bayesian methods permit prior information to be included in analyses and produce the information needed for the basis for projections (the probability associated with alternative parameter vectors and even models).
Sensitivity tests	These should be as broad as possible, ideally divided into 'more plausible' and 'less plausible' sets.
Simulation evaluation	Test the performance of the estimation method using simulations prior to their application in a management context.

by which the number of calves can differ from the expected value given by equations such as equation 1. Punt *et al*. (2014) recognised this and formulated the function defining recruitment variation to impose an upper bound on the numbers of calves-per-female in any year and the model of Cooke (2007) shows that large reductions in population size can occur on an annual basis, but this is not the case for increases owing to population demography. In general, stochasticity in calf numbers has limited impact on population trajectories when calf survival is larger than 0.9. However, such stochasticity must be modelled if the model is to be fitted to age-, size- or stage-composition data or if calf survival is to be linked to an environmental variable such as ice cover.

The choice between using a production model and an age- and sex-structured population dynamics model is semi-arbitrary although analyses for stocks with age-, size- or stage-composition data would logically be based on models that have this type of structure. Nevertheless, the choice between basing an analysis on an age-structured population dynamics model or a production model is often a pragmatic (computational) one, especially when the aim is to quantify uncertainty using Bayesian methods, there are multiple stocks of the species of interest in the region, or there is a substantial amount of informative data.

Experience has shown that there is often little justification for the inclusion of sex-structure in analyses. However, it is prudent to explicitly model sex-structure for species for which the catch sex-ratio can be markedly different from 1:1 (such as Antarctic and common minke whales and gray whales), because the relative reduction of the two sexes could differ markedly. Obviously, the number of calves will be directly related to the number of mature females, but social behaviour related to reproduction might result in the number of males also markedly impacting reproduction rates, particularly in odontocetes.

Most early analyses assumed that the region under consideration contained only a single stock. However, the available data (including mark-recapture, telemetry and genetics data) often suggest that multiple stocks of a given species may be found in a region, and these stocks may mix where catches and surveys occur. In such cases, it is necessary to develop multi-stock population dynamics models. The present models that allow for multiple areas and movement do not model movement explicitly but rather treat the proportions of each stock in each modelled area as estimable parameters (or pre-specify these parameters); this seems reasonable.

Finally, most models ignore within-year dynamics. This is reasonable for cetaceans, which are long-lived and for which removals are generally a small proportion of total abundance. The operating model developed for the western North Pacific common minke whales was the only one that allowed for seasonal dynamics; this was needed because catches occur during migration, and consequently the stock-, sex-, and age-composition of the catches in some areas changes during the year.

In general, estimation performance (measured by the precision with which parameters such as *K* is estimated) is improved if the stock is assumed to be at *K* at the start of the first year for which substantial catches are available. However, the benefits of improved estimation ability may be lost if the historical catches are subject to considerable uncertainty or if there are regime shifts in carrying capacity. In such cases, it may not be possible to provide reasonable estimates of population size relative to reference points such as carrying capacity and MSYL.

Parameterisation of processes

Most of analyses for cetacean stocks are based on models that represent the age- and sex-structure of the population (the analyses for Southern Hemisphere humpback whales being a notable exception). Age- and sex-structured models require specifications for how density-dependence is represented, as well as how survival, maturity and fishery selectivity are modelled as a function of age or sex.

Most past analyses have assumed that density-dependence impacts calf survival/fecundity/age-at-maturity (the effects of which tend to be difficult to distinguish) and whilst it is reasonable for this to remain the default, assuming density-dependence in adult survival can lead to different population dynamics so this source of density-dependence is worth at least considering in analyses.

Natural mortality is probably age- (or at least stage) specific. This can be modelled by assuming that calf survival differs from that for non-calf animals (assuming that calf survival is the square of adult survival is a simple way to force this to be true). However, if there are age-composition data, it may be possible to model age-specific natural mortality using a functional form such as the Siler model (Siler, 1979). Moore and Read (2008) used age-composition data to fit the Siler model for harbour porpoises. Punt *et al*. (2014) considered the Siler model as well as that natural mortality changes as an auto-regressive process with age, but eventually selected a piecewise linear model for natural mortality-at-age with breakpoints based on the results of initial model runs, for simplicity.

The way selectivity is modelled will be largely inconsequential owing to the longevity of most cetaceans. However, selectivity should be estimated rather than being pre-specified if (a) historical removals were very large and (b) if age- (or size-) composition data are included in the likelihood function. This is because composition data can provide information on absolute abundance, but such estimates are sensitive to misspecification of selectivity. In general, it is reasonable to assume that selectivity is an asymptotic function of age or size. However, this assumption should be tested if there are fleets for which the assumption that selectivity is asymptotic is likely to be invalid, and there are data for those fleets.

In principle, parameters for natural mortality, growth, selectivity, *K* and distribution could be linked (perhaps with error to environmental variables [Brandon and Punt, 2013]). However, selecting the correct variables can be challenging. Thus, in general, it is better to treat parameters that may vary over time as random effects, possibly (as in Brandon and Punt, 2013) linked to an environmental variable.

Main sources of uncertainty/quantification of uncertainty

Assessments for cetacean species and stocks are subject to a wide variety of sources of uncertainty. The major source of uncertainty is likely to be stock-specific. Punt *et al*. (2016) identify the categories of uncertainty that should be considered for inclusion in the operating models on which MSEs are based. The uncertainties that usually have the greatest impact on estimates of current abundance, and current abundance relative to reference points are: (a) model structure uncertainty, in particular in the context of analyses of cetaceans, uncertainty about stock structure (number of stocks, where they are found, how they move, and whether there is permanent movement among them); (b) uncertainty about the constant of proportionality between estimates of abundance and abundance itself; and (c) uncertainty about historical catches (particularly if these are large relative to sustainable yields). The performance of management strategies usually depends on the uncertainties that impact estimation of current abundance, but also on uncertainties related to (a) the quality and frequency of future data, and (b) regime shifts in productivity, natural mortality and carrying capacity.

Care needs to be taken to ensure that the way the uncertainties are characterised is plausible. This is particularly the case for uncertainties that relate to possible future events (e.g. future changes in carrying capacity and productivity, an increased frequency of episodic events), as current data may not shed much light on the likelihood of such events. Butterworth *et al*. (1996) outline a scheme for evaluating the relative plausibility of alternative hypotheses that could form the basis for sensitivity analyses in MSEs. In general, as is the case for recent MSEs undertaken by the IWC, it is advisable to divide sensitivity tests into a reference set (called ‘Evaluation’ trials in IWC parlance) that consists of the more plausible sets of assumptions and a less plausible set (called ‘Robustness’ trials in IWC parlance) that includes scenarios that are of interest to examine the behaviour of the management strategies in more ‘extreme’ circumstances.

Several ways have been used to quantify uncertainty (Tables 7 and 8), but the trend for cetacean assessments is towards the use of Bayesian approaches, notwithstanding the challenges associated with specifying defensible prior distributions. This is because (a) Bayesian methods permit the inclusion of prior information, in particular about the intrinsic rate of growth (or equivalently the MSYR) and (b) because the outputs of a Bayesian analysis are the inputs for decision analysis (i.e. the probability of alternative parameter vectors and even alternative models).

Data

In general, it is better to consider using as many sources of data as possible in assessments, although as mentioned earlier catch per unit of effort data are unlikely to be representative of changes in population size. However, it must be recognised that model misspecification, including incorrect assumptions about sampling error, can degrade results when multiple data sources are used for parameter estimation. In addition, inclusion of multiple data sources, can lead to identification of data conflicts, and hence the need to weight different data sources. In general, it is advisable to follow the recommendation of Francis (2011) that assessments should always try to mimic the trends in the index of abundance best, if they are representative of the stock, perhaps at the expense of fits to age-composition data. Age- (or size-) composition data are required if selectivity (or natural mortality) is to be estimated (although given the demographics of whales, the value for adult survival can often be informed by the rate of increase).

Simulation testing

Although many of the earlier methods of assessment for cetacean stocks were subject to evaluation using simulation, the use of simulation to evaluate estimation methods is now less common that was the case 20–30 years ago. While this perhaps reflects the complexity of some of the estimation methods, it is not good practice and is counter to the improved trend in fisheries assessment where most of the key methods have been subject to some form of simulation evaluation (e.g. Dichmont *et al*., 2016).

Some future directions

It is beyond the scope of this paper to provide a full analysis of improvements in assessments methods and MSEs that are or might be forthcoming. A short, annotated list of some key areas is presented below.

(1) Multi-species modelling to provide management advice

The analyses outlined in the paper ignore biological interactions among species – multi-species modelling is certainly an avenue to be explored but for a number of reasons is not yet at the stage of being able to provide robust management advice (e.g. Mori and Butterworth, 2006; Schweder *et al*., 1998).

(2) Use of individual-based models

In principle, it is possible to apply individual-based models to cetacean assessments and MSEs, especially for 'small' populations. In effect, this is close to the approach of the existing mark-recapture-based assessments for southwest and southeast Atlantic right whales and Sakhalin Island gray whales. Punt and Breiwick (2002) outlined an assessment and MSE framework that is based on an individual-based population dynamics model. This framework was developed to evaluate management strategies for small stocks, but has not been used to date.

(3) Incorporating non-lethal and cumulative effects data

Few analyses explicitly address the issue of the cumulative impacts of non-lethal impacts (such as the impact of the Gulf of Mexico oil spill on bottlenosed dolphins and the reduction in salmon numbers on killer whale survival in Puget Sound). In large part, this is because of the lack of available data (and hence understanding) of non-lethal factors individually and cumulatively to assess their impact on cetacean dynamics. Efforts are underway with respect to chemical pollutants (e.g. Hall *et al.,* 2016), noise and other forms of disturbance (e.g. King *et al.,* 2015), and food availability (de la Mare, 2017). The latter model is individual-based and has been used to better understand population-level yield curves.

(4) Incorporating 'raw' data in assessments

Most assessments fit the population model to estimates of abundance when these are determined from surveys. Recently, there has been a move to include data sources in assessments in their raw form (e.g. the integration of mark-recapture histories directly into the population models for right whales in the southwest and southeast Atlantic and for gray whales off Sakhalin Island). Nadeem *et al*. (2016) outline an approach in which raw sightings data for fin whales off the US west coast are fitted within a state-space population dynamics model. The state-space model used is based on an age- and sex-aggregated model, with production based on a Gompertz model and no allowance for historical removals. In principle, this approach could be extended to account for age, sex and catches, but this might come at a substantial computational cost.

FINAL THOUGHTS

Model-based assessments of cetaceans, especially baleen whales, remain the gold standard for providing management advice. Assessments for cetaceans usually have (and rely on) at least one estimate of absolute abundance. This is stark contrast to fisheries assessments where absolute abundance must be inferred from changes in relative abundance and age-composition. That being said, estimation of trends in abundance (and hence the values for parameters such as MSYR) in fishery assessments rely on information such as trends in relative abundance or age-composition, the latter of which is rare for cetacean stocks.

The ability to estimate stock status relative to reference points such as carrying capacity or MSYL for cetaceans is challenging in those cases where the catch history is long and uncertain and/or carrying capacity may have changed since the start of substantial catches. This issue is also a concern for fisheries (e.g. those in Europe and the east coast of North America) where exploitation started many centuries before the establishment of monitoring programmes. However, this problem can be partially overcome for these fisheries given the availability of often substantial amounts of catch and survey age-composition data during periods when exploitation rates and biomass changed substantially.

This review has shown that there are generally fewer data available for parameter estimation purposes for cetaceans than for fish and invertebrates (although better independent estimates of absolute abundance). Fisheries science has much to learn from analyses conducted for cetaceans, in particular the way MSE has been applied, the use of data independent of commercial catches, and the attempts to better understand/evaluate the implications of alternative stock structure hypotheses.

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REFERENCES

Alvarez-Flores, C.M. 2006. A review of the analysis to evaluate the recovery of bowhead whales, *Balaena mysticetus*, in the eastern Canadian Arctic. DFO Canadian Science Advisory. Research Document 2006/054. iv+36pp.

Anon. 2009. Updated estimate of NMIN and stock mortality limits. Document SAB-07-05 presented to the 7th Meeting of the Scientific Advisory Board of the International Dolphin Conservation Program, 30 October 2009, La Jolla, CA. 12pp. [Available from: *https://www.iattc.org/PDFFiles2/SAB-07-05-Nmin-and-Stock-Mortality-Limits.pdf*]

Beddington, J.R. and Cooke, J.G. 1981. Development of an assessment technique for male sperm whales based on the use of length data from the catches, with special reference to the North-west Pacific stock. *Rep. int. Whal. Commn* 31: 747–60.

Bøthun, G. and Øien, N. 2011. Report of the Scientific Committee. Annex D. Report of the Sub-Committee on the Revised Management Procedure. Appendix 7. Estimates used for catch limit calculations in northeast Atlantic minke whales. *J. Cetacean Res. Manage.* (Suppl.) 12: 107–10.

Brandão, A., Butterworth, D.S., Ross-Gillespie, A. and Best, P.B. 2013. Application of a photo-identification based assessment model to southern right whales in South African waters, now including data up to 2012. Paper SC/65a/BRG17 presented to the IWC Scientific Committee, June 2013, Jeju Island, Republic of Korea (unpublished). 15pp. [Paper available from the Office of this Journal].

Brandon, J.R. and Punt, A.E. 2013. Testing the Gray Whale Strike Limit Algorithm (SLA): allowing environmental variability to influence population dynamics. *J. Cetacean Res. Manage.* 13(1): 81–8.

Brandon, J.R. and Wade, P.R. 2006. Assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales using Bayesian model averaging. *J. Cetacean Res. Manage*. 8(3): 225–39.

Brandon, J.R., Breiwick, J.M., Punt, A.E. and Wade, P.R..2007. Constructing a coherent joint prior while respecting biological bounds: application to marine mammal stock assessments. *ICES J. Mar. Sci.* 64: 1,085–1,100.

Breiwick, J.M. 1977. Analysis of the Antactic fin whale stock in Area I. *Rep. int. Whal. Commn* 27: 124–27.

Butterworth, D.S. and Punt, A.E. 1992. Assessments of the East Greenland-Iceland fin whale stock. *Rep. int. Whal. Commn* 42: 671–96.

Butterworth, D.S. Korrubel, J.L. and Punt, A.E. 2002. What is needed to make a simple density-dependent response population model consistent with data for eastern North Pacific gray whales? *J. Cetacean Res. Manage.* 4(1): 63–76.

Butterworth, D.S., Punt, A.E. and Smith, A.D.M. 1996. On plausible hypotheses and their weighting, with implications for selection between variants of the Revised Management Procedure. *Rep. int. Whal. Commn* 46: 637–40.

Butterworth, D.S., Punt, A.E., Geromont, H.F., Kato, H. and Fujise, Y. 1999. Inferences on the dynamics of Southern Hemisphere minke whales from ADAPT analyses of catch-at-age information. *J. Cetacean Res. Manage.* 1(1): 11–32.

Cañadas, A., Fortuna, C. and Hammond, P.S. 2006. Modelling techniques to investigate the impact of changes in habitat on cetacean distribution and abundance. Paper SC/58/E21 presented to the IWC Scientific Committee, May 2006, St. Kitts and Nevis, West Indies (unpublished). 11pp. [Paper available from the Office of this Journal].

Cooch, E. and White, G. 2007. *Program MARK: A Gentle Introduction.* 900pp. [Available at *www.phidot.org/software/mark/docs/book/*].

Cooke, J.G. 1986. On the net recruitment rate of gray whales with reference to inter-specific comparisons. *Rep. int. Whal. Commn* 36: 363–6.

Cooke, J.G. 1993. Further analyses of minke whale CPUE in the Northeast Atlantic, with estimates of yield rates. Paper SC/45/NA7 presented to the IWC Scientific Committee, April 1993 (unpublished). 18pp. [Paper available from the Office of this Journal]

Cooke, J.G. 2007. The influence of environmental variability on baleen whale sustainable yield curves. Paper SC/59/RMP10 presented to the IWC Scientific Committee, May 2007, Anchorage, USA (unpublished). 15pp. [Paper available from the Office of this Journal]

Cooke, J.G. 2016. A note on the selection of stock recruitment relationships for western Atlantic Bluefin tuna, with reference to temporal variation in the relationship. *Collect. Vol. Sci. Pap. ICCAT.* 72: 1,449–56.

Cooke, J.G. and de la Mare, W.K. 1983. Description of and simulation studies on the length-specific sperm whale assessment technique. *Rep. int. Whal. Commn* 33: 741–6.

Cooke, J., Rowntree, V. and Payne, R. 2003. Analysis of inter-annual variation in reproductive success of South Atlantic right whales (*Eubalaena australis*) from photo-identification of calving females observed off Península Valdés, Argentina, during 1971–2000. Paper SC/55/O23 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 16pp. [Paper available from the Office of this Journal].

Cooke, J.G., de la Mare, W.K. and Beddington, J.R. 1983. An extension of the sperm whale model for the simulation of the male population by length and age. *Rep. int. Whal. Commn* 33: 731–4.

Cooke, J.G., Weller, D.W., Bradford, A.L., Sychenk, O., Burdin, A.M., Lang, A.R. and Brownell, R.L., Jr. 2016. Updated population assessment of the Sakhalin gray whale aggregation based on a photoidentification study at Piltun, Sakhalin, 1995–2015. Paper SC/66b/BRG225 presented to the IWC Scientific Committee, Bled, Slovenia, June 2016 (unpublished). 13pp. [Paper available from the Office of this Journal]

Davies, N., Bian, R., Starr, P., Lallemand, P., Gilbert, D. and Mckenzie, J. 2008. Risk analysis of Hector's dolphin and Maui's dolphin subpopulations to commercial set net fishing using a temporal-spatial age-structured model. Final Research Report to the Ministry of Fisheries, Wellington, NZ. 113pp.

De la Mare, W.K. 1986. Fitting population models to time series of abundance data. *Rep. int. Whal. Commn* 36: 399–418.

De la Mare, W.K. 1988. Extended sensitivity trials on the length-specific method for estimating the size of exploited sperm whale populations. *Rep. int. Whal. Commn* 38: 243–8.

De la Mare, W.K. 1989. Report of the Scientific Committee. Annex L. The model used in the HITTER and FITTER programs (Program FITTER.SC40). *Rep. int. Whal. Commn* 39: 150–51.

De la Mare, W.K. 2016. Simulation studies on the properties of estimates from statistical catch at age models. Paper SC/66b/IA8 presented to the IWC Scientific Committee, Bled, Slovenia, June 2016. 34pp. Paper available from the Office of this Journal]

De la Mare, W.K. 2017. Further developments of the individual based energetics model and progress on the development of an emulation model. Paper SC/67a/RMP2 presented to the IWC Scientific Committee, Bled, Slovenia, May 2017 (unpublished). [Paper available from the Office of this Journal]

De la Mare, W.K. and Cooke, J.G. 1984. A new model for the female sperm whale incorporating aspects of the reproductive cycle. *Rep. int. Whal. Commn* 34: 251–4.

Dichmont, C.M., Deng, R., Punt, A.E., Brodziak, J., Chang, Y-J, Cope, J.M., Ianelli, J.N., Legault, C.M., Methot, R.D., Porch, C.E., Prager, M.H. and Shertzer, K. 2016. A review of stock assessment packages in the United States. *Fisheries Research* 183: 447–60.

Donovan, G. P. 1991. A review of IWC stock boundaries. *Rep. int. Whal. Commn* (Special Issue 13): 39–68.

Dueck, L. and Richard, P. 2008. Preliminary evaluation of selective hunting and recovery of Eastern Canadian Arctic-West Greenland bowhead whales. Canadian Science Advisory Secretariat Research Document 2008/088. 17pp.

Fifas, S., Goujon, M. and Antoine, L. 1998. Application of Leslie's model on a population of common dolphns (*Delphinus delphis*): Senstivity study. *Aquat. Liv. Res.* 11: 359–69.

Fournier, D.A., Skaug, H.G., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A., and Sibert, J. 2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27: 233–49.

Francis, R.I.C.C. 2011. Data weighting in statistical fisheries stock assessment models. *Can. J. Fish. Aquat. Sci.* 68: 1,124–38.

Gerrodette, T. and Forcada, J. 2005. Non-recovery of two spotted and spinner dolphin populations in the eastern tropical Pacific Ocean. *Marine Ecology Progress Series* 291: 1–12.

Givens, G.H., Zeh, J.E. and Raftery, A.E. 1995. Assessment of the Bering Chukchi-Beaufort Seas stock of bowhead whales using the BALEEN II model in a Bayesian Synthesis Framework. *Rep. int. Whal. Commn* 45: 345–64.

Government of Japan. 2016. Results of the analytical work on NEWREP-A recommendations on sample size and relevance of age information for the RMP. Paper SC/66b/SP10 presented to the IWC Scientific Committee, Bled, Slovenia, June 2016 (unpublished). 23pp. [Paper available from the Office of this Journal]

Hall, A.J., Schwacke, L.H. and Rowles, T.K. 2016. Assessing the effects of petroleum-associated compound exposure on cetacean populations using the Pollution 2020 individual based modelling approach. Paper SC/66b/E04 presented to the IWC Scientific Committee, June 2016, Bled, Slovenia (unpublished). 10pp. [Paper available from the Office of this Journal]

Hammill, M.O., Kingsley, M.C.S, Lesage, V. and Gosselin, J-F. 2009. Abundance of Eastern Hudson Bay beluga. DFO Canadian Science Advisory. Secretariat Research Document. 2009/009. iv+18 p.

Horwood, J.W. 1980. Population biology and stock assessment of Southern Hemisphere sei whales. *Rep. int. Whal. Commn* 30: 519–30.

Hobbs, R.C. and Shelden, K.E.W. 2008. Supplemental status review and extinction assessment of Cook Inlet belugas (*Delphinapterus leucas*). AFSC Processed Rep. 2008-08, Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE, Seattle WA 98115. 76pp.

Hobbs, R.C, Wade, P.R. and Sheldon, K.W. 2016. Viability of a small, geographically-isolated population of beluga whales, *Delphinapterus leucas*: Effects of hunting, predation, and mortality events in Cook Inlet, Alaska. *Mar. Fish. Rev.* 77: 59–88.

Hoyle, S.D. and Maunder, M.N. 2004. A Bayesian integrated population dynamics model to analyse data for protected species. *Animal Biodiversity and Conservation* 27: 247–66.

International Whaling Commission. 1989. Report of the Comprehensive Assessment Workshop on Catch per Unit Effort (CPUE), Reykjavik, 16–20 March. *Rep. int. Whal. Commn* (Special Issue 11): 15–28.

International Whaling Commission. 2003. Report of Standing Working Group on the Aboriginal Subsistence Whaling Management Procedure. *J. Cetacean Res. Manage.* (Suppl.) 5: 154–225.

International Whaling Commission. 2005. Report of Standing Working Group on the Aboriginal Subsistence Whaling Management Procedure. *J. Cetacean Res. Manage.* (Suppl.) 7: 115–87.

International Whaling Commission. 2008a. Report of Standing Working Group on the Aboriginal Subsistence Whaling Management Procedure. *J. Cetacean Res. Manage.* (Suppl.) 8: 121–49.

International Whaling Commission. 2008b. Report of Sub-Committee on the Revised Management Procedure. *J. Cetacean Res. Manage.* (Suppl.) 10: 90–119.

International Whaling Commission. 2012. The Revised Management Procedure (RMP) for Baleen Whales. *J. Cetacean Res. Manage.* (Suppl.) 13: 485–94.

International Whaling Commission. 2013. Report of the Standing Working Group on the Aboriginal Subsistence Whaling Management Procedure. *J. Cetacean Res. Manage*. (Suppl.) 13: 130–53.

International Whaling Commission. 2014a. Report of the Standing Working Group on the Aboriginal Subsistence Whaling Management Procedure. *J. Cetacean Res. Manage.* (Suppl.) 15: 189–213.

International Whaling Commission. 2014b. Report of Sub-Committee on the Revised Management Procedure. *J. Cetacean Res. Manage.* (Suppl.) 15: 87–188.

International Whaling Commission. 2014c. Report of the Fourth Intersessional Workshop on the Review of Maximum Sustainable Yield Rates (MSYR) in Baleen Whales, 26–28 March 2013, La Jolla, California, USA. *J. Cetacean Res. Manage*. (Suppl.) 15: 507–518.

International Whaling Commission. 2015. Report of Sub-Committee on the Revised Management Procedure. *J. Cetacean Res. Manage.* (Suppl.) 15: 87–111.

International Whaling Commission. 2017. Report of Sub-Committee on the Revised Management Procedure. *J. Cetacean Res. Manage.* (Suppl.) 18: 123–73.

Jackson, J.A., Caroll, E.L., Smith, T.D., Zerbini, A.N., Patenaude, N.J. and Baker, C.S. 2016. An integrated approach to historical population assessment of the great whales: case of the New Zealand southern right whale. *Royal Society Open Science* 3: 150669.

Jackson, J., Olavarria, C. and Baker. 2006. Estimating the minimum historical population size of Southern Hemisphere humpback whales using diversity of mtDNA haplotypes. Paper SC/58/SH22 presented to the IWC Scientific Committee, May 2006, St. Kitts and Nevis, West Indies (unpublished). 11pp. [Paper available from the Office of this Journal].

Johnston, S.J. and Butterworth, D.S. 2010. New breeding stock C sabbatical model reference case and sensitivity tests. *J. Cetacean Res. Manage.* (Suppl. 2) 11: 244–8.

Johnston, S.J., Zerbini, A.N. and Butterworth, D.S. 2011. A Bayesian approach to assess the status of Southern Hemisphere humpback whales (*Megaptera novaeangliae*) with an application to Breeding Stock G. *J. Cetacean Res. Manage.* (Special Issue 3): 309–17.

Jones, R. 1980. Population assessments of sei whales using a modified VPA technique. *Rep. int. Whal. Commn* 30: 545–8.

King, S.L., Schick, R.S., Donovan, C., Booth, C.G., Burgman, M., Thomas, L. and Harwood, J. 2015. An interim framework for assessing the population consequences of disturbance. *Methods in Ecology and Evolution* 6(10): 1,150–8.

Kingsley, M.C.S., Richard, P. and Ferguson, S.H. 2012. Stock-dynamic model for the northern Hudson Bay narwhal population based on 1982–2008 aerial surveys. DFO Canadian Science Advisory. Secretariat Research Document. 2012/020. iv+20pp.

Kirkwood, G.P. 1981. Estimation of stock size using relative abundance data – a simulation study. *Rep. int. Whal. Commn* 31: 729–35.

Laake, J.L., Punt, A.E., Hobbs, R., Ferguson, M., Rugh, D. and Breiwick, J. 2012. Gray whale southbound migration surveys 1967–2006: an integrated re-analysis. *J. Cetacean Res. Manage.* 12: 287–306.

Leaper, R., Peel, S., Peel, D. and Gales, N. 2011. Exploring the assumptions of multi-stock assessment models for humpback whales (Megaptera novaeangliae) in the Southern Hemisphere: using Breeding Stocks D and E as an example. *J. Cetacean Res. Manage.* (Special Issue 3): 119–28.

Lennert-Cody, C.E., Rusin, J.D., Maunder, M.N., Everett, E.H., Largacha Delgado, E.D and Tomlinson, P.K. 2013. Studying small purse-seine vessel fishing behavior with tuna catch data: Implications for eastern Pacific Ocean dolphin conservation. *Mar. Mamm. Sci.* 29: 643–68.

Lewison, R.L., Crowder, L.B., Read, A. J. and Freeman, S.A. 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution* 19: 598–604.

Maunder, M.N. and Punt, A.E. 2013. A review of integrated analysis in fisheries stock assessment. *Fish. Res.* 142: 61–74.

McAllister, M.K. and Ianelli, J.N. 1997. Bayesian stock assessment using catch-age data and the sampling/importance resampling algorithm. *Can. J. Fish. Aquat. Sci.* 54: 284–300.

Maunder, M.N., Starr, P.J. and Hilborn, R. 2000. A Bayesian analysis to estimate loss in squid catch due to implementation of a sea lion population management plan. *Mar. Mamm. Sci.* 16: 413–26.

Monnahan, C., Branch, T.A. and Punt, A.E. 2015. Do ship strikes threaten the recovery of endangered eastern North Pacific blue whales? *Marine Mammal Science* 31: 279–97.

Moore, J.E. and Read, A.J. 2008. A Bayesian uncertainty analysis of cetacean demography and bycatch mortality using age-at-death data. *Ecol. Appl.* 18: 1914–31.

Moore, J.E. and Barlow, J.P. 2013. Declining abundance of beaked whales (family Ziphiidae) in the California current large marine ecosystem. *PLoS ONE* 8:e52770.

Mori, M. and Butterworth, D.S. 2006. A first step towards modelling the krill-predator dynamics of the Antarctic ecosystem. *CCAMLR Sci.* 13: 217–77.

Muller, A., Butterworth, D.S. and Johnston, S.J. 2011. Assessments of the Southern Hemisphere humpback whale Breeding Stock B: results for the models and sensitivities proposed at and following the 62nd meeting of the Scientific Committee of the IWC. Paper SC/63/SH26 presented to the IWC Scientific Committee, June 2011, Tromsø, Norway (unpublished). 45pp. [Paper available from the Office of this Journal].

Nadeem, K., Moore, J.E., Zhang, Y. and Chipman, H. 2016. Integrating population dynamics models and distance sampling data: a spatial hierarchical state-space approach. *Ecology* 97: 1,735–45.

Oleson, E.M., Boggs, C.H., Forney, K.A., Hanson, M.B., Kobayashi, D.R., Taylor, B.L., Wade, P.R. and Ylitalo, G.M. 2010. Status review of Hawaiian insular false killer whales (*Pseudorca crassidens*) under the Endangered Species Act. US Dep. Commerce, NOAA Tech. Memo., NOAA-TM-NMFS-PIFSC-22. 237 pp.

Punt, A.E 1999. Report of the Scientific Committee. Annex R. A full description of the standard BALEEN II model and some variants thereof. *J. Cetacean Res. Manage.* (Suppl.) 1: 267–76.

Punt, A.E. 2006. Assessing the Bering-Chukchi-Beaufort Seas stock of bowhead whales using abundance data together with data on length or age. *J. Cetacean Res. Manage*. 8(2): 127–37.

Punt, A.E. 2015a. Initial evaluation of two options for addressing infrequent surveys of the Bering-Beaufort Seas bowhead whales. Paper SC/D15/AWMP01 presented to the AWMP Workshop for Develop SLAS for the Greenland Hunts, 14–17 December 2015, Copenhagen, Denmark (unpublished). 22pp. [Paper available from the Office of this Journal].

Punt, A.E. 2015b. An investigation of the relationship between $\mathrm{MSYR}_{\mathrm{MAT}}$ and MSYR1+ based on a non-individual-based model. *J. Cetacean Res. Manage.* (Suppl.) 16: 110–11.

Punt, A.E. 2016. A revised age-structured model for exploring the conceptual models developed for gray whales in the North Pacific. IWC. Paper SC/A16/GW2 presented to the Third Workshop on the Rangewide Review of the Population Structure and Status of North Pacific Gray Whales, 18–20 April 2016, La Jolla, California (unpublished). 24pp. [Paper available from the Office of this Journal]

Punt, A.E. 2017. Some insights into data weighting in integrated stock assessments. *Fish. Res.* 192: 52–65.

Punt, A.E. and Breiwick, J.M. 2002. A framework for evaluating Strike Limit Algorithms for population reduced to small numbers. *J. Cetacean Res. Manage.* 4(2): 165–77.

Punt, A.E. and Butterworth, D.S. 1997. Assessments of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena mysticetus*) using maximum likelihood and Bayesian methods. *Rep. int. Whal. Commn* 47: 603–18.

Punt, A.E. and Donovan, G. 2007. Developing management procedures that are robust to uncertainty: Lessons from the International Whaling Commission. *ICES J. Mar. Sci.* 64: 603–12.

Punt, A.E. and Polacheck, T. 2008. Further analyses related to application of statistical catch-at-age analysis to Southern Hemisphere minke whales. Paper SC/60/IA2 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 46pp. [Paper available from the Office of this Journal].

Punt, A.E. and Wade, P.R. 2012. Population status of the eastern North Pacific stock of gray whales in 2009. *J. Cetacean Res. Manage.* 12(1): 15–28.

Punt, A.E., Butterworth, D.S., de Moor, C.L., De Oliveira, J.A.A. and Haddon, M. 2016. Management Strategy Evaluation: Best Practices. *Fish and Fisheries* 17: 303–34.

Punt, A.E., Friday, N.A. and Smith, T.D. 2006. Reconciling data on the trends and abundance of North Atlantic humpback whales within a population modelling framework. *J. Cetacean Res. Manage.* 8(2): 145–59.

Punt, A.E., Haung, T-C. and Maunder, M.N. 2013. Review of integrated size-structured models for stock assessment of hard-to-age crustacean and mollusc species. *ICES J. Mar. Sci.* 70: 16–33.

Punt, A.E., Hakamada, T., Bando, T. and Kitakado, T. 2014. Assessment of Antarctic minke whales using statistical catch-at-age analysis. *J. Cetacean Res. Manage.* 14: 93–116.

Reeves, R.R. and Brownell, R.L. (Eds). 2009. Indo-Pacific bottlenose dolphin assessment workshop report: Solomon Islands case study of *Tursiops aduncus*. Occasional Papers of the Species Survival Commission, No. 40, IUCN, Gland, Switzerland. 53pp.

Reilly, S.B. 1981. Population assessment and population dynamics of the California gray whale (*Eschrichtius robustus*). Ph.D. thesis. University of Washington, Seattle.

Reilly, S.B. 1992. Population biology and status of eastern Pacific gray whales: recent developments. pp.1,062–72. *In*: D.R. McCullough and R.H. Barrett (Eds). *Wildlife 2001: populations.* Elsevier Science, Essex, United Kingdom.

Ross-Gillespie, A., Butterworth, D.S. and Findlay, K. 2014. Assessment results for humpback breedings stocks D, E1 and oceania following recommendations from SC 65a. Paper SC/65b/SH04Rev presented to the IWC Scientific Committee, Bled, Slovenia, May 2014 (unpublished). 28pp. [Paper available from the Office of this Journal]

Ross-Gillespie, A., Butterworth, D.S. and Findlay, K. 2015. Final results for the final 'base case' three-stock DSB, BSE1 and BSO model, with sensitivity runs. *J. Cetacean Res. Manage*. (Suppl.) 16: 215–21.

Schweder, T., Hagen, G.S. and Hatlebakk, E. 1998. On the effect on cod and herring fisheries of retuning the Revised Management Procedure for minke whaling in the greater Barents Sea. *Fish. Res.* 37: 77–95.

Shirakihara, K. and Tanaka, S. 1984. Simulation studies on length-specific population assessment techniques for western North Pacific sperm whales. *Rep. int. Whal. Commn* 34: 259–64.

Shirakihara, K., Tanaka, S. and Nakano, T. 1983. The revised age-specific model for population assessment of the Western North Pacific sperm whales. *Rep. int. Whal. Commn* 33: 757–9.

Shirakihara, K., Tanaka, S. and Nakano, T. 1985. Further simulation studies on length-specific population assessment techniques for western North Pacific sperm whales. *Rep. int. Whal. Commn* 35: 199–203.

Siler, W. 1979. A competing-risk model for animal mortality. *Ecology* 64: 750–7.

Simeoni, C. 2014. Bottlenosed dolphins in the northern Adriatic Sea: A long-term assessment of the population dynamics. MS thesis, Department of Industrial Mathematics, University of Padua. vi+103pp,

Slooten, E. 2015. Effectiveness of partial protection for Maui's dolphin. Paper SC/66a/SM12rev1 presented to the IWC Scientific Committee, May 2015, San Diego, CA, USA (unpublished). 9pp. [Paper available from the Office of this Journal].

Smith, T.D. and Polacheck, T. 1979. Analysis of a simple model for estimating historical population sizes. *Fish. Bull.*, *US* 76: 771–9.

Smith, T.D. 1983. Changes in size of three dolphin (Stenella spp.) populations in the eastern tropical Pacific. *Fish. Bull., US* 81: 1–13.

Smith, T.D. and Reeves, R.R. 2003. Estimating historic humpback removals from the North Atlantic: an update. *J. Cetacean Res. Manage.* (Suppl.) 5: 301–11.

Stolen, M.K. and Barlow, J. 2003. A model life table for bottlenose dolphins (*Tursiops truncates*) from the Indian River lagoon system Florida, USA *Marine Mammal Science* 19: 630–49.

Tilman, M.F. 1977. Estimates of population size for the North Pacific sei whale. *Rep. int. Whal. Commn* (Special Issue 1): 98–106.

Wade, P.R. 1993. Estimation of historical population size of the eastern stock of spinner dolphin (*Stenella longirostris orientalis*). Fish. *Bull. US* 91: 775–87.

Wade, P.R. 1999. A comparison of statistical methods for fitting population models to data. pp.249–70 *In:* G.W Garner, S.C. Amstrup, J.L Laake, B.F.J. Manly, L.L. Mcdonald and D.G Robertson (Eds.) *Marine Mammal Survey and Assessment Methods*. Balkema, Rotterdam.

Wade, P.R. 2002. A Bayesian stock assessment of the eastern Pacific gray whale using abundance and harvest data from 1967–1996. *J. Cetacean Res. Manage*. 4(1): 85–98.

Wade, P.R., Reilly, S.B. and Gerrodette, T. 2002. Assessment of the population dynamics of the northeastern offshore spotted dolphin and the eastern spinner dolphin populations through 2002. SWFSC Administrative Report LJ-02-13. 58pp.

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

Witting, L. 2013. Assessment runs for harbour porpoise in West Greenland. NAMMCO Document. NAMMCO/SC/20/HP/05. 24pp.

Witting, L. 2015. Meta population modelling of narwhals in East Canada and West Greenland. NAMMCO Document NAMMCO/SC/22/JCNB/SWG/2015-JWG/10. 20pp.

Witting, L. and Heidi-Jørgensen, M.P. 2015a. Population model for West Greenland beluga. NAMMCO Document. NAMMCO/SC/22/JCNB/SWG/2015-JWG/09. 12pp.

Witting, L. and Heidi-Jørgensen, M.P. 2015b. Assessment of East Greenland narwhals. NAMMCO Document NAMMCO/SC/22/JCNB/SWG/2015-JWG/16. 14pp.

Zerbini, A.N., Clapham, P.J. and Wade, P.R. 2010. Assessing plausible rates of population growth in humpback whales from life-history data. *Mar. Biol*. 157: 1,225–36.

Zerbini, A.N., Ward, E.J., Kinas, P.G., Engel, M.H. and Andriolo, A. 2011. A Bayesian assessment of the conservation status of humpback whales (*Megaptera novaenangliae*) in the western South Atlantic Ocean (Breeding Stock A). *J. Cetacean Res. Manage.* (Special Issue 3): 131–44.

Zeh, J.E. and Punt, A.E. 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.

Modelling whale-vessel encounters: the role of speed in mitigating collisions with humpback whales (*Megaptera novaeangliae*)

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ABSTRACT

Increasing whale populations and vessel traffic worldwide has led to an increase in reported whale-vessel collisions. This paper reports on factors that affect the rate of whale-vessel collisions in the four-island region of Maui, Hawai'i. More specifically, it aims at quantifying the probability of a whale-vessel collision with varying vessel speeds using encounter distances as a proxy. A change point model was used to identify a speed threshold of 12.5kts (6.4m/s), which showed a significant change in the relationship between speed and mean sighting distance. A 3.4-fold decrease in close encounters with humpback whales was observed when vessels travelled at speeds of 12.5kts (6.4m/s) or less. Furthermore, results indicate that lone adult whales and calves are the most likely to be involved in a collision. A speed limit of 12.5kts (6.4m/s) is warranted in areas and/or during seasons where a high density of whales occurs. This limit aligns with a reduction in lethal vessel strikes with speed from previous studies which found a significant increase in the likelihood of mortality when vessel speed exceeds 12kts.

KEYWORDS: MODELLING; SHIP STRIKES; HUMPBACK WHALE; PACIFIC OCEAN; SURVEY–VESSEL; CONSERVATION

INTRODUCTION

Vessel collisions with cetacean species are a growing concern worldwide (IWC, 2011; Douglas *et al*., 2008; Laist *et al*., 2001; Van Waerebeek *et al*., 2007). Although a wide range of cetacean species are struck by vessels, collisions are a key mortality factor for larger whale species, including those found on the endangered species list (Laist *et al*., 2001; Redfern *et al*., 2013). Large whales, including humpback whales (*Megaptera novaeangliae*) are more susceptible to collisions in areas where their habitat overlaps with heavy vessel traffic. This risk is increased when whales are resting or moving slowly at the surface (Constantine *et al*., 2015; Laist *et al*., 2001; Vanderlaan and Taggart, 2007).

The increased rate of whale-vessel collisions over the past few decades constitutes an important conservation issue (IWC, 2011; Douglas *et al*., 2008; Laist *et al*., 2001; Silber *et al*., 2010), as they can often be lethal to the animal. Collisions which seriously injure or kill large whales are an important factor threatening the viability of certain populations or sub-populations (Knowlton and Kraus, 2001; Panigada *et al*., 2009).

Increased vessel traffic globally, as well as an increase in size and speed of vessels, has contributed to the rise in whale-vessel collisions (Dolman *et al*., 2009; Jensen and Silber, 2004; Vanderlaan *et al*., 2009). Vessels of all types and sizes are known to be involved in collisions with cetaceans, but larger and faster vessels account for higher instances of lethal collisions (Laist *et al*., 2001; Panigada *et al*., 2006; Silber *et al*., 2010; Vanderlaan and Taggart, 2007). At a speed of 12kts (6.2m/s), 45–60% of collisions between a vessel with mass significantly exceeding that of the whale are lethal; at speeds $\geq$ 19kts (9.8m/s) 100% of collisions are lethal (Vanderlaan and Taggart, 2007).

While various models provide insight into the survivability of vessel strikes among large whales, our understanding of the true frequency of strikes and the factors that lead to them is limited. Published figures for the frequency of vessel strikes are likely to be underestimates, owing to under reporting, whether intentional or unintentional (Van Waerebeek *et al*., 2007; Neilson *et al*., 2012). In addition, population level effects of collision mortality are also not well understood for most whale species (van der Hoop *et al*., 2013).

Hawai'i is an area where humpback whale habitat and high human use overlap. Over 8.1 million people visited Hawai'i in 2014 (DBEDT, 2015), with vessel-based activities being a major source of revenue for the tourism sector (Lammers *et al*., 2013) owing to the thousands of humpback whales that migrate to Hawai'i each winter to breed and calve. More than half, 53.6%, of the North Pacific humpback whale population migrates to Hawai'i each year (Calambokidis *et al*., 2008) with the population growing by 5.5–7.0% annually (Calambokidis and Barlow, 2004; Mobley *et al*., 2001). As humpback whale numbers continue to grow, so too does the concern about potential increases in whale-vessel collisions.

The majority of whale-vessel collisions reported in Hawai'ian waters by NOAA occur between the islands of Maui, Moloka'i, Kaho'olawe, and Lana'i, collectively referred to as the four-island region of Maui (Laist *et al*., 2001; Lammers *et al*., 2013). From 2013 to 2015, 17 vessel collisions were reported to NOAA, of which 82% (n = 14) were recorded in the four-island region of Maui (Ed Lyman, NOAA/HIHWNMS, pers. comm., 2015). The high percentage of whale vessel strikes within the Hawai'ian Islands Humpback Whale National Marine Sanctuary (HIHWNMS) is not surprising, given that the greatest density of humpback whales occurs within this region (Mobley *et al*., 2001); which is in conjunction with over half of the Hawai'ian whalewatching operations (O'Connor *et al*., 2009) and a multitude of other commercial and non-commercial vessels (Appendix Figs 1 and 2).

Increasing reports of whale-vessel collisions in Hawai'i are likely to be caused in part by an increasing number of humpback whales and increased monitoring efforts over the last 20 years (Lammers *et al*., 2013). However, the incidence of reported collisions is increasing more than would be expected for these reasons alone. Other potential factors include an increase in registered vessels between 7.9 and 19.8m, the size class which is responsible for more than two thirds of strikes in Hawai'i (Lammers *et al*., 2013).

Although mostly limited to vessels that have the ability to avoid collisions, to date very few studies have attempted to quantify the risk of collisions by taking into account not only distance to whale (Gende *et al*., 2008) but also vessel speed at the time of initial sighting. A better understanding of specific factors that influence the incidence of collisions, particularly in the seconds prior to contact, is crucial to reduce this threat. This paper looks at data collected from a dedicated research platform that recorded distances to first sightings of humpback whales travelling at different speeds. These data were then used to assess the frequency and proximity of encounters between small vessels (<10m) and humpback whales in relation to vessel speed and to identify a speed guideline for the Hawai'i regions or similar areas. To our knowledge, this is the first systematic study aimed at better understanding how speed influences the encounter distance between humpback whales and small vessels, utilising an *in situ* approach to developing a whale-vessel collision model for management purposes.

METHODS

Study area

The study region covered an area of 798.0km^2 located within the four-island region of Maui, Hawai'i, and was chosen to cover a large section of the HIHWNMS (Fig. 1). The area experiences high levels of vessel traffic during the whalewatching season from December to April each year (DBEDT, 2015).

Data collection

Surveys were conducted from an 8m *Power Cat* research vessel equipped with two 150 horsepower outboard engines. Data were collected using systematic line transect methodologies (Buckland *et al*., 2004) during the winter months from 2013 to 2016. Observations were undertaken by two experienced observers and the boat operator using a continuous scanning methodology by naked-eye or reticle binoculars (Bushnell 7x50), while a fourth person acted as a data recorder. Only whales sighted within 300m or less, forward and abeam of the vessel, were recorded to represent whales at risk of collision. Within this distance, encounters were further classified into surprise encounters (SE) and near misses (NM) defined as sighting within 80–300m and 0–80m respectively, as outlined in Stack *et al*. (2013). In the context of this paper and throughout the remaining text, SE and NM will be collectively referred to as 'encounters' and refers to whales sighted within 0–300m forward and abeam of the

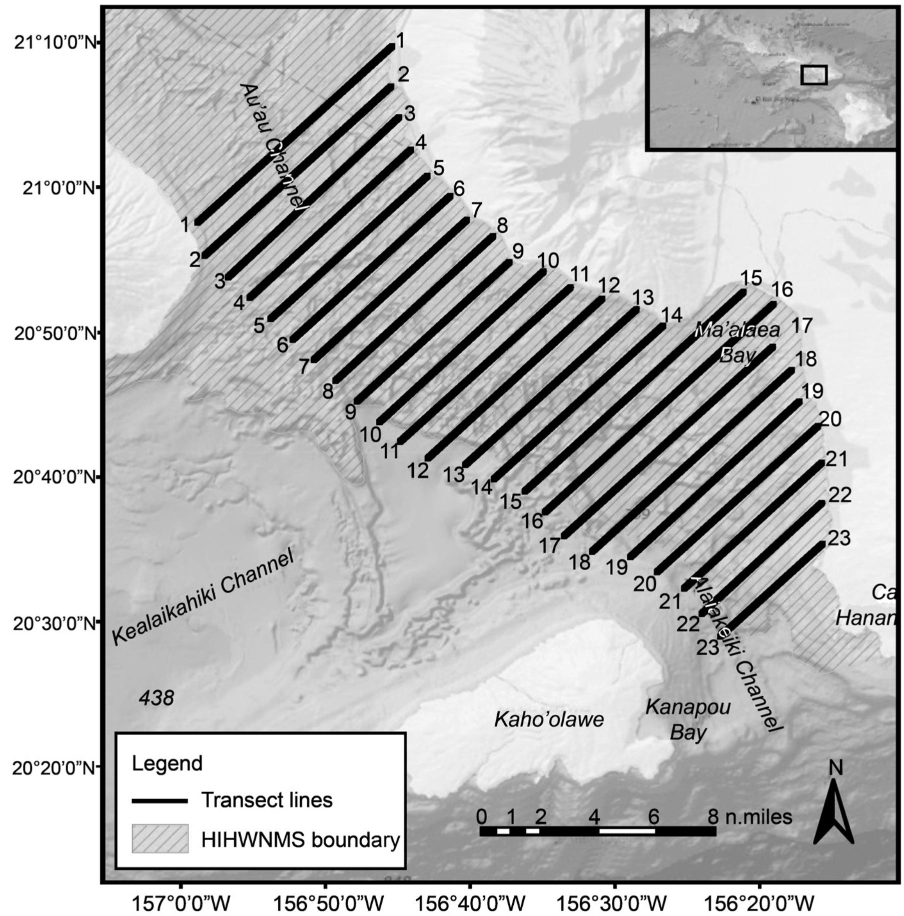

Fig. 1. Transect lines depicting survey area in the four-island region of Maui, Hawai'i, between 2 February 2013 and 31 March 2016 including the Hawai'ian Islands Humpback Whale National Marine Sanctuary (HIHWNMS) boundary.

vessel. The division of encounters into SE and NM allowed for subsequent analysis to determine if specific age classes were more susceptible to NM and/or SE. In addition, the following data were also recorded: time and location (latitude and longitude) of sighting, vessel speed, age-class of whale, number of whales in the pod, angle to pod (measured in magnetic degrees), and direction of travel by the whale. Additional environmental variables including Beaufort Sea state (BSS) as a measure of wind speed and Douglas Sea state (DSS) as a measure of wave height, were recorded at the start of each transect line, and updated as they changed throughout the survey.

To quantify rate encounters with varying vessel speed, a total of seven different speeds were randomly selected for the start of each transect, and speed was increased at 5kt (1.3m/s) increments every 15 minutes until the transect was completed. Depending on the length of the transect line, between two and three speed intervals were completed for each transect. Speeds used were 5.0, 7.5, 10, 12.5, 15, 17.5 and 20.0kts (2.6–10.3m/s) and this range was chosen to best represent the most frequently travelled vessel speeds in the study area.

Analysis

Analyses performed were: (1) assess the composition of SE and NM with varying age class and group composition; (2) change-point modelling to determine a threshold speed at which a change in mean distance at initial sighting of the whale occurred for all encounters; (3) quantification and distribution of encounters above and below identified threshold speed; (4) probabilities of encounters with varying vessel speed.

Change-point modelling

To determine if there was a threshold speed which caused a change in the mean encounter distance a change-point analysis was completed (Gende *et al*., 2011) using the ‘changepoint’ package in R (Killick and Eckley, 2014). Encounter data from 2013–2016 were binned into 2.5 knot speed increments, which were summarised by the mean sighting distance derived from a minimum of 30 observations. Encounter data for each set of changes were then checked for normality and independence to ensure adherence to change-point distribution assumptions. As the goal of the analysis was to identify a speed threshold and assess the frequency of encounters above and below this threshold, the At-Most-One-Change method was considered most appropriate for the change-point model fit with a normal distribution:

$$En_i \sim (\beta_j, \sigma^2)$$

Where En_i are the encounters (i) including a speed (kts) and distance (m) with mean (β_j) and variance (σ^2), and j is the mean distance of sighting above and below the identified change point.

Distribution of encounters above and below the threshold speed

To determine the location and frequency of encounters, all on effort sighting and GPS track data collected from February 2013 to April 2016 were combined. Data were then subdivided into two groups: encounters above and below the threshold speed identified using the change-point model. To determine the density of encounters, the study area was divided into 184 grid cells measuring 1.5x1.5km, each with an area of 2.25km^2. Each grid cell was summarised by the count of encounters occurring in that cell and the total on effort distance travelled in that cell. Density of encounters was calculated by dividing the total number of encounters by the on effort distance per grid cell. Only grid cells that had a total on effort distance of ≥ 5km were included in final density estimates. Maps and grid were created using ArcGIS 10.1 (ESRI, 2011).

Probability of encounters with varying vessel speed and month

A General Linear Model (GLM) with a binomial error distribution and logit link function was used to model the relationship between encounters and vessel speed:

$$P_{SE} = e^{\beta_0 + \beta_{sp}} + \varepsilon$$

where P_{SE} is the probability of encounter, β_0 is the intercept, β_{sp} is the speed ranging from 5.0 to 20.0kts (2.6 to 10.3 m/s), and ε is the binomial error.

To account for the variation in number of humpback whales from December to April resulting from a progressive influx in numbers leading to peak season (Baker and Herman, 1981), analysis was divided into five months to represent the primary mating/birthing season in Hawai’i waters: December, January, February, March and April.

Model fit

All computations were completed using the ‘stats’ package in R (Wood, 2011). Final model selection was based on minimizing the AIC values (Akaike, 1973). To ensure proper model fit and adherence to assumptions, model residuals were graphed and visually checked for violations.

RESULTS

Survey effort

Between 2 February 2013 and 31 March 2016, 143 survey days allowed for sampling of 608 transect lines in the four-island region of Maui. Each transect line was surveyed a minimum of 23 and maximum of 29 times throughout the study period. This corresponded to a total of 4,477.6 nautical miles (n.mi) on effort and 5,009.4 n.mi off effort survey distances.

Composition of SE and NM

A total of 529 SE and 25 NM were recorded during the study period. Calves were present in 23.1% (n = 122) of SE and 48.0% (n = 12) of NM. Of all SE and NM involving calves, 54.5% (n = 73) were mother-calf pairs, 26.1% (n = 35) were mother-calf-escort pods, and 19.4% (n = 26) were lone calves (i.e. mother did not surface). Lone adults accounted for 48.3% (n = 255) of SE and 32.0% (n = 8) of NM, while pods consisting of ≥ 2 adults, accounted for 22.3% (n = 118) of SE and 44.0% (n = 11) of NM.

Change-point modelling

The change point model identified a change in the relationship between speed and mean sighting distance at 12.5kts (6.4m/s) (Fig. 2). The mean sighting distance before and after the change point was 211.2m and 189.4m,

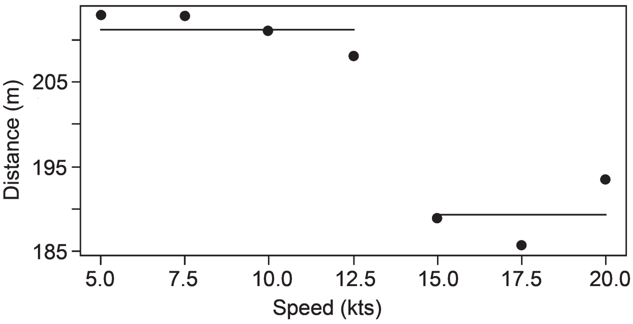

Fig. 2. Mean sighting distance of humpback whales with increasing speed (points) and the identified change point (solid line) recorded within the four-island region of Maui, Hawai'i between 2 February 2013 and 31 March 2016.

respectively. In the field, encounters were reduced 3.4 fold when the vessel travelled at speeds of 12.5kts (6.4m/s) or less. As such, encounters occurred for every 37.0 on effort nautical miles when travelling 12.5kts or less and every 10.9 on effort nautical miles when travelling faster than 12.5kts.

Distribution of encounters above and below the threshold speed

There was no clear trend in distribution of encounters when travelling at speeds below 12.5kts (6.4m/s) (Fig. 3). However, when travelling at speeds greater than 12.5kts (6.4m/s), a higher frequency of encounters was observed in the Au'Au Channel, which is covered by transect lines 1–9.

Probability of encounters with varying vessel speed by month

A significant positive relationship between speed and probability of encounter was identified (p = value: < 0.001, Res.df = 798). When data were further divided by month, three months were found to significantly vary from intercept only models showing a postive relationship between encounters and speed: December (p-value: 0.03, Res.df = 76), February (p-value: 0.006, Res.df = 213), and March (p-value: 0.003, Res.df = 275) (Fig. 4).

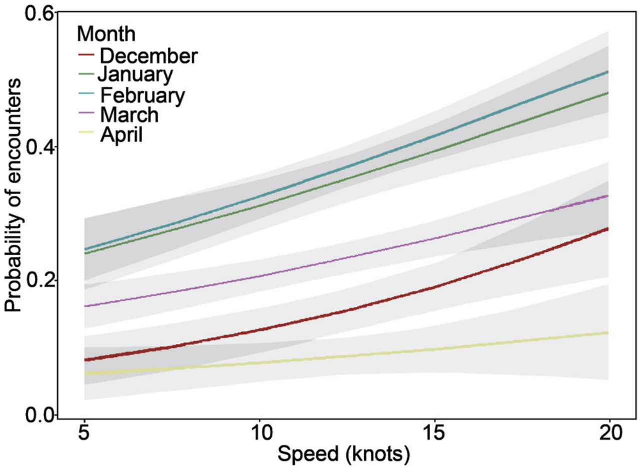

Fig. 4. Probabilities of encounters with humpback whales at varying vessel speeds, where lines represent monthly predictions based on binomial regression and the shaded area represents the 95% confidence interval.

DISCUSSION

Whale-vessel collisions are a matter of concern globally. To date, very few studies have attempted to quantify the risk of a whale being struck by a vessel by taking into account the frequency of close encounters at varying vessel speeds (Richardson *et al.*, 2011). Previous studies have assessed the risk of whale-vessel collisions by establishing co-occurrence of whales within major shipping routes (Redfern *et al.*, 2013). The implications of speed on mortality rate (Vanderlaan *et al.*, 2009) and encounter distance (Gende *et al.*, 2011) has also been investigated. This study aimed at assessing the rate of close encounters (<300m) with humpback whales at varying vessel speeds.

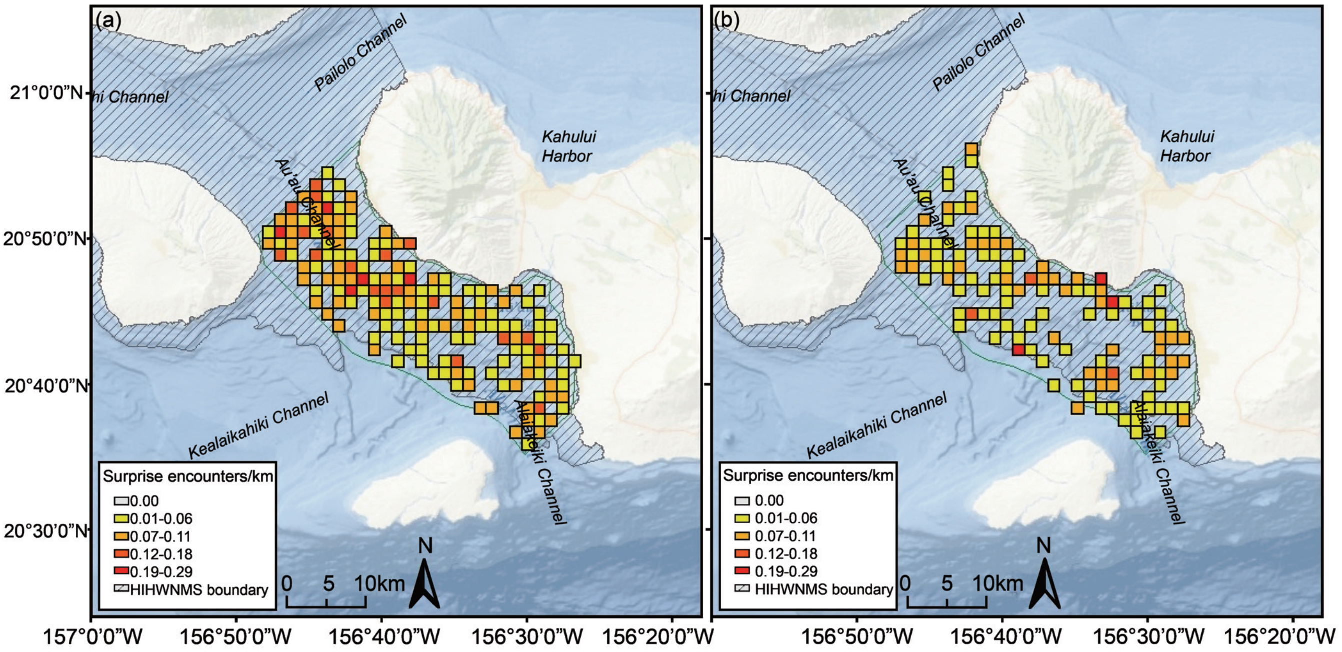

Fig. 3. Encounters per km travelled at speeds (A) above and (B) below the identified 12.5kts (6.4m/s) threshold within the four-island region of Maui, Hawai'i between 2 February 2013 and 31 March 2016.

Change-point modelling

Despite the relatively small change in mean sighting distance identified using the change point model, the speed threshold of 12.5kts (6.4m/s) showed a significant decrease in the frequency of encounters when traveling below this threshold. The small change in mean sighting distance is likely a result of analysing only whales that were sighted within 300m of the vessel. The speed threshold of 12.5kts (6.4m/s) is similar to results presented in Gende *et al*. (2011), which identified a threshold speed of 11.8kts (6.1m/s), despite utilising large cruise ships and including encounter distances up to 1000m. These results suggest that speeds in excess of ~12kts (6.2m/s), regardless of vessel size, will significantly increase the likelihood of whale-vessel collisions.

Distribution of encounters above and below the threshold speed

A reduction in speed may be favorable for preventing whale-vessel collisions over other options, such as reduced or closed traffic areas, as we observed a threefold reduction in encounters when vessel speeds were reduced to 12.5kts (6.4m/s) or less, and noted no clear trends in distribution of encounters for the four-island region. Furthermore, the implementation of a speed limit is much easier and is more likely to become adopted rather than trying to minimise traffic within an area.

Probability of encounters with varying vessel speed by month

The contrast in the monthly rate of encounters suggests that the risk of a whale-vessel collision varies with month and whale abundance. During February, the peak humpback whale season in Hawai'i, the probability of encounter increases from ~35% to 50% when vessel speed is increased from below 12.5kts (6.4m/s) to above. Similarly, a probability analysis modelling the lethality of vessel strikes with speed found a significant increase in the likelihood of lethality when vessel speed exceeds 12kts (6.2m/s) (Vanderlaan and Taggart, 2007). As such, vessel speed restrictions are being used as mitigation measures in various locations (e.g. USA: Gulf of Maine and Glacier Bay, Alaska; New Zealand: Hauraki Gulf, Auckland) to reduce the occurrence and/or severity of whale-vessel collisions with large whale species (Constantine *et al*., 2015; Gende *et al*., 2011; Vanderlaan *et al*., 2009).

Combining information on the rate of near collisions with the severity (Vanderlaan *et al*., 2009) of whale vessel collisions based on differing vessel speeds provides insight into the efficacy of speed restrictions as a management tool. Reduced speed will not only allow whales more time to manoeuvre, but also increases reaction time for a vessel to stop or change course if they are able (Stack *et al*., 2013). Consequently, this could reduce the incidence of collisions. The average speed of whale-vessel collisions reported from 1979–2011 in Maui was 14.7kts (7.6m/s) and, of these collisions, 52.9% were at speeds ≥ 15kts (7.7m/s) (Lammers *et al*., 2013). Current results suggest implementation of a speed guideline in the four-island region of Maui would be most effective during peak whale season (February–March).

The defining of SE and NM at distances of 300m and 80m respectively (Stack *et al*., 2013) differs from the term near miss defined in IWC (2011) as 100m. The IWC-ACCOBAMS workshop on ship strikes noted that there could be many interpretations of a near miss and a clear definition is required (IWC, 2011). The terms as outlined in this study were designed to quantify the risk of vessel strikes by using close encounters (<300m) as proxies for whale-vessel collisions. Results from this study relating speed to probability of encounters, in conjunction with other studies relating speeds to encounter distance and lethality (Gende *et al*., 2011; Vanderlaan and Taggart, 2007), all point to similar speed thresholds of 11–13kts (5.7–6.7m/s).

Age-class and susceptibility to whale-vessel collisions

SE occurred across all age-classes. However, lone adults were more likely to be involved in a SE than other compositions recorded. This differs from other findings which show a significantly greater proportion of calves and sub-adults involved in SE than the general population (e.g. Richardson *et al*., 2011). The number of lone adult SE increased from 2014 to 2015, suggesting that there are yearly variations in the population, as shown by Tonachella *et al*. (2012). If some years are peak years for calving, there will be more young whales present and therefore an increased susceptibility of that age class to a collision. If, however, there are lulls in the calving rate, the opposite will be true and more SE with adult whales would be expected.

The age-class composition of NM revealed that 48.0% of all NM involved a calf, and yet calves comprise only 7.0–9.0% of the Hawai'ian population of humpback whales (Mobley *et al*., 2001). This supports earlier research findings indicating that calves and juveniles are highly vulnerable to vessel strikes (Laist *et al*., 2001; Lammers *et al*., 2013). This is likely due to a combination of calf related traits such as: more time spent at the surface to breathe than adults, surfacing often without the mother if the pod is stationary, being less visible than adults, and being relatively naive to interactions with vessels (Laist *et al*., 2001; Lammers *et al*., 2013). In Hawai'ian waters, 63.5% of the 52 collisions with humpback whales between 1975–2011, in which age-class was specified, involved either a calf or juvenile (Lammers *et al*., 2013).

Recommendations

Although data were collected within the four-island region, results from previous literature (Constantine *et al*., 2015; Currie *et al*., 2014; Guzman *et al*., 2013; Laist *et al*., 2014; Lammers *et al*., 2013; Richardson *et al*., 2011; Stack *et al*., 2013; van der Hoop *et al*., 2014; Vanderlaan and Taggart, 2007) suggest implementation of a 12–13kts (6.2–6.7m/s) speed limit is warranted in areas and/or in seasons with high densities of humpback whales. Furthermore, speed restrictions have been proven a successful mitigation measure (Gende *et al*., 2011; Vanderlaan *et al.,* 2009). Instances of whale-vessel collisions still occur at speeds below this threshold (Laist *et al.,* 2001; Vanderlaan and Taggart, 2007) and adoption of programs such as the 'Be Whale Aware' by Pacific Whale Foundation (PWF, 2015) and 'Ocean Etiquette' by NOAA (NOAA, 2015b) should continue to be implemented to help further mitigate whale-vessel collisions. As both whale and human populations increase, with a concurrent increase in anthropogenic activities in the marine environment, more scientific research leading to sound management strategies will ensure that both humans and animals can safely co-exist.

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REFERENCES

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. pp.267–81. *In*: B.N. Petrov and F. Csáki (eds.) Proceedings of the 2nd International Symposium on Information Theory, Tsahkadsor, Armenia, USSR, 2–8 September 1971, Budapest: Akadémiai Kiadó.

Baker, C.S. and Herman, L.M. 1981. Migration and local movement of humpback whales (*Megaptera novaeangliae*) through Hawaiian waters. *Can. J. Zool.* 59(3): 460–9.

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. 434pp.

Calambokidis, J., Falcone, E.A., Quinn, T.J., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Mattila, D., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urbán, J.R., Weller, D., Witteveen, B.H., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggings, J., Maloney, N., Barlow, J. and Wade, P.R. 2008. SPLASH: Structure of populations, levels of abundance and status of humpback whales in the North Pacific. Report submitted by Cascadia Research Collective to USDOC, Seattle, WA, USA. Contract AB133F-03-RP-0078 (unpublished). [Available from the author – JC].

Calambokidis, J. and Barlow, J. 2004. Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. *Mar. Mamm. Sci.* 20(1):63–85.

Constantine, R., Johnson, M., Riekkola, L., Jervis, S., Kozmian-Ledward, L., Dennis, T., Torres, L.G. and Aguilar de Soto, N. 2015. Mitigation of vessel-strike mortality of endangered Bryde's whales in the Hauraki Gulf, New Zealand. *Biol. Conserv.* 186:149–57.

Currie, J.J., Stack, S.H., Davidson, E., Kaufman, G.D., Martinez, E. 2014. Results from two years of line transect surveys utilizing surprise encounters and near-misses as proxies of vessels collisions with humpback whales (*Megaptera novaeangliae*) in the four-island region of Maui, Hawai'i, USA. Paper SC/65b/HIM01 presented to the IWC Scientific Committee, 12–24 May 2014, Bled, Slovenia (unpublished). 21pp. [Available from the Office of this Journal].

Department of Business, Economic Development and Tourism (DBEDT). 2015. Research Economics and Analysis. Accessed May 2015. [Available at: *http://hawaii.gov/dbedt/info/economic/databook/*].

Dolman, S.J., Weir, C.R. and Jasny, M. 2009. Comparative review of marine mammal guidance implemented during naval exercises. *Mar. Poll. Bull.* 58:465–77.

Douglas, A.B., Calambokidis, J., Raverty, S., Jeffries, S.J., Lambourn, D.M. and Norman, S.A. 2008. Incidence of ship strikes of large whales in Washington State. *J. Mar. Biol. Ass. U.K.* 88(06): 1,121–32.

ESRI. 2011. ArcGIS Desktop: Release 10.: Environmental Systems Research Institute, Redlands, CA. [Available from: *https://www.esri.com*]

Gende, S.M., Hendrix, A.N., Harris, K.R., Eichenlaub, B., Nielson, J. and Pyare S. 2011. A Bayesian approach for understanding the role of ship speed in whale-ship encounters. *Ecol. Appl.* 21:2,232–40.

Guzman, H.M., Gomez, C.G., Guevara, C.A. and Kleivane, L. 2013. Potential vessel collisions with southern hemisphere humpback whales wintering off Pacific Panama. *Mar. Mamm. Sci.* 29(4):629–42. [Available at: *http://bit.ly/2lTfaec*].

International Whaling Commission. 2011. Report of the Joint IWC-ACCOBAMS Workshop on Reducing Risk of Collisions between Vessels and Cetaceans, 21–24 September 2010, Beaulieu-Sur-Mer, France. Paper IWC/63/CC8 presented to the IWC Conservation Committee, July 2011, Jersey, Channel Islands, UK. 41pp. [Paper available from the Office of this Journal]

Jensen, A.S. and Silber, G.K. 2004. Large whale ship strike database. US Department of Commerce, National Oceanic and Atmospheric Administration (NOAA) Technical Memorandum NMFS-OPR-25. 37pp. [Available from: *http//www.nmfs.noaa.gov*].

Killick, R. and Eckley, I.A. 2014. changepoint: An R Package for Changepoint Analysis. *J. Stat. Softw.* 58(3):1–19.

Knowlton, A.R. and Kraus, S.D. 2001. Mortality and serious injury of northern right whales (*Eubalaena glacialis*) in the western North Atlantic Ocean. *J. Cetacean Res. Manage.* 2:193–208.

Laist, D.W., Knowlton, A.R., Mead, J.G., Collet, A.S. and Podesta, M. 2001. Collisions between ships and whales. *Mar. Mamm. Sci.* 17(1):35–75.

Laist, D.W., Knowlton, A.R. and Pendelton, D. 2014. Effectiveness of mandatory vessel speed limits for protecting North Atlantic right whales. *Endanger. Species Res.* 23:133–147.

Lammers, M.O., Pack, A.A., Lyman, E.G. and Espiritu, L. 2013. Trends in collisions between vessels and North Pacific humpback whales (*Megaptera novaeangliae*) in Hawaiian waters (1975–2011). *J. Cetacean Res. Manage.* 13(1):73–80.

Mobley, J.M., Spitz, S., Grotefendt, R., Forestell, P., Frankel, A. and Bauer, G. 2001. Abundance of humpback whales in Hawaiian waters: Results of 1993–2000 aerial surveys. Report to the Hawaiian Islands Humpback Whale National Marine Sanctuary. 9pp.

Neilson, J.L., Gabriele, C.M., Jensen, A.S., Jackson, K. and Straley, J.M. 2012. Summary of reported whale-vessel collisions in Alaskan waters. *J. Mar. Biol.* 2012:1–18.

NOAA. 2015. Ocean Etiquette. [Available at: *http://oceanservice.noaa.gov/facts/ocean-etiquette.html* Accessed on 15 April 2015.]

O'Connor, S., Campbell, R., Cortez, H. and Knowles, T. 2009. Whale Watching Worldwide: tourism numbers, expenditures and expanding economic benefits. Special report from the International Fund for Animal Welfare. Yarmouth, International Fund for Animal Welfare, Yarmouth, MA, USA.

Pacific Whale Foundation. Be Whale Aware. Accessed on 15 October 2015. 295pp. [Available at: *https://www.pacificwhale.org/be-whale-aware*, accessed 15 October 2015]

Panigada, S., Pesante, G., Zanardelli, M., Capoulade, F., Gannier, A. and Weinrich, M.T. 2006. Mediterranean fin whales at risk from fatal ship strikes. *Mar. Poll. Bull.* 52(10): 1,287–98.

Panigada, S., Leaper, R. and Arcerdillo, A. 2009. Ship strikes in the Mediterranean Sea: Assessment and identification of mitigation measures. Paper SC/61/BC2 presented to the IWC Scientific Committee, 22–25 June 2009, Madeira, Portugal (unpublished). 5pp. [Available from the Office of this Journal].

Redfern, J.V., McKenna, M.F., Moore, T.J., Calambokidis, J., Deangelis, M.L., Becker, E. A., Barlow, J., Forney, K.A., Fiedler, P.C. and Chivers, S.J. 2013. Assessing the risk of ships striking large whales in marine spatial planning. *Conserv. Biol.* 27(2):292–302.

Richardson, D.T., Silva, I.F., Macie, A., Rankin, R.W., Maldini, D. and Kaufman, G.D. 2011. Whale surprise encounters and near misses: proxies of vessel strikes in Maui County waters. Document SC/63/BC2 presented to the IWC Scientific Committee, Tromso, Norway (unpublished). 19pp. [Available from the Office of this Journal]

Silber, G.K., Slutsky, J. and Bettridge, S. 2010. Hydrodynamics of a ship/whale collision. *J. Exp. Mar. Biol. Ecol.* 391:10–19.

Smultea, M.A. 1994. Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. *Can. J. Zool.* 72(5):805–11.

Stack, S.H., Currie, J.J., Davidson, E.H., Frey, D., Maldini, D., Martinez, E. and Kaufman, G.D. 2013. Preliminary results from line transect surveys utilizing surprise encounters and near-misses as proxies of vessels collisions with humpback whales (*Megaptera novaeangliae*) in Maui County waters, Hawaii, USA. Paper SC/65a/WW04 presented to the IWC Scientific Committee, 3–15 June 2013, Jeju, Korea (unpublished). 20pp. [Available from the Office of this Journal]

Tonachella, N., Nastasi, A., Kaufman, G., Maldini, D. and Rankin, R. W. 2012. Predicting trends in humpback whale (*Megaptera novaeangliae*) abundance using citizen science. *Pac. Conserv. Biol.* 18(4):297–309.

Van der Hoop, J.M., Moore, M.J. and Barco, S.G., Colde, T.V.N., Daoust, P-Y., Henry, A., McAlpine, D.F., McLellan, W.A., Winner, T. and Solow, A.R. 2013. Assessment of management to mitigate anthropogenic effects on large whales. *Conserv. Biol.* 27:121–133.

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. *Latin Am. J. Aquat. Mamm.* 6:43–69.

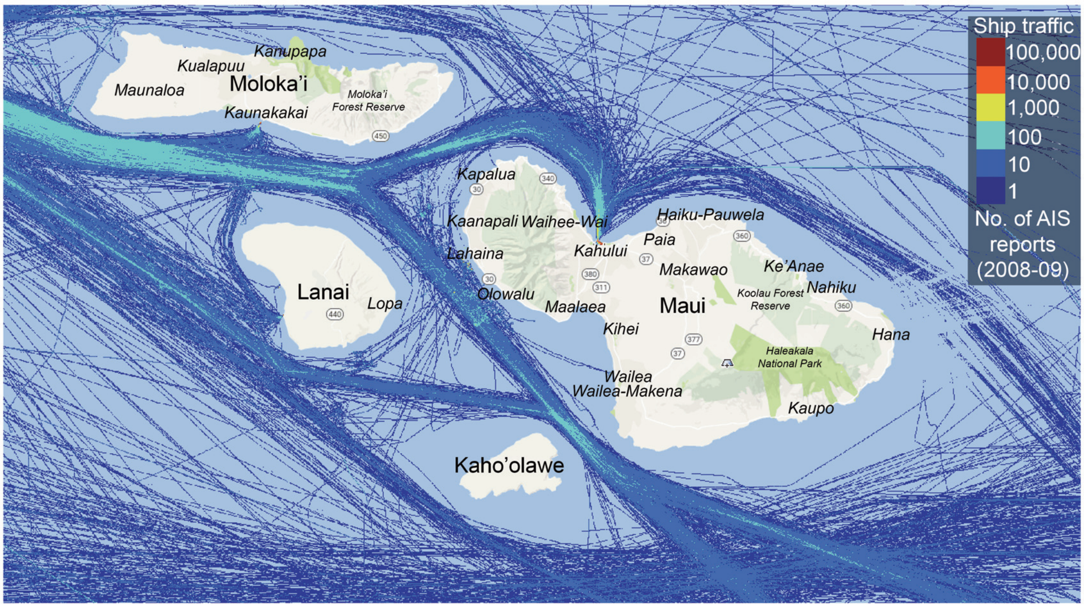
Vanderlaan, A.S.M., and Taggart, C.T. 2007. Vessel collisions with whales: the probability of lethal injury based on vessel speed. *Mar. Mamm. Sci.* 23(1):144–156.

Vanderlaan, A.S., Corbett, J.J., Green, S.L., Callahan, J.A., Wang, C., Kenney, R.D., Taggart, C.T. and Firestone, J. 2009. Probability and mitigation of vessel encounters with North Atlantic right whales. *Endanger. Species Res.* 6(3):273–285.

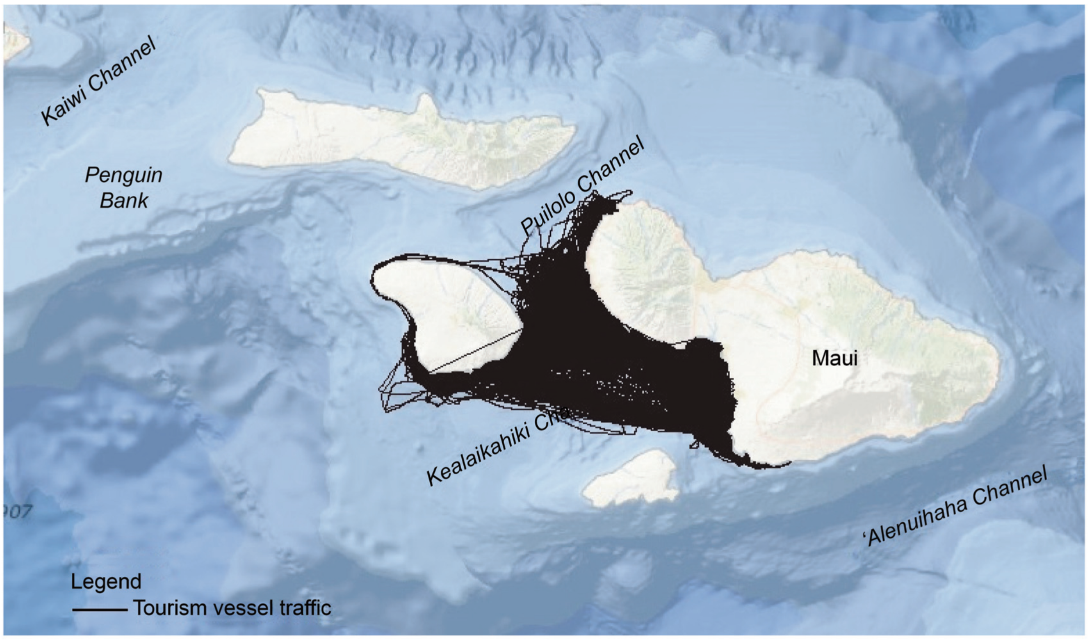
Weinrich, M., Pekarcik, C. and Tackaberry, J. 2010. The effectiveness of dedicated observers in reducing risks of marine mammal collisions with ferries: A test of the technique. *Mar. Mamm. Sci.* 26(2):460–70.

Wood, S.N. 2006. *Generalized Additive Models: An Introduction with R.* Taylor and Francis, UK. 384pp.

APPENDIX 1



Appendix Fig. 1. Map depicting ship traffic densities of vessels equipped with AIS transceivers in the four-island region of Maui, Hawai'i over a one year period. Source: Data for map provided by PacIOOS (*http://www.pacioos.org*), which is a part of the US Integrated Ocean Observing System (IOOS), funded in part by National Oceanic and Atmospheric Administration (NOAA) Awards, NA11NOS0120039 and NA16NOS0120024.



Appendix Fig. 2. Map depicting tourism vessel traffic densities of eight vessels in the four-island region of Maui, Hawai'i over a one year period.

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