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Article *in* Mammal Review · August 2019

DOI: 10.1111/mam.12168

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Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

North Atlantic killer whale *Orcinus orca* populations: a review of current knowledge and threats to conservation

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Keywords
connectivity, distribution, ecological structuring, harvest, killer whale *Orcinus orca*, movement, North Atlantic Ocean

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Submitted: 6 March 2019
Returned for revision: 10 April 2019
Revision accepted: 15 July 2019
Editor: DR

doi: 10.1111/mam.12168

ABSTRACT

1. The first comprehensive review on North Atlantic killer whales *Orcinus orca* was published in 1988. Since then, a significant increase in published studies has substantially improved our understanding of occurrence patterns, major food sources, abundance and population structuring in the North-east Atlantic. Dedicated studies on killer whales in the Mid- and West Atlantic were undertaken beginning in 2006, mainly following an increase in their presence due to rapidly changing environmental conditions in the Arctic regions of Canada and Greenland.
2. Compiling 111 scientific articles and reports published from 1957 to date, this review assesses the current state of knowledge of North Atlantic killer whale populations. We reviewed distribution, abundance, movements, genetic structure, acoustics, population parameters, and threats, whilst highlighting the connection among regions from east to west.
3. Our results indicated that, while North Atlantic killer whales should be recovering following the end of the harvest, culling and live captures in the 1980s, new emerging threats including chemical pollution, anthropogenic noise and increasing unregulated subsistence harvest in Greenland could be hampering this rebound.
4. There is an urgent need to collect data on the abundance and population structure of killer whales in Greenland and Eastern Canada. A lack of information across most regions of the North Atlantic Ocean has prevented regional status assessments from being conducted. Ongoing and future studies should be aimed at collecting relevant data to undertake these assessments, particularly genetic samples and photo-identification.

INTRODUCTION

The killer whale *Orcinus orca* is the largest delphinid and an apex predator widely distributed in the world's oceans (Forney & Wade 2006). Based on abundance estimates from multiple regions, a worldwide minimum abundance of 50000 killer whales has been suggested, though this is likely to be an underestimate (Reeves et al. 2017). Although currently considered to be a single species, the morphological, behavioural, dietary, and genetic diversity among different groups or populations of killer whales suggests that separate (sub-) species may exist (Pitman & Ensor 2003, Leduc et al. 2008, Morin et al. 2010). Due to taxonomic uncertainty (Reeves et al. 2004) and a lack of baseline data on the populations, the conservation status of the killer whale in the *IUCN Red List of Endangered Species* has remained Data Deficient (Reeves et al. 2017). The main threats to wild populations include past harvest, live-captures, lethal interactions with fisheries, marine chemical pollution and subsequent toxic effects, and prey depletion (Reeves et al. 2017).

In the North Atlantic Ocean, the status of the killer whale was first reviewed in 1993 by the North Atlantic Marine Mammal Commission (NAMMCO). A substantial data deficiency on stock identity and abundance was highlighted, especially for Western Greenland (NAMMCO 1993). In the meantime, global warming became increasingly recognised as a force altering marine ecosystems and leading to significant changes in available habitats and prey resources utilised by killer whales (Higdon & Ferguson 2009, Ferguson et al. 2010). Such changes, more pronounced in rapidly changing Arctic ecosystems, further resulted in changes in killer whale occurrence patterns and eventually promoted co-occurrence and conflicts with humans (Westdal et al. 2013), as well as increased (unregulated) harvest in Greenland (Ugarte et al. 2013). These emerging threats largely underline the importance of acquiring baseline information for the development of mitigation solutions. Despite a significant increase in killer whale studies during the decades since 1993 (Foote et al. 2014), NAMMCO once again called attention to the persisting lack of information about the killer whale population (or populations) harvested off Western Greenland, and found off Eastern Canada in 2004 (NAMMCO 2005). While reviewing the status of the species worldwide, the International Whaling Commission expressed similar concerns in 2007 (IWC 2007).

After a new decade of scientific findings, NAMMCO requested an updated review to inform a full assessment of North Atlantic killer whales (NAMMCO 2017). By compiling information relating to distribution, movements, population structure, acoustics, abundance, population parameters and threats, this review assesses the current state of knowledge of North Atlantic killer whale populations. Current conservation status is discussed, remaining knowledge gaps are identified, and priorities for future research are outlined.

METHODS

We searched for publications relating to killer whales in the North Atlantic Ocean. The North Atlantic is defined as the geographic area that stretches from the East to the West Atlantic, bounded to the south by the Strait of Gibraltar in the east and the Caribbean in the west, and to the north by the continuous sea-ice extent from Svalbard in the east and by the Eastern Canadian Arctic (ECA) in the west. References focusing on distribution, movement, and association with prey resources, population structure, acoustics, abundance, population parameters, and threats were compiled.

In order to assess the distribution of effort among research topics and regions, publications were first categorised by topic as follows: 1) distribution (investigations of occurrence and distribution patterns); 2) abundance (estimates or patterns of abundance); 3) movements (investigations of movement patterns and association with prey resources); 4) genetic structure (studies on populations structure); 5) acoustics (investigations of acoustic behaviours); 6) population parameters (photo-identification, survival, and calving rates); and 7) threats (reports on impacts from human activities, climate change, chemical pollution, and other threats). The origin or origins of samples that had been collected and/or of observations was used to assign the investigations described in each publication to one or multiple study regions.

Each publication was assigned to as many topics and/or regions as relevant: more than one, if the investigations (resulting in observations, samples, records, etc.) pertained to multiple topics or were conducted in multiple regions. Publication content was summarised for each topic in order to assess and discuss the current status of knowledge of North Atlantic killer whale populations.

RESULTS AND DISCUSSION

A total of 111 scientific publications, published from 1957 to early 2019, were used in this review. Of these 111 publications, 61% dealt with the research topic 'distribution', 15% with 'abundance', 46% with 'movements', 5% with 'genetic structure', 12% with 'acoustics', 25% with 'population parameters', and 33% with 'threats' (Fig. 1). Most studies (72%) were published since 2005 (Fig. 2). Studies were largely focused on the North-east Atlantic

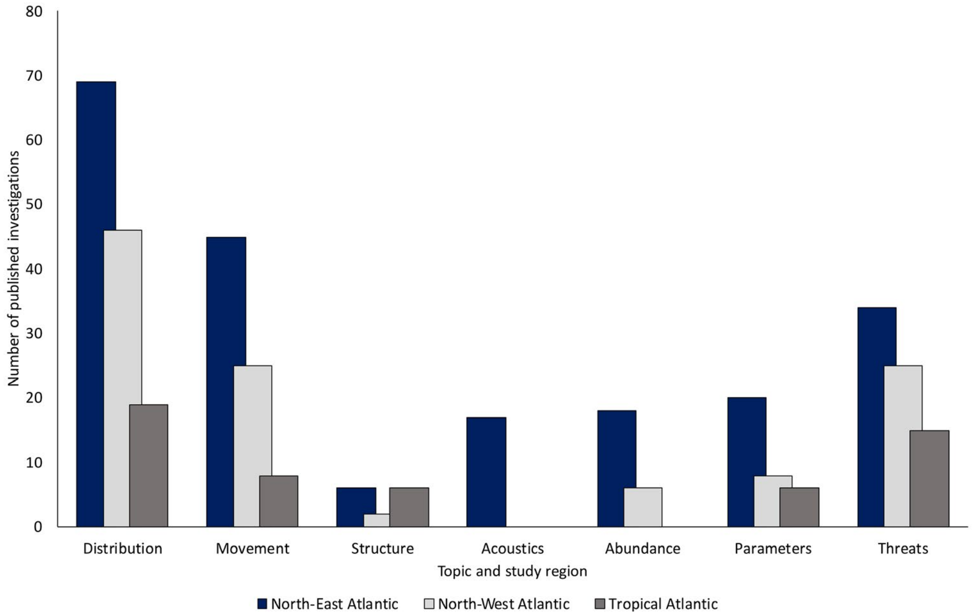

Fig. 1. Distribution and number of published investigations of killer whales *Orcinus orca* (see Methods), as cited in the present review, per topic and per study region across the North Atlantic. In total, 111 publications were included, but many pertained to more than one topic or region. The North-east Atlantic includes Norway, Iceland, Faroe Islands, Denmark, British Isles; the North-west Atlantic includes Greenland, Eastern Canadian Arctic, and Newfoundland-Labrador; the Tropical Atlantic refers to waters south of 35°N, which includes Western and Eastern Tropical regions of the North Atlantic.

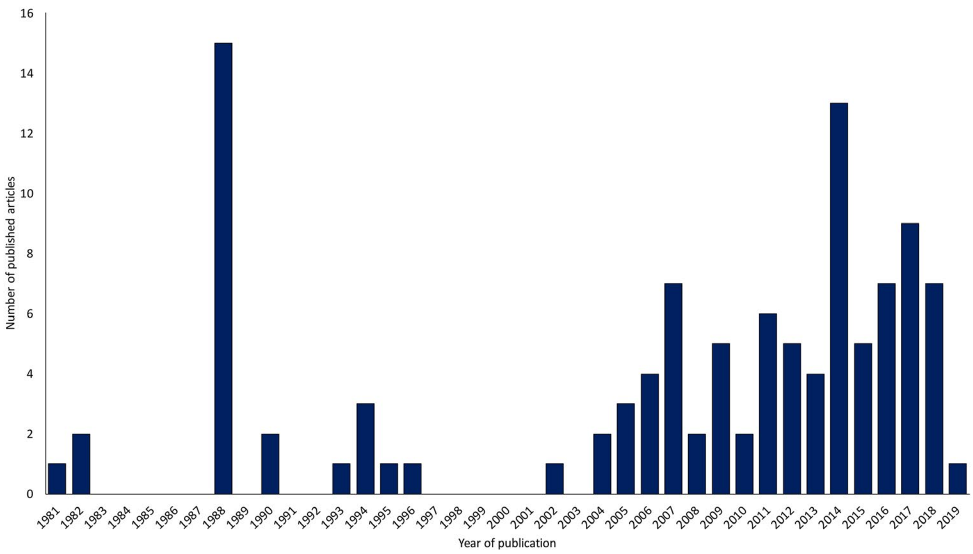

Fig. 2. Number of articles on killer whales *Orcinus orca* cited in the present review and published in each year.

(Norway, Iceland, Faroe Islands, Denmark, British Isles, and North Sea), accounting for 59% of the investigations, while 27% were focused on the North-west Atlantic (ECA, Labrador, Newfoundland, Nova Scotia) and Greenland, and 14% on tropical regions south of 35°N (Gulf of Mexico/Caribbean, Azores, Canary Islands, Madeira and Gibraltar; Fig. 1).

Distribution

Occurrence records from the literature spanned the entire North Atlantic Ocean (Hammond & Lockyer 1988, Øien 1988, Reeves & Mitchell 1988a), though records are likely to be biased towards coastlines and seasons with the greatest sighting effort. Killer whale occurrence was documented along the entire Norwegian coast, throughout the year, in nearshore and offshore areas (Christensen 1982, 1988, Øien 1988, 1990). Killer whales are known to be infrequent seasonal visitors around Svalbard, where they swim right up to the ice edge and into fjords (e.g. Kovacs & Lydersen 2008, Storrie et al. 2018); they also occur throughout the Barents Sea (Kovacs et al. 2009). Killer whales are also found all around Iceland and in deep waters of the central North Atlantic (e.g. Øien 1988, Sigurjónsson et al. 1988, Gunnlaugsson & Sigurjónsson 1990, Vikingsson 2004, Pike et al. 2009).

Around the Faroe Islands, coastal sightings were recorded in spring and summer (Bloch & Lockyer 1988). Killer whales also occur offshore, possibly in large aggregations interacting with both summer herring *Clupea harengus* and winter mackerel *Scomber scombrus* fisheries, north and south-west of the Faroes, respectively (Bloch & Lockyer 1988). A continuous distribution from the north of Scotland and Shetland throughout the Faroes is likely, as supported by individual killer whales photographed multiple times around Caithness, Orkney, and Shetland and inshore of the Faroes (Foote et al. 2010, Foote unpublished data).

Killer whales occur throughout the year around the British Isles, but sightings peak in north-western parts of the North Sea and in the summer around the Western, Shetland, and Orkney Isles (Evans 1988, Weir 2002, Bolt et al. 2009, Foote et al. 2010, Deecke et al. 2011, Robinson et al. 2017). In contrast, sightings have been rare in the English Channel (Weir 2002). A small assemblage of killer whales preferentially ranges west of Scotland, Ireland, and Wales (Foote et al. 2010, Beck et al. 2014). Large aggregations of killer whales were also reported offshore, north of Shetland and around Ireland in the winter, when they are foraging around the mackerel trawl-fishing fleet (Couperus 1994, Luque et al. 2006, Foote et al. 2010, Pinfield et al. 2012).

In Greenland, killer whales have been sighted near all inhabited locations (Heide-Jørgensen 1988, APNN unpublished data). Since 2009, killer whales have been increasingly seen and are hunted every summer off Tasiilaq, southeast Greenland (Foote et al. 2013, Ugarte et al. 2013, Lennert & Richard 2017).

Killer whales in Labrador, Newfoundland, and Nova Scotia, hereafter referred to as North-west Atlantic (NWA) killer whales, were mainly sighted during June-September, with sightings likely limited by winter-forming sea ice (Lien et al. 1988, Lawson et al. 2007). Yet, cases of ice entrapments suggest year-round killer whale presence (Lien et al. 1988, Mitchell & Reeves 1988, Lawson et al. 2007, see Westdal et al. 2017 for a review of recorded cases). Killer whale sightings seem to have increased over recent decades, possibly reflecting changes in killer whale abundance and distribution, and/or increased awareness of the species (Lawson et al. 2007, Lawson & Stevens 2014).

Killer whales occurring as far north as the Baffin Bay and Lancaster Sound regions (Reeves & Mitchell 1988b) are hereafter referred to as ECA killer whales, although the possibility of shared population(s) between NWA, ECA, and West Greenland cannot be excluded. Based on Inuit ecological knowledge (Ferguson et al. 2012a, Westdal et al. 2013, Higdon et al. 2014), sightings started and then increased in the western part of Hudson Bay after the 1950s (Higdon & Ferguson 2009). Declining sea ice and the resulting increase in open habitat, as generated by warming oceans, correlated with increasingly frequent and longer killer whale visits (Higdon & Ferguson 2009, Higdon et al. 2014, Matthews et al. 2019).

The scarcity of published studies for regions south of latitude 35°N suggests low killer whale densities compared to the northern regions. A small assemblage of killer whales occurs in the Strait of Gibraltar and adjacent waters throughout the year. Sightings peak between April and September and coincide with the migration of the Atlantic bluefin tuna *Thunnus thynnus* (Esteban et al. 2014). In the Canary Islands, killer whales are only rarely sighted (Foote et al. 2011). Whaling logbooks (Clarke 1981) document killer whale occurrence from the 1950s to the 1970s around the islands of Azores and Madeira (Hammond & Lockyer 1988). Infrequent sightings and strandings in 1990–2010 also support killer whale presence in the Mid-Atlantic (Silva et al. 2014) and in the tropical NWA (Katona et al. 1988, Reeves & Mitchell 1988b). Anecdotal killer whale sightings and strandings were recorded in the Caribbean, including around Florida, the Bahamas, the Dominican Republic, Puerto Rico, the Virgin Islands, St. Vincent and the Grenadines, and Dominica (Bolanos-Jimenez et al. 2014, Dunn & Claridge 2014).

Abundance

The 1987–2016 North Atlantic Sightings Surveys (NASS) series was initiated in 1987 by cooperative efforts of several countries in the North-east and central North Atlantic, and coordinated through the Scientific Committees of the International Whaling Commission and NAMMCO. NASS enabled cetacean abundance estimates to be generated for the North-east Atlantic (Øien 1990, 1993, Foote et al. 2007, Lockyer & Pike 2009). Even though methods were optimised for estimation of specific target species, such as the larger baleen whales and pilot whales *Globicephala* spp., surveys provided valuable information about the offshore distribution and abundance of killer whales in remote Atlantic regions. The four NASS conducted between 1987 and 2001 covered an average of 2613420 km^2, recorded a total of 91 killer whale sightings, and produced a mean abundance estimate of 13615 killer whales (Table 1).

Table 1. Estimates of the abundance of North Atlantic killer whales *Orcinus orca*, produced from North Atlantic Sighting Surveys 1987-2001 (modified from Foote et al. 2007). Coefficients of variation (CV) and confidence intervals (CI) are given. Effort is measured in km of transect lines surveyed

Year	Area (km^2)	Effort (km)	No. sightings	Abundance (CV)	95% CI
1987	2285353	26545	21	8260 (0.45)	3516–19408
1989	3011133	17226	23	26774 (0.63)	8341–85943
1995	2428812	12648	5	4413 (1.21)	575–33990
2001	2728383	15891	42	15014 (0.42)	6637–33964

Aerial and ship-based surveys were not effective in informing population size estimates of killer whales in ECA, NWA, and Greenland, where low sighting rates prevented any comprehensive abundance estimates from being produced (Lien et al. 1988, Lawson et al. 2007, Hansen et al. 2018). Therefore, killer whale abundance appears to be strikingly lower in the North-western Atlantic and mid-Atlantic than in the North-eastern Atlantic. This was supported by low counts of individuals in Greenland, NWA and ECA (Nielsen 2011, Young et al. 2011, Lawson & Stevens 2014; Table 2). Regional populations number several hundreds of individuals off Iceland (Samarra et al. 2017b) and Norway (Kuningas et al. 2014, Jourdain & Karoliussen 2018; Table 2). The total absence of killer whale records during sighting surveys conducted in tropical waters is certainly indicative of lower abundance relative to higher northern latitudes (Mullin & Fulling 2003).

Movements and genetic structure

Association with dynamic prey resources is known to determine movement patterns, site fidelity, and dispersal in killer whales (e.g. Foote et al. 2010), so feeding ecology is relevant for the assessment of connectivity between geographic communities. A broad-scale molecular study that included tissue samples from Norway (n = 40), Iceland (n = 13), Gibraltar (n = 11), the Canary Islands (n = 9), the British Isles (n = 10), and the North Sea (n = 1; Fig. 3) supported at least three differentiated killer whale populations, the distribution of each of which coincides with that of major fish stocks (Foote et al. 2011). Spatial clustering of individuals assigned to each population is consistent with field observations of predation, and suggests that population A (individuals from Iceland, Norway and Scotland) is associated with the North Atlantic herring, population B (individuals from Scotland, Ireland, Iceland, and the North Sea) is associated with the North-east Atlantic mackerel, and population C (individuals from Gibraltar and the Canary Islands) is associated with the eastern stock of the Atlantic bluefin tuna. While there is potential contact between populations A and B and between populations B and C based on prey movement, allopatric populations A and C appear to be the most differentiated populations of the three (Foote et al. 2011).

Table 2. Minimum counts of identified individual killer whales *Orcinus orca* (excluding calves) per region

Location	Number of individuals	Year(s)	Reference
Northern Norway	971	2007–2018	Jourdain & Karoliussen (2018)
Iceland	432	2006–2015	Samarra et al. (2017b)
Northern Scotland	37	2008–2009	Beck et al. (2011) Foote et al. (2010)
Western Ireland	10	1992–2011	Beck et al. (2014)
Eastern Greenland	7	2009	Nielsen (2011)
Western Greenland	7	2010–2011	Nielsen (2011)
Eastern Canadian Arctic	53	2004–2009	Young et al. (2011)
North West Atlantic	67	2012	Lawson & Stevens (2014)
Canary Islands	16	2009	Esteban et al. (2016c)
Gibraltar	47	1999–2011	Esteban et al. (2016c)
Bahamas	14	1996–2010	Dunn & Claridge (2014)

Variations in tooth wear and nitrogen stable isotopes that are correlated with differences in morphological traits indicate a minimum of two wide-ranging and sympatric killer whale ecotypes throughout the North Atlantic (Foote et al. 2009). Generalist ecotype 1 appears to associate with regional mackerel or herring stocks as its main prey resource(s), but there are group-specific variations in the proportions of prey items taken, including high trophic level prey. In contrast, little isotopic variation was measured for ecotype 2, suggesting this ecotype to be highly specialised and mainly foraging on baleen whales (Foote et al. 2009).

Ecotype 1 includes killer whales off Norway and Iceland that associate with the Norwegian spring-spawning and Icelandic summer-spawning stocks of Atlantic herring as their main prey resources, respectively (e.g. Jonsgård & Lyshoel 1970, Sigurjónsson & Leatherwood 1988, Similä et al. 1996). In both regions, at least some killer whale groups appear to follow these fish stocks' seasonal migration, as confirmed by re-sightings of photographically identified individuals at herring wintering and spawning

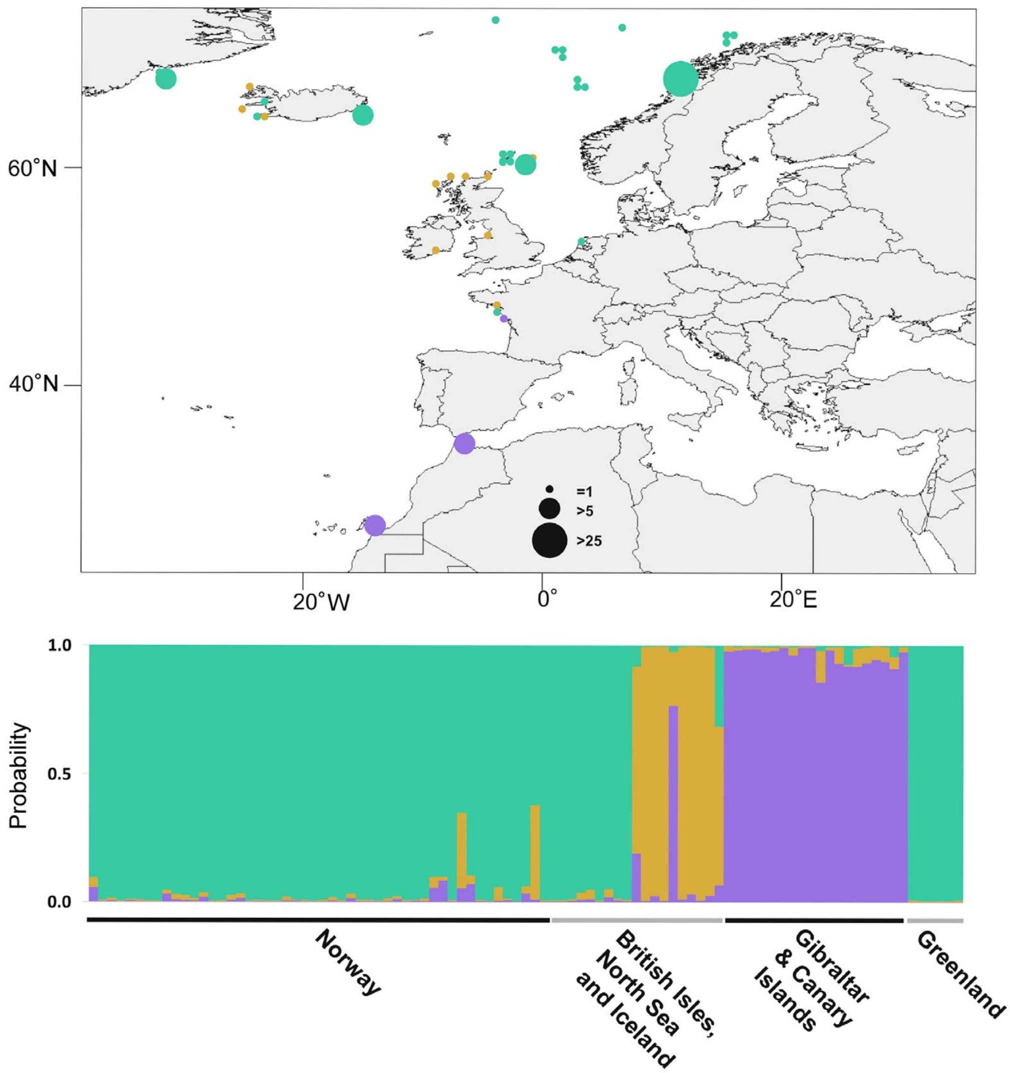

Fig. 3. Map of sampling locations and population structure for a data set of 103 killer whales *Orcinus orca* belonging to three putative populations. Each individual is represented by a column and a sampling point on the map, and the probability of that individual belonging to each population is indicated by shaded segments. Only samples from which high-quality DNA could be obtained were included, so museum specimens and degraded stranded specimens were excluded (figure adapted from Fig. 5 in Foote et al. 2013).

grounds (Lyrholm 1988, Bisther & Vongraven 1994, Samarra et al. 2017a) and satellite tracks of seven individuals (Similä 2006). Killer whales are known to also feed on herring around the Faroe and Shetland Islands (Bloch & Lockyer 1988, Deecke et al. 2011).

Until the 1960s, the distributions of the Norwegian spring-spawning, Icelandic summer-spawning and Icelandic spring-spawning herring stocks overlapped seasonally, in the summer (Jakobsson & Østvedt 1999). Confirmed killer whale presence within their common distribution area suggested a potential past contact zone between the Norwegian and Icelandic killer whale communities (Jonsgård & Lyshoel 1970, Øien 1988). However, after the collapse of the Norwegian spring-spawning herring stock in 1970, its migration patterns changed and there was no longer overlap between the Icelandic and Norwegian herring stocks (Jakobsson & Østvedt 1999). Consistently, comparisons of killer whale identification photographs collected in 1981–2007 off Iceland and in 1986–2006 off Norway did not reveal any match (Foote et al. 2010), suggesting that these communities now have separate ranges. The Norwegian spring-spawning herring has reappeared in killer whale feeding grounds east of Iceland since 2004 and north of Iceland since 2012 (Óskarsson 2018). Cross-matching of recent photo-identification catalogues is warranted, to assess if connectivity between the Norwegian and Icelandic killer whale communities has also been re-established.

Some of the killer whales seasonally feeding on herring off Iceland have been photographically recaptured when foraging on seals *Phoca vitulina* (and possibly *Halichoerus grypus*) and herring off the Shetland Islands and North-east Scotland (Foote et al. 2010, Deecke et al. 2011). This suggests variations in movement patterns and connections between Icelandic and North Sea killer whale communities (Samarra & Foote 2015), which is in further support of contact between populations A and B.

Atlantic mackerel constitutes another apparent prey resource for killer whales in the Norwegian and North Seas (Luque et al. 2006, Pinfield et al. 2012, Nøttestad et al. 2014, Nøttestad et al. 2015). Between 2007 and 2014, the abundance of the North-east Atlantic mackerel stock increased from 1.6 million tons (Mt) to 9.0 Mt (ICES 2013, 2014) and its north-western range expanded (e.g. Astthorsson et al. 2012). Numbers of killer whales recorded during fish stock assessment surveys in July and August in the Norwegian Sea showed a sharp increase, and groups were largely observed in association with mackerel, even when herring were present (Nøttestad et al. 2015).

The Eastern stock of the Atlantic bluefin tuna has been suggested as a third major fish-prey resource for North Atlantic killer whales, as supported by field observations from Gibraltar (Foote et al. 2011, Esteban et al. 2014). Tuna, and possibly other higher trophic level prey, could also be part of the diet of killer whales around the Canary Islands, as suggested by dietary markers and contaminant loads from biopsy samples (Esteban et al. 2016c). However, no movement between the two locations has been documented so far and the two communities are socially, ecologically, and genetically different.

The description of ecotype 2 baleen-whale-eating killer whales was based on only five stranded specimens found in northern European waters (Foote et al. 2009). The actual distribution and ecology of this ecotype are yet to be fully assessed. The current classification of killer whale ecological diversity in the North Atlantic into only two ecotypes is based on relatively few data. Increasing evidence for killer whales switching prey in Norway and Iceland (e.g. Vongraven & Bisther 2014, Jourdain et al. 2017, Samarra et al. 2017c, Samarra et al. 2018) and further variations in feeding behaviour observed in the NWA (e.g. Heide-Jørgensen 1988, Ferguson et al. 2012a, Bourque et al. 2018) may suggest an ecological gradient instead.

Genetic analyses were used to assign six marine-mammal-eating killer whales harvested off eastern Greenland to herring-associated population A (Foote et al. 2013), suggesting recent divergence or a lack of assortative mating, despite ecological differences in the North Atlantic. A recent study in Iceland also revealed weak differentiation among whales with different feeding strategies (Tavares et al. 2018). Social groups overlapping in ecological niche and geographical ranges may associate seasonally, thus preventing social isolation and genetic segregation.

Killer whales off Greenland appear to forage on fish (Heide-Jørgensen 1988, Laidre et al. 2006), pinnipeds, and other cetaceans (Heide-Jørgensen 1988, Ugarte et al. 2013, Bourque et al. 2018), though blubber contamination profiles support marine mammals as the major dietary component (Pedro et al. 2017). The declining summer sea ice in the Arctic environment, including around Greenland over the past decade (Kern et al. 2010), may have promoted access to new marine mammal prey resources and led to increased killer whale presence in these profitable habitats. Inter-individual dietary variations measured from fatty acid signatures (Bourque et al. 2018) suggest that the killer whales that have recently moved into the Arctic could be fish-eaters from the North Atlantic that have diversified their diet and home ranges.

Samples from the NWA ($n = 1$) and the Gulf of Mexico ($n = 1$) were assigned to population B by Foote et al. (2011), but more samples from the NWA are needed to understand population structure in these regions. Dietary analyses conducted on a small number of ECA and NWA killer whales supported foraging in distinct food webs within low-latitude regions and suggested connectivity between northern and southern regions of the NWA (Matthews & Ferguson 2014).

NWA killer whales feed on both fish and marine mammals, but variations in dietary preferences and related movement patterns remain unknown (Lien et al. 1988, Lawson et al. 2007). Conversely, only predation on marine mammals has been recorded for ECA killer whales (Laidre et al. 2006, Ferguson et al. 2012b, Higdon et al. 2012, Westdal et al. 2016). Temporary fidelity to areas with seasonal high-density cetacean prey such as Foxe Basin and Western Hudson Bay further suggest association with preferred marine mammal prey resources (see Figure 5 in Galicia et al. 2016). Satellite tagging of one individual killer whale in 2009 for 90 days, another in 2013 (for 59 days), and a third in 2018 (for 10 days) off Baffin Island confirmed wide-range movements within the Arctic (DFO unpublished data). The 2009 whale travelled 5400 km, from ECA waters south nearly to the Azores between August and November (Matthews et al. 2011). The timing of the telemetry tracks supported seasonal migration out of the Arctic by autumn, presumably in order to avoid heavy ice formation (Sergeant & Fisher 1957, Mitchell & Reeves 1988). Based on this 2009 track, which suggested connectivity between whales at northern high latitudes and low latitudes, the area including the open North Atlantic

Ocean, south to the Caribbean and Western Greenland was suggested as a winter range for ECA killer whales (Matthews & Ferguson 2014).

Despite an apparently large geographic range, there has been no photo-identification evidence of individual killer whales moving among NWA, ECA, and Greenland (Young et al. 2011). This lack of evidence suggests that wide-ranging, potentially non-overlapping populations or sub-populations may inhabit these regions. However, given the proximity of and ecological connections between these regions and the limited data available, conclusions must remain elusive until genomic analyses are completed.

Acoustics

As for other cetaceans, acoustic communication plays a crucial role for killer whale feeding and social cohesiveness. Call repertoires from some populations can provide insights into relatedness, and are relevant tools for the assessment of population structure.

As shown in the north-eastern Pacific Ocean (Ford 1991), early studies of killer whale acoustics confirmed the existence of group-specific call repertoires in Norway, and suggested their existence in Icelandic waters as well (Moore et al. 1988, Strager 1995). Culturally transmitted call repertoires can provide insights into relatedness (Deecke et al. 2010). A few shared calls between the Icelandic and Norwegian killer whale communities suggested past or ongoing contact (Strager 1995), consistent with historic overlap in herring stock distributions (Jakobsson & Østvedt 1999).

More recently, research has emphasised the importance of sound production for foraging by fish-eating killer whales in both Norway and Iceland (e.g. Simon et al. 2006, Samarra 2015, Samarra et al. 2016). However, killer whales in these regions often occur in large aggregations where social groups are challenging to dissociate acoustically. As a result, investigations so far have largely promoted knowledge about context-specific call use (Van Parijs et al. 2004, Van Opzeeland et al. 2005, Simon et al. 2007a, Simon et al. 2007b, Samarra & Miller 2015) rather than group-specific call repertoires. Herring-eating killer whales in Norway and Iceland present similar (Simon et al. 2005, Simon et al. 2007a), but not identical (Simon et al. 2006) acoustic behaviours, supporting the assumption of past contact between killer whales in both areas. Similar to ecotypic variation in the north-eastern Pacific Ocean, variation in acoustic signals suggest behavioural adaptation in relation to feeding specialisation in fish-eating and mammal-eating killer whales in Scotland (Deecke et al. 2011). Acoustic studies have been lacking in Greenland, NWA, and ECA.

Population parameters

In northern Norway and Gibraltar, apparent survival rates of adult killer whales ranging from 0.971 to 0.977 (1986-2003; Kuningas et al. 2014), and from 0.901 to 0.991 (1999-2011; Esteban et al. 2016b), respectively, fell within the range of estimates produced for regions worldwide (Olesiuk et al. 2005, Poncelet et al. 2010; Table 3). Sympatric social groups adopting different foraging strategies in Gibraltar differed in both survival and calving rates, and were shown to follow divergent demographic trends (Esteban et al. 2016b). This highlights the need to assess variations in both ecology and demographics of groupings within regions.

Table 3. Demographic parameters estimated for killer whales *Orcinus orca* of Norway and Gibraltar, compared to those of other populations. Standard errors (SE) are given; y = year. 'INT' refers to killer whales known to interact with dropline tuna fishery while 'NOT' refers to killer whales never seen interacting with dropline tuna fishery

Region and reference	Years	Adult survival	Calving interval (y)	Calving rate (calves/y)
Norway Kuningas et al. 2014	1986–2003	Females: 0.977 (SE = 0.009) Males: 0.971 (SE = 0.008)	5.06 (SE = 0.722)	0.197 (SE = 0.065)
Gibraltar Esteban et al. 2016b	1999–2011	INT*: 0.991 (SE = 0.014) NOT**: 0.901 (SE = 0.067)	INT*: 6 to 8	INT*: 0.219 (SE = 0.034) NOT**: 0.020 (SE = 0.013)
Northeastern Pacific Olesiuk et al. 2005	1973–1995	Females: 0.984 (SE = 0.004) Males: 0.959 (SE = 0.008)	4.88 (SE = 0.793)	0.205
	1996–2004	Females: 0.971 (SE = 0.007) Males: 0.909 (SE = 0.017)	5.53 (SE = 1.103)	0.180
Crozet Archipelago Poncelet et al. 2010	1977	Females: 0.942 Males: 0.935	_	_
	2002	Females: 0.901 Males: 0.895	_	_

Threats

HARVEST

Between 1938 and 1981, a total of 2435 killer whales was caught by Norwegian whalers throughout the North Atlantic. The average annual catch was 55 animals, and catches peaked at 231 and 246 animals taken in 1969 and 1970, respectively (Christensen et al. 1982, Christensen 1988, Øien 1988). From 1976 to 1988, a total of 59 killer whales was live-captured in Iceland in order to provision aquaria. Of these, eight were released, three died and 48 were exported (Sigurjonsson & Leatherwood 1988). In the mid-1950s, there were reports that killer whales in Iceland were destroying fisheries equipment. Consequently, the U.S. navy reduced the numbers of killer whales using machine guns from fishing boats, and later with rockets and depth charges from the air (Naval Aviation News 1956). Campaigns in 1954, 1955, and 1956 killed hundreds of killer whales (Naval Aviation News 1956). In ECA, an estimated 21 killer whales were caught between 1950 and 2007, mainly as a result of entrapments in ice or salt lakes (Higdon 2007). In Greenland, catches, including unreported kills and animals struck and lost, were estimated to be a total of 75 killer whales during 1950–1988 (Heide-Jørgensen 1988). From 1996, after it became mandatory to report killer whale catches in the Greenlandic catch data base called Piniarneq (i.e. the hunt), reports indicated that a total of 59 killer whales was harvested during 1996–2006 (Greenland Institute of Natural Resources, unpublished data). For this period, reported landings varied from one to six killer whales per year, with the exception of 2002 when unusual winter killer whale presence led to 21 catches in Disko Bay. Catches in southeast Greenland increased dramatically between 2009 and 2017 (Ugarte et al. 2013), when a minimum of 47 killer whales were landed in Tasiilaq and surrounding settlements (see Table 1 in Lennert & Richard 2017). Killer whale catches were also recorded in the Caribbean islands of St. Vincent and the Grenadines ($n = 22$), in Trinidad and Tobago ($n = 2$), and in Colombia ($n = 1$) between 1968 and 2011 (Bolanos-Jimenez et al. 2014). One source further cited nine landings between 2015 and 2018 off the town of Barrouallie on the island of St. Vincent (iWitness News 2018).

CHEMICAL POLLUTION

High polychlorinated biphenyl (PCBs) concentrations were measured in full blubber-depth and biopsy samples taken from North Atlantic killer whales (McHugh et al. 2007, Wolkers et al. 2007, Jepson et al. 2016, Pedro et al. 2017, Desforges et al. 2018, see Table 4). Contamination patterns are variable across regions and are presumably a reflection of differences in diet, trophic level, and proximity to industrialised coastlines. The most heavily contaminated killer whales are those sampled in Gibraltar, Canary Islands, UK and Ireland (Jepson et al. 2016), and marine-mammal-eating killer whales sampled around Greenland (Pedro et al. 2017). There was an indication of reproductive failure in female killer whales sampled around the very industrialised regions of the Canary Islands and Gibraltar (Jepson et al. 2016). The distribution of critically small killer whale populations (<50 individuals; e.g. Beck et al. 2014, Esteban et al. 2016a) with low-to-no recruitment also coincides with the most industrialised European regions. PCBs, along with the next most common groups of contaminants (chlordanes and DDT), occur in blubber concentrations exceeding thresholds that cause physiological, reproductive and immune impairments (McHugh et al. 2007, Wolkers et al. 2007, Jepson et al. 2016, Pedro et al. 2017).

Table 4. Blubber PCB concentrations measured in killer whales *Orcinus orca* sampled in various regions (all units in mg/kg per lipid weight; N = number of individuals)

Region	Reference	Sex	Age class	N	Mean	Minimum	Maximum
Norway	Wolkers et al. (2007)	Male	Adult	8	26.9	16.6	43.7
Iceland	Desforges et al. (2018)	Male	Adult	13	99.7	9.7	436
		Female	Adult	1	28.9	–	–
		Female	Foetus/calf	3	83.9	15	164
Greenland	Pedro et al. (2017)	Male	Adult	1	140.1	–	–
		Female	Adult	6	63.8	24	121
Faroes	Pedro et al. (2017)	Female	Sub/Ad	2	5.16	2.75	7.57
United Kingdom	Jepson et al. (2016)	Male	Adult	5	312	23.6	778
		Female	Adult	9	271	16.9	957
Canaries	Jepson et al. (2016)	Male	Adult	1	180.2	–	–
		Female	Adult	7	108.1	27.5	247.2
Gibraltar	Jepson et al. (2016)	Male	Sub/Ad	2	243.4	171.5	315.4
		Female	Adult	6	186.7	43.3	857.9

CLIMATE CHANGE AND PREY AVAILABILITY

Climate change and the subsequent loss of sea ice promote pelagic-dominated habitats and make new prey resources available to killer whales in Polar regions (Higdon & Ferguson 2009, Ferguson et al. 2010). Consistent with their marked ice-avoidance, satellite tracking of individual killer whales tagged around Baffin Island supported consistent routes and schedules to exit the region prior to heavy ice formation (Matthews et al. 2011, DFO unpublished data). However, variable timing of sea ice formation combined with possible lack of matrilineal knowledge of geographic patterns for newly invading killer whale groups appear to have resulted in increased ice entrapments (Westdal et al. 2017, Matthews et al. 2019). As these events are usually fatal to entire groups, ice entrapments represent a significant source of mortality with suspected long-term demographic impacts (Matthews et al. 2019). Ice entrapments were also reported in the NWA (Reeves & Mitchell 1988a, Higdon 2007, see Westdal et al. 2017 for a review), Disko Bay (Heide-Jørgensen 1988), Iceland (Vikingsson 2004), and Norway (Bisther et al. 1994). Colonisation of new regions by killer whales and subsequent predation on species of commercial and/or cultural importance to humans (Westdal et al. 2016, Breed et al. 2017) may result in new conflicts with human communities in Greenland (Lennert & Richard 2017) and in ECA (Westdal et al. 2013).

The recently warming marine climate has promoted major shifts in the distribution and abundance of killer whale prey resources in the North Atlantic (e.g. Astthorsson et al. 2012). Plasticity in killer whale feeding behaviours suggests adaptability and possible resilience to changing prey availability in this region (e.g. Vongraven & Bisther 2014, Samarra & Miller 2015). However, low prey supplies may lead to decreasing body condition in specialist individuals (Christensen 1982) and to potential population-level consequences through lower survival and reproduction rates (Ward et al. 2009, Ford et al. 2010).

INTERACTIONS WITH FISHERIES

Killer whales have been observed scavenging on discarded fish around herring purse-seiners off Iceland (Sigurjonsson & Leatherwood 1988) and Norway (Similä 2005), around mackerel trawlers in the North Sea (Couperus 1994, Luque et al. 2006, Pinfield et al. 2012), around Greenland halibut *Reinhardtius hippoglossoides* longliners off northern Labrador and in the Davis Strait, and around trawlers (Lawson et al. 2007) and gillnets in NWA (Lien et al. 1988). Depredation was confirmed during longline fishing for Atlantic halibut *Hippoglossus hippoglossus* and Greenland halibut off Iceland (Bloch & Lockyer 1988, Samarra et al. 2018), tuna in Newfoundland (Lawson et al. 2007) and in the Strait of Gibraltar (Esteban et al. 2016b), and pelagic fish in Colombia (Bolanos-Jimenez et al. 2014).

To date, the frequency with which killer whales forage in proximity to or directly interact with fisheries has only been assessed in Gibraltar (Esteban et al. 2015, Esteban et al. 2016b). Depredation on fisheries provides access to prey capture with less effort, and has been shown to be culturally transmitted within killer whale populations (Esteban et al. 2015). Lethal outcomes following entanglement in fishing gear has been reported in NWA (Lawson et al. 2007), Norway (EJ unpublished data), and Gibraltar, indicating a need for regional assessments of these interactions and induced mortality, if any.

ACOUSTIC DISTURBANCE

Sound production by killer whales during foraging activities (e.g. Samarra 2015) highlights the potential for anthropogenic noise to impact functional behaviour. Acoustic disturbance from anthropogenic sources such as sonar sounds used in naval activities results in responses of variable severity by North Atlantic killer whales (e.g. Miller et al. 2014). These include disruption of diving behaviour and feeding, separation of group members, and source avoidance leading to displacement; subsequent costs relate to loss of habitat and reduced foraging success (Miller et al. 2012, Kuningas et al. 2013, Samarra & Miller 2016). Vessel traffic has been shown to affect activity budgets and possibly reduce foraging success in Pacific Ocean fish-eating killer whales (e.g. Williams et al. 2006, Lusseau et al. 2009). However, the noise levels that killer whales are exposed to and the effects of vessel noise and physical disturbance on North Atlantic killer whales have not been assessed to date.

Conservation status

The conservation status of the killer whale in the *IUCN Red List of Endangered Species* is Data Deficient (Reeves et al. 2017). Gibraltar killer whales were classified as Critically Endangered in the Agreement on the Conservation of Cetaceans in the Black Sea Mediterranean Sea and Contiguous Atlantic Area, due to social, genetic, and ecological isolation, small population size, low recruitment, and the decline of their primary prey (Esteban et al. 2016a). A conservation plan was urgently recommended and is currently under revision (Esteban et al. 2016a). Similarly, the critically small West Coast killer whale community off the British Isles has been suggested as a separate conservation unit (Beck et al. 2011). In the ECA and NWA, killer whales were classified as Special Concern by the Committee on the Status of Endangered Wildlife in Canada, due to low abundance and potential direct harvest if there was any movement to Greenland (COSEWIC 2008). Killer whales are categorised as Data Deficient in the Greenland Red List (Boertmann & Bay 2018).

CONCLUSION

A growing body of studies has substantially improved our understanding of North Atlantic killer whales. However, due to patchy knowledge, how the various regional populations or lineages are genetically, socially, and ecologically differentiated remains unknown. Further photo-identification and genetic work is crucial to delineate the various populations and subpopulations, and to resolve taxonomic uncertainties across regions. Efforts should also be directed towards regional status assessments and towards monitoring killer whale resilience to changing habitats. Characterisation of both context-specific and group-specific acoustic repertoires is needed, and would support other research approaches, e.g. passive acoustic monitoring to assess seasonality, distribution, and behavioural activities. This would be particularly beneficial in areas where it is logistically challenging and costly to carry out fieldwork.

Historic whaling, culling, and live captures depleted killer whale populations in the North Atlantic until 1989 to an unknown extent. High numbers of removals over small areas may have impacted social integrity and resulted in long-lasting demographic effects, and expected recovery may continue to be jeopardised by new emerging threats. Despite a ban on the use of PCBs during the 1980s in most European countries, PCB concentrations in killer whale blubber have remained stable and at levels exceeding toxicity thresholds. Subsequent impairment of reproduction could lead to population decline or lack of recovery in some regions, especially for small, demographically closed populations. Despite these multiple threats, killer whales are locally seasonally abundant around Norway and Iceland, and their numbers appear to be stable or increasing around Norway, Iceland, eastern Greenland, and the ECA. This could be due to recovery from past removals, increased access to prey due to better management of fisheries, whaling and sealing activities reducing predator competition, shifts in prey availability and habitat due to climate change. Apparent increases may also reflect increasing numbers of records, due to greater awareness or effort by potential observers, rather than increases in abundance.

Information related to abundance and population identity is still missing from Greenland, where harvest has been increasing. The Special Concern status of the killer whales therefore remains unchanged (NAMMCO 2017, 2018). With no current advice on sustainable harvest levels, there is an immediate need for catch data to be validated and reported reliably, as well as for improved sampling for comparative molecular studies (NAMMCO 2018). Not only could heterogeneity in individual catch probabilities alter genetic and ecological diversities, it could also have substantial effects on long-term population dynamics. High contamination levels and subsequent risks of reproductive failure could further reduce the potential for a sustainable harvest. Research should urgently address status assessment-relevant questions in the NWA and Greenland, where killer whale abundance appears to be strikingly lower than in the north-eastern regions.

ACKNOWLEDGEMENTS

This work was conducted under contract (EJ) with the North Atlantic Marine Mammal Commission. We thank Andy Foote and three anonymous reviewers for their suggestions that greatly improved the manuscript.

REFERENCES

Astthorsson OS, Valdimarsson H, Gudmundsdottir A, Óskarsson GJ (2012) Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. *Ices Journal of Marine Science* 69: 1289–1297. https://doi.org/10.1093/icesjms/fss084.

Beck S, Foote AD, Kotter S, Harries O, Mandleberg L, Stevick PT, Whooley P, Durban JW (2014) Using opportunistic photo-identification to detect a population decline of killer whales (*Orcinus orca*) in British and Irish waters. *Journal of the Marine Biological Association of the United Kingdom* 94: 1327–1333. https://doi.org/10.1017/s0025315413001124.

Beck S, Kuningas S, Esteban R, Foote AD (2011) The influence of ecology on sociality in the killer whale (*Orcinus orca*). *Behavioral Ecology* 23: 246–253. https://doi.org/10.1093/beheco/arr151.

Bisther A, Amundin M, Rian J (1994) *A group of killer whales (Orcinus orca) entrapped behind an ice barrier in Norway November/December 1993 – conclusions for the future*. European Association for Aquatic Mammals, Kolmården, Sweden.

Bisther A, Vongraven D (1994) *Killer whales off the mid-Norwegian coast*. Final Report, NFFR-PROJECT 4001-319.016. Trondheim, Norway.

Bloch D, Lockyer C (1988) Killer whales (*Orcinus orca*) in Faroese waters (Atlantic Ocean). *Rit Fiskideildar* 11: 55–64.

Boertmann D, Bay C (2018) Grønlands rødliste 2018: Fortegnelse over grønlandske dyr og planters trusselstatus. Grønlands Naturinstitut, Aarhus Universitet, Aarhus, Denmark.

Bolanos-Jimenez J, Mignucci-Giannoni AA, Blumenthal J, Bogomolni A, Casas JJ, Henriquez A et al. (2014) Distribution, feeding habits and morphology of killer whales *Orcinus orca* in the Caribbean Sea. *Mammal Review* 44: 177–189. https://doi.org/10.1111/mam.12021.

Bolt HE, Harvey PV, Mandleberg L, Foote AD (2009) Occurrence of killer whales in Scottish inshore waters: temporal and spatial patterns relative to the distribution of declining harbour seal populations. *Aquatic Conservation-Marine and Freshwater Ecosystems* 19: 671–675. https://doi.org/10.1002/aqc.1030.

Bourque J, Dietz R, Sonne C, St Leger J, Iverson S, Rosing-Asvid A, Hansen M, McKinney MA (2018) Feeding habits of a new Arctic predator: insight from full-depth blubber fatty acid signatures of Greenland, Faroe Islands, Denmark, and managed-care killer whales *Orcinus orca*. *Marine Ecology Progress Series* 603: 1–12. https://doi.org/10.3354/meps12723.

Breed GA, Matthews CJD, Marcoux M, Higdon JW, LeBlanc B, Petersen SD, Orr J, Reinhart NR, Ferguson SH (2017) Sustained disruption of narwhal habitat use and behavior in the presence of Arctic killer whales. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 2628–2633. https://doi.org/10.1073/pnas.1611707114.

Christensen I (1982) Killer whales in Norwegian coastal waters. *Report of the International Whaling Commission* 32: 633–641.

Christensen I (1988) Distribution, movements and abundance of killer whales (*Orcinus orca*) in Norwegian coastal waters, 1982-1987, based on questionnaire surveys. *Rit Fiskideildar* 11: 79–88.

Christensen I, Jonsgård Å, Rørvik CJ (1982) Catch statistics for minke whales (*Balaenoptera acutorostrata*) and killer whales (*Orcinus orca*) caught by Norway in 1980. *Report of the International Whaling Commission* 32: 487–489.

Clarke R (1981) Whales and dolphins of the Azores and their exploitation. *Report of the International Whaling Commission* 31: 607–615.

COSEWIC (2008) *Cosewic assessment and update status report on the killer whale* Orcinus orca, *southern resident population, northern resident population, west coast transient population, offshore population and northwest Atlantic/eastern Arctic population, in Canada*. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada.

Couperus AS (1994) Killer whales (*Orcinus orca*) scavenging on discards of freezer trawlers north east of the Shetland Islands. *Aquatic Mammals* 20: 47–51.

Deecke VB, Barrett-Lennard LG, Spong P, Ford JKB (2010) The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus orca*). *Naturwissenschaften* 97: 513–518. https://doi.org/10.1007/s00114-010-0657-z.

Deecke VB, Nykanen M, Foote AD, Janik VM (2011) Vocal behaviour and feeding ecology of killer whales *Orcinus orca* around Shetland, UK. *Aquatic Biology* 13: 79–88. https://doi.org/10.3354/ab00353.

Desforges J-P, Hall A, McConnell B, Rosing-Asvid A, Barber JL, Brownlow A et al. (2018) Predicting global killer whale population collapse from PCB pollution. *Science* 361: 1373–1376. https://doi.org/10.1126/science.aat1953.

Dunn C, Claridge D (2014) Killer whale (*Orcinus orca*) occurrence and predation in the Bahamas. *Journal of the Marine Biological Association of the United Kingdom* 94: 1305–1309. https://doi.org/10.1017/s0025315413000908.

Esteban R, Verborgh P, Gauffier P, Alarcón D, Salazar-Sierra JM, Giménez J, Foote AD, de Stephanis R (2016a) Conservation status of killer whales, *Orcinus orca*, in the Strait of Gibraltar. In: *Advances in Marine Biology* 75, 141–172. Academic Press. https://doi.org/10.1016/bs.amb.2016.07.001.

Esteban R, Verborgh P, Gauffier P, Gimenez J, Afan I, Canadas A et al. (2014) Identifying key habitat and seasonal patterns of a critically endangered population of killer whales. *Journal of the Marine Biological Association of the United Kingdom* 94: 1317–1325. https://doi.org/10.1017/s002531541300091x.

Esteban R, Verborgh P, Gauffier P, Giménez J, Foote AD, de Stephanis R (2015) Maternal kinship and fisheries interaction influence killer whale social structure. *Behavioral Ecology and Sociobiology* 70: 111–122. https://doi.org/10.1007/s00265-015-2029-3.

Esteban R, Verborgh P, Gauffier P, Giménez J, Guinet C, de Stephanis R (2016b) Dynamics of killer whale, bluefin tuna and human fisheries in the Strait of Gibraltar. *Biological Conservation* 194: 31–38. https://doi.org/10.1016/j.biocon.2015.11.031.

Esteban R, Verborgh P, Gauffier P, Giménez J, Martín V, Pérez-Gil M et al. (2016c) Using a multi-disciplinary approach to identify a critically endangered killer whale management unit. *Ecological Indicators* 66: 291–300. https://doi.org/10.1016/j.ecolind.2016.01.043.

Evans PGH (1988) Killer whales (*Orcinus orca*) in British (UK) and Irish waters. *Rit Fiskideildar* 11: 42–54.

Ferguson SH, Higdon JW, Chmelnitsky EG (2010) The rise of killer whales as a major Arctic predator. In: Ferguson SH, Loseto LL & Mallory ML (eds) *A Little Less Arctic: Top Predators in the World's Largest Northern Inland Sea, Hudson Bay*, 117–136. Springer Netherlands, Dordrecht, the Netherlands. https://doi.org/10.1007/978-90-481-9121-5_6.

Ferguson SH, Higdon JW, Westdal KH (2012a) Prey items and predation behavior of killer whales (*Orcinus orca*) in Nunavut, Canada based on Inuit hunter interviews. *Aquatic Biosystems* 8: 3–3. https://doi.org/10.1186/2046-9063-8-3.

Ferguson SH, Kingsley MCS, Higdon JW (2012b) Killer whale (*Orcinus orca*) predation in a multi-prey system. *Population Ecology* 54: 31–41. https://doi.org/10.1007/s10144-011-0284-3.

Foote AD, Kuningas S, Samarra FIP (2014) Foreword: North Atlantic killer whale research; past, present and future. *Journal of the Marine Biological Association of the United Kingdom* 94: 1245–1252. https://doi.org/10.1017/s0025315414000800.

Foote AD, Newton J, Ávila-Arcos MC, Kampmann M-L, Samaniego JA, Post K, Rosing-Asvid A, Sinding M-HS, Gilbert MTP (2013) Tracking niche variation over millennial timescales in sympatric killer whale lineages. Proceedings of the Royal Society B 280: 20131481. https://doi.org/10.1098/rspb.2013.1481.

Foote AD, Newton J, Piertney SB, Willerslev E, Gilbert MTP (2009) Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. *Molecular Ecology* 18: 5207–5217. https://doi.org/10.1111/j.1365-294X.2009.04407.x.

Foote AD, Similä T, Vikingsson G, Stevick PT (2010) Movement, site fidelity and connectivity in a top marine predator, the killer whale. *Evolutionary Ecology* 24: 803–814. https://doi.org/10.1007/s10682-009-9337-x.

Foote AD, Vikingsson G, Øien N, Bloch D, Davis CG, Dunn TE et al. (2007) Distribution and abundance of killer whales in the north east Atlantic. Paper SC/59/SM5 presented to the IWC Scientific Committee.

Foote AD, Vilstrup JT, de Stephanis R, Verborgh P, Nielsen SCA, Deaville R et al. (2011) Genetic differentiation among north Atlantic killer whale populations. *Molecular Ecology* 20: 629–641. https://doi.org/10.1111/j.1365-294x.2010.04957.x.

Ford JKB (1991) Vocal traditions among resident killer whales *Orcinus orca* in coastal waters of British Columbia. *Canadian Journal of Zoology* 69: 1454–1483.

Ford JKB, Ellis GM, Olesiuk PF, Balcomb KC (2010) Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? *Biology Letters* 6: 139–142. https://doi.org/10.1098/rsbl.2009.0468.

Forney KA, Wade PR (2006) Worldwide distribution and abundance of killer whales. In: Estes JA, Demaster DP, Doak DF, Williams TM, Brownell RL (eds) *Whales, Whaling, and Ocean Ecosystems*, 145–162. University of California Press, Berkeley and Los Angeles, California, USA. https://doi.org/10.1525/california/9780520248847.003.0012.

Galicia MP, Thiemann GW, Dyck MG, Ferguson SH, Higdon JW (2016) Dietary habits of polar bears in Foxe Basin, Canada: possible evidence of a trophic regime shift mediated by a new top predator. *Ecology and Evolution* 6: 6005–6018. https://doi.org/10.1002/ece3.2173.

Gunnlaugsson T, Sigurjónsson J (1990) Nass-87: Estimation of whale abundance based on observations made onboard Icelandic and Faroese survey vessels. *Report of the International Whaling Commission* 40: 571–580.

Hammond PS, Lockyer C (1988) Distribution of killer whales in the eastern north Atlantic. *Rit Fiskideildar* 11: 24–41.

Hansen RG, Boye TK, Larsen RS, Nielsen NH, Tervo O, Nielsen RD, Rasmussen MH, Sinding MHS, Heide-Jørgensen MP (2018) Abundance of whales in west and east Greenland in summer 2015. *NAMMCO Scientific Publications* 11: https://doi.org/10.7557/3.4689.

Heide-Jørgensen MP (1988) Occurrence and hunting of killer whales in Greenland. *Rit Fiskideildar* 11: 115–135.

Higdon J (2007) Status of knowledge on killer whales *(Orcinus orca)* in the Canadian Arctic. Research Document 2007/048, Canadian Science Advisory Secretariat, Winnipeg, Canada.

Higdon JW, Ferguson SH (2009) Loss of Arctic sea ice causing punctuated change in sightings of killer whales (*Orcinus orca*) over the past century. *Ecological Applications* 19: 1365–1375. https://doi.org/10.1890/07-1941.1.

Higdon JW, Hauser DDW, Ferguson SH (2012) Killer whales (*Orcinus orca*) in the Canadian Arctic: distribution, prey items, group sizes, and seasonality. *Marine Mammal Science* 28: E93–E109. https://doi.org/10.1111/j.1748-7692.2011.00489.x.

Higdon JW, Westdal KH, Ferguson SH (2014) Distribution and abundance of killer whales (*Orcinus orca*) in Nunavut, Canada - an Inuit knowledge survey. *Journal of the Marine Biological Association of the United Kingdom* 94: 1293–1304. https://doi.org/10.1017/s0025315413000921.

ICES (2013) Report of the working group on widely distributed stocks (wgwide). ICES CM 2013/ACOM:15,950, Copenhagen, Denmark.

ICES (2014) Report of the working group on widely distributed stocks (wgwide). ICES CM 2014/ACOM:15,971, Copenhagen, Denmark.

IWC (2007) Report of the scientific committee. *Journal of Cetacean Research and Management* 10(Suppl.): 1–74.

iWitness News (2018) Whalers kill 3 more orcas in St. Vincent (video at: Https://bit.Ly/2hirzqc).

Jakobsson J, Østvedt OJ (1999) A review of joint investigations on the distribution of herring in the Norwegian and Iceland seas 1950-1970. *Rit Fiskideildar* 16: 209–238.

Jepson PD, Deaville R, Barber JL, Aguilar A, Borrell A, Murphy S et al. (2016) PCB pollution continues to impact populations of orcas and other dolphins in European waters. *Scientific Reports* 6: 18573. https://doi.org/10.1038/srep18573.

Jonsgård Å, Lyshoel PB (1970) A contribution to the knowledge of the biology of the killer whale *Orcinus orca* l. *Nytt Magasin for Zoologi* 18: 41–48.

Jourdain E, Karoliussen R (2018) Identification catalogue of Norwegian killer whales: 2007–2018. https://doi.org/10.6084/m9.figshare.4205226.

Jourdain E, Vongraven D, Bisther A, Karoliussen R (2017) First longitudinal study of seal-feeding killer whales (*Orcinus orca*) in Norwegian coastal waters. *Plos One* 12: e0180099. https://doi.org/10.1371/journal.pone.0180099.

Katona SK, Beard JA, Girton PE, Wenzel F (1988) Killer whales *Orcinus orca* from the Bay of Fundy (Southeast Canada) to the equator, including the Gulf of Mexico. *Rit Fiskideildar* 11: 205–224.

Kern S, Kaleschke L, Spreen G (2010) Climatology of the Nordic (Irminger, Greenland, Barents, Kara and White/Pechora) seas ice cover based on 85 GHz satellite microwave radiometry: 1992–2008. *Tellus A* 62: 411–434. https://doi.org/10.3402/tellusa.v62i4.15709.

Kovacs KM, Haug T, Lydersen C (2009) Marine mammals of the Barents Sea. In: Sakshaug E, Johnsen G, Kovacs KM (eds) *Ecosystem Barents Sea*, 453–497. Tapir Academic Press, Trondheim, Norway.

Kovacs KM, Lydersen C (2008) Climate change impacts on seals and whales in the north Atlantic and adjacent shelf areas. *Science Progress* 91: 117–150. https://doi.org/10.3184/003685008x324010.

Kuningas S, Kvadsheim PH, Lam FPA, Miller PJO (2013) Killer whale presence in relation to naval sonar activity and prey abundance in northern Norway. *Ices Journal of Marine Science* 70: 1287–1293. https://doi.org/10.1093/icesjms/fst127.

Kuningas S, Similä T, Hammond PS (2014) Population size, survival and reproductive rates of northern Norwegian killer whales (*Orcinus orca*) in 1986-2003. *Journal of the Marine Biological Association of the United Kingdom* 94: 1277–1291. https://doi.org/10.1017/s0025315413000933.

Laidre KL, Heide-Jorgensen MP, Orr JR (2006) Reactions of narwhals, *Monodon monoceros,* to killer whale, *Orcinus orca*, attacks in the eastern Canadian Arctic. *Canadian Field-Naturalist* 120: 457–465. https://doi.org/10.22621/cfn.v120i4.355.

Lawson JW, Stevens TS, Snow D (2007) *Killer whales of Atlantic Canada, with particular reference to the Newfoundland and Labrador region*. Research Document. Department of Fisheries and Oceans, Canadian Science Advisory Secretariat.

Lawson JW, Stevens TS (2014) Historic and current distribution patterns, and minimum abundance of killer whales (*Orcinus orca*) in the North-west Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 94: 1253–1265. https://doi.org/10.1017/s0025315413001409.

Leduc RG, Robertson KM, Pitman RL (2008) Mitochondrial sequence divergence among Antarctic killer whale ecotypes is consistent with multiple species. *Biology Letters* 4: 426–429. https://doi.org/10.1098/rsbl.2008.0168.

Lennert AE, Richard G (2017) At the cutting edge of the future: unravelling depredation, behaviour and movement of killer whales in the act of flexible management regimes in Arctic Greenland. *Ocean & Coastal Management* 148: 272–281. https://doi.org/10.1016/j.ocecoaman.2017.08.016.

Lien J, Stenson GB, Jones PW (1988) Killer whales (*Orcinus orca*) in waters off Newfoundland and Labrador, (Canada) 1978-1986. *Rit Fiskideildar* 11: 194–201.

Lockyer C, Pike D (eds; 2009) *North Atlantic sightings surveys: counting whales in the North Atlantic 1987–2001*. Scientific Committee, North Atlantic Marine Mammal Commission, The Arctic University of Norway, Tromsø, Norway.

Luque PL, Davis CG, Reid DG, Wang JJ, Pierce GJ (2006) Opportunistic sightings of killer whales from Scottish pelagic trawlers fishing for mackerel and herring off North Scotland (UK) between 2000 and 2006. *Aquatic Living Resources* 19: 403–410. https://doi.org/10.1051/alr:2007009.

Lusseau D, Bain DE, Williams R, Smith JC (2009) Vessel traffic disrupts the foraging behavior of southern resident killer whales *Orcinus orca*. *Endangered Species Research* 6: 211–221. https://doi.org/10.3354/esr006211.

Lyrholm T (1988) Photoidentification of individual killer whales, *Orcinus orca*, off the coast of Norway, 1983-1986. *Rit Fiskideildar* 11: 89–94.

Matthews CJD, Ferguson SH (2014) Spatial segregation and similar trophic-level diet among eastern Canadian Arctic/North-west Atlantic killer whales inferred from bulk and compound specific isotopic analysis. *Journal of the Marine Biological Association of the United Kingdom* 94: 1343–1355. https://doi.org/10.1017/s0025315413001379.

Matthews CJD, Luque SP, Petersen SD, Andrews RD, Ferguson SH (2011) Satellite tracking of a killer whale (*Orcinus orca*) in the Eastern Canadian Arctic documents ice avoidance and rapid, long-distance movement into the North Atlantic. *Polar Biology* 34: 1091–1096. https://doi.org/10.1007/s00300-010-0958-x.

Matthews CJD, Raverty SA, Noren DP, Arragutainaq L, Ferguson SH (2019) Ice entrapment mortality may slow expanding presence of Arctic killer whales. *Polar Biology*. https://doi.org/10.1007/s00300-018-02447-3.

McHugh B, Law RJ, Allchin CR, Rogan E, Murphy S, Foley MB, Glynn D, McGovern E (2007) Bioaccumulation and enantiomeric profiling of organochlorine pesticides and persistent organic pollutants in the killer whale (*Orcinus orca*) from British and Irish waters. *Marine Pollution Bulletin* 54: 1724–1731. https://doi.org/10.1016/j.marpolbul.2007.07.004.

Miller PJO, Antunes RN, Wensveen PJ, Samarra FIP, Alves AC, Tyack PL et al. (2014) Dose-response relationships for the onset of avoidance of sonar by free-ranging killer whales. *Journal of the Acoustical Society of America* 135: 975–993. https://doi.org/10.1121/1.4861346.

Miller PJO, Kvadsheim PH, Lam F-PA, Wensveen PJ, Antunes R, Alves AC et al. (2012) The severity of behavioral changes observed during experimental exposures of killer (*Orcinus orca*), long-finned pilot (*Globicephala melas*), and sperm (*Physeter macrocephalus*) whales to naval sonar. *Aquatic Mammals* 38: 362–401. https://doi.org/10.1578/am.38.4.2012.362.

Mitchell E, Reeves RR (1988) Records of killer whales in the western North Atlantic, with emphasis on eastern Canadian waters. *Rit Fiskideildar* 11: 161–193.

Moore SE, Francine JK, Bowles AE, Ford JKB (1988) Analysis of calls of killer whales, *Orcinus orca*, from Iceland and Norway. *Rit Fiskideildar* 11: 225–250.

Morin PA, Archer FI, Foote AD, Vilstrup J, Allen EE, Wade P et al. (2010) Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. *Genome Research* 20: 908–916. https://doi.org/10.1101/gr.102954.109.

Mullin KD, Fulling GL (2003) Abundance of cetaceans in the southern US North Atlantic Ocean during summer 1998. *Fishery Bulletin* 101: 603–613.

NAMMCO (1993) Report of the scientific committee working group on northern bottlenose and killer whales NAMMCO-SC2/Report - Appendix 8, SC-WG/NBK1/Report.

NAMMCO (2005) Report of the 12th meeting of the NAMMCO scientific committee. NAMMCO/14/5.

NAMMCO (2017) Report of the 24th meeting of the NAMMCO scientific committee. NAMMCO SC/24/Report.

NAMMCO (2018) Report of the 25th scientific committee meeting 13–16 November, Norway.

Naval Aviation News (1956) Killer whales destroyed. *Naval Aviation News,* 00-75R-3: 19.

Nielsen J (2011) Photo-id of killer whales (*Orcinus orca*) in Greenland waters. http://descna.Com/images/knowledge_base/egne_artikler/photoid%20killer%20whale.Pdf.

Nøttestad L, Krafft BA, Anthonypillai V, Bernasconi M, Langård L, Mørk HL, Fernö A (2015). *Frontiers in Ecology and Evolution* 2 (83). https://doi.org/10.3389/fevo.2014.00083.

Nøttestad L, Sivle LD, Krafft BA, Langard L, Anthonypillai V, Bernasconi M, Langoy H, Ferno A (2014) Prey selection of offshore killer whales *Orcinus orca* in the northeast Atlantic in late summer: spatial associations with mackerel. *Marine Ecology Progress Series* 499: 275–283. https://doi.org/10.3354/meps10638.

Øien N (1988) The distribution of killer whales (*Orcinus orca*) in the North Atlantic based on Norwegian catches, 1938-1981, and incidental sightings, 1967-1987. *Rit Fiskideildar* 11: 65–78.

Øien N (1990) Sightings surveys in the northeast Atlantic in July 1988: distribution and abundance of cetaceans. *Report of the International Whaling Commission* 40: 499–511.

Øien N (1993) Abundance of killer whales (*Orcinus orca*) in waters off Norway. *Working Paper* SC-WG/NBK1/4.

Olesiuk PF, Ellis GM, Ford JKB (2005) Life history and population dynamics of northern resident killer whales (*Orcinus orca*) in British Columbia. CSAS Research Document 2005/045. Fisheries and Oceans Canada, Nanaimo, Canada.

Óskarsson GJ (2018) The existence and population connectivity of Icelandic spring-spawning herring over a 50-year collapse period. *Ices Journal of Marine Science* 75: 2025–2032. https://doi.org/10.1093/icesjms/fsy120.

Pedro S, Boba C, Dietz R, Sonne C, Rosing-Asvid A, Hansen M, Provatas A, McKinney MA (2017) Blubber-depth distribution and bioaccumulation of PCBs and organochlorine pesticides in Arctic-invading killer whales. *Science of the Total Environment* 601–602: 237–246. https://doi.org/10.1016/j.scitotenv.2017.05.193.

Pike DG, Paxton CG, Gunnlaugsson T, Víkingsson GA (2009) Trends in the distribution and abundance of cetaceans from aerial surveys in Icelandic coastal waters, 1986-2001. *NAMMCO Scientific Publications*: 117–142.

Pinfield R, Enright J, McCarthy A, Rogan E (2012) Interactions between killer whales *(Orcinus orca)* and the Irish pelagic trawl fisheries during the winter 2010/2011 fishing season. 26th Annual Conference of the European Cetacean Society, Galway, Ireland.

Pitman RL, Ensor P (2003) Three forms of killer whales in Antarctic waters. *Journal of Cetacean Research and Management* 5: 131–139.

Poncelet E, Barbraud C, Guinet C (2010) Population dynamics of killer whales (*Orcinus orca*) in the Crozet Archipelago, southern Indian Ocean: a mark–recapture study from 1977 to 2002. *Journal of Cetacean Research and Management* 11: 41–48.

Reeves RR, Mitchell E (1988a) Distribution and seasonality of killer whales in the Eastern Canadian Arctic. *Rit Fiskideildar* 11: 136–160.

Reeves RR, Mitchell E (1988b) Killer whale sightings and takes by American pelagic whalers in the North Atlantic. *Rit Fiskideildar* 11: 7–23.

Reeves RR, Perrin WF, Taylor BL, Baker CS, Mesnick SL (2004) Report of the workshop on shortcomings of cetacean taxonomy in relation to needs of conservation and management, April 30–May 2, 2004, La Jolla, California. NOAA-TM-NMFS-SWFSC-363.

Reeves R, Pitman RL, Ford JKB (2017) *Orcinus orca*. The IUCN Red List of Threatened Species 2017: e.T15421A50368125. http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T15421A50368125.en.

Robinson KP, Bamford CCG, Airey A, Bean TS, Bird C, Haskins GN, Sim TMC, Evans PGH (2017) Killer whale (*Orcinus orca*) occurrence in the Moray Firth, Northeast Scotland: incidental sightings, behavioural observations, and photo-identification. *Aquatic Mammals* 43: 26–32. https://doi.org/10.1578/AM.43.1.2017.26.

Samarra FIP (2015) Variations in killer whale food-associated calls produced during different prey behavioural contexts. *Behavioural Processes* 116: 33–42. https://doi.org/10.1016/j.beproc.2015.04.013.

Samarra FIP, Bassoi M, Beesau J, Eliasdottir MO, Gunnarsson K, Mrusczok MT et al. (2018) Prey of killer whales (*Orcinus orca*) in Iceland. *Plos One* 13: e0207287. https://doi.org/10.1371/journal.pone.0207287.

Samarra FIP, Deecke VB, Miller PJO (2016) Low-frequency signals produced by northeast Atlantic killer whales (*Orcinus orca*). *Journal of the Acoustical Society of America* 139: 1149–1157. https://doi.org/10.1121/1.4943555.

Samarra FIP, Foote AD (2015) Seasonal movements of killer whales between Iceland and Scotland. *Aquatic Biology* 24: 75–79. https://doi.org/10.3354/ab00637.

Samarra FIP, Miller PJO (2015) Prey-induced behavioural plasticity of herring-eating killer whales. *Marine Biology* 162: 809–821. https://doi.org/10.1007/s00227-015-2626-8.

Samarra FIP, Miller PJO (2016) Identifying variations in baseline behavior of killer whales (*Orcinus orca*) to contextualize their responses to anthropogenic noise. In: Popper AN, Hawkins A (eds) *Effects of Noise on Aquatic Life ii*, 963–968. Springer Science+Business Media, New York, USA.

Samarra FIP, Tavares SB, Beesau J, Deecke VB, Fennell A, Miller PJO, Petursson H, Sigurjonsson J, Vikingsson GA (2017a) Movements and site fidelity of killer whales (*Orcinus orca*) relative to seasonal and long-term shifts in herring (*Clupea harengus*) distribution. *Marine Biology* 164: https://doi.org/10.1007/s00227-017-3187-9.

Samarra FIP, Tavares SB, Miller PJO, Vikingsson GA (2017b) Killer whales of Iceland 2006–2015. HV 2017-005, Report of the Marine and Freshwater Research in Iceland.

Samarra FIP, Vighi M, Aguilar A, Vikingsson GA (2017c) Intra-population variation in isotopic niche in herring-eating killer whales off iceland. *Marine Ecology Progress Series* 564: 199–210. https://doi.org/10.3354/meps11998.

Sergeant DE, Fisher HD (1957) The smaller cetacea of eastern Canadian waters. *Journal of the Fisheries Research Board of Canada* 14: 83–115. https://doi.org/10.1139/f57-003.

Sigurjonsson J, Leatherwood S (1988) The Icelandic live-capture fishery for killer whales, 1976-1988. *Rit Fiskideildar* 11: 307–316.

Sigurjónsson J, Leatherwood S (eds; 1988) North Atlantic killer whales. Rit Fiskideildar vol. XI, Marine Research Institute, Reykjavik, Iceland, 317 pp.

Sigurjónsson J, Lyrholm T, Leatherwood S, Jonsson E, Vikingsson G (1988) Photoidentification of killer whales, *Orcinus orca*, off Iceland, 1981 through 1986. *Rit Fiskideildar* 11: 99–114.

Silva MA, Prieto R, Cascao I, Seabra MI, Machete M, Baumgartner MF, Santos RS (2014) Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Marine Biology Research* 10: 123–137. https://doi.org/10.1080/17451000.2013.793814.

Similä T (2005) Interactions between herring fishery and killer whales in northern Norway. International Council for the Exploration of the Sea. *CM* 2005/R: 03.

Similä T (2006) Satellite tracking study of movements and diving behaviour of killer whales in the Norwegian Sea. *Fourth International Orca Symposium and Workshops*, Sep 23–28, 2002, 134-135, CEBC-CNRS, France.

Similä T, Holst JC, Christensen I (1996) Occurrence and diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 769–779.

Simon M, McGregor PK, Ugarte F (2007a) The relationship between the acoustic behaviour and surface activity of killer whales (*Orcinus orca*) that feed on herring (*Clupea harengus*). *Acta Ethologica* 10: 47–53. https://doi.org/10.1007/s10211-007-0029-7.

Simon M, Ugarte F, Wahlberg M, Miller LA (2006) Icelandic killer whales *Orcinus orca* use a pulsed call suitable for manipulating the schooling behaviour of herring *Clupea harengus*. *Bioacoustics* 16: 57–74. https://doi.org/10.1080/09524622.2006.9753564.

Simon M, Wahlberg M, Miller LA (2007b) Echolocation clicks from killer whales (*Orcinus orca*) feeding on herring (*Clupea harengus*) (l). *Journal of the Acoustical Society of America* 121: 749–752. https://doi.org/10.1121/1.2404922.

Simon M, Wahlberg M, Ugarte F, Miller LA (2005) Acoustic characteristics of underwater tail slaps used by Norwegian and Icelandic killer whales (*Orcinus orca*) to debilitate herring (*Clupea harengus*). *Journal of Experimental Biology* 208: 2459–2466. https://doi.org/10.1242/jeb.01619.

Storrie L, Lydersen C, Andersen M, Wynn RB, Kovacs KM (2018) Determining the species assemblage and habitat use of cetaceans in the Svalbard archipelago, based on observations from 2002 to 2014. *Polar Research* 37: 1463065. https://doi.org/10.1080/17518369.2018.1463065.

Strager H (1995) Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca* Linnaeus, 1758, in the waters of northern Norway. *Canadian Journal of Zoology* 73: 1037–1044.

Tavares SB, Samarra FIP, Pascoal S, Graves JA, Miller PJO (2018) Killer whales (*Orcinus orca*) in Iceland show weak genetic structure among diverse isotopic signatures and observed movement patterns. *Ecology and Evolution* 1–14: https://doi.org/10.1002/ece3.4646.

Ugarte F, Simon M, Laidre K (2013) Recent increase of catches of killer whales in southeast Greenland - is there a need for NAMMCO advise? NAMMCO SC/20/20. *Rosing-Asvid A*.

Van Opzeeland IC, Corkeron PJ, Leyssen T, Similä T, Van Parijs SM (2005) Acoustic behaviour of Norwegian killer whales, *Orcinus orca*, during carousel and seiner foraging on spring-spawning herring. *Aquatic Mammals* 31: 110–119. https://doi.org/10.1578/am.31.1.2005.110.

Van Parijs SM, Leyssen T, Similä T (2004) Sounds produced by Norwegian killer whales, *Orcinus orca*, during capture. *Journal of the Acoustical Society of America* 116: 557–560. https://doi.org/10.1121/1.1763954.

Vikingsson GA (2004) Háhyrningur. In: Hersteinsson P (ed) *Islensk spendýr*, 150–153. Vaka-Helgafell, Reykjavik, Iceland.

Vongraven D, Bisther A (2014) Prey switching by killer whales in the north-east Atlantic: observational evidence and experimental insights. *Journal of the Marine Biological*

Association of the United Kingdom 94: 1357–1365. https://doi.org/10.1017/s0025315413001707.

Ward EJ, Holmes EE, Balcomb KC (2009) Quantifying the effects of prey abundance on killer whale reproduction. *Journal of Applied Ecology* 46: 632–640. https://doi.org/10.1111/j.1365-2664.2009.01647.x.

Weir CR (2002) Killer whales (*Orcinus orca*) in UK waters. *British Wildlife* 14: 106–108.

Westdal KH, Davies J, MacPherson A, Orr J, Ferguson SH (2016) Behavioural changes in belugas (*Delphinapterus leucas*) during a killer whale (*Orcinus orca*) attack in southwest Hudson Bay. *Canadian Field-Naturalist* 130: 315–319. https://doi.org/10.22621/cfn.v130i4.1925.

Westdal KH, Higdon JW, Ferguson SH (2013) Attitudes of Nunavut Inuit toward killer whales (*Orcinus orca*). *Arctic* 66: 279–290. https://doi.org/10.14430/arctic4307.

Westdal KH, Higdon JW, Ferguson SH (2017) Review of killer whale (*Orcinus orca*) ice entrapments and ice-related mortality events in the northern hemisphere. *Polar Biology* 40: 1467–1473. https://doi.org/10.1007/s00300-016-2019-6.

Williams R, Lusseau D, Hammond PS (2006) Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biological Conservation* 133: 301–311. https://doi.org/10.1016/j.biocon.2006.06.010.

Wolkers H, Corkeron PJ, van Parijs SM, Similä T, van Bavel B (2007) Accumulation and transfer of contaminants in killer whales (*Orcinus orca*) from Norway: indications for contaminant metabolism. *Environmental Toxicology and Chemistry* 26: 1582–1590. https://doi.org/10.1897/06-455r1.1.

Young BG, Higdon JW, Ferguson SH (2011) Killer whale (*Orcinus orca*) photo-identification in the eastern Canadian Arctic. *Polar Research* 30: 7203. https://doi.org/10.3402/polar.v30i0.7203.