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FOREWORD

North Atlantic killer whale research; past, present and future

ANDREW D. FOOTE[1], SANNA KUNINGAS[2] AND FILIPA I.P. SAMARRA[2,3]

[1]Centre for GeoGenetics, Natural History Museum of Denmark, University of Copenhagen, Øster Volgade 5-7, DK-1350 Copenhagen, Denmark, [2]Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, UK, [3]Marine Research Institute, Skulagata 4, PO Box 1390, 121 Reykjavík, Iceland

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INTRODUCTION

Studying wide-ranging top predators requires a multidisciplinary and transnational approach to efficiently identify population structure, movement patterns, ecology and population parameters for effective monitoring and conservation of the populations. A recent workshop was held at the European Cetacean Society Conference, Galway Ireland, on 25 March 2012, on one of the most wide-ranging of top predators in the North Atlantic, the killer whale *Orcinus orca*. The workshop had as its main aims, to summarize the current state of knowledge, strengthen cooperation by evaluating the potential to share data and combine field efforts, and discuss the advances to date and future priorities for killer whale research in the North Atlantic. A selection of the presentations from this workshop is included within this special section as well as other contributions that contain relevant information on the status of killer whale research in this broad geographical area. In this Foreword, whilst not attempting to thoroughly review all published work to date, we look back at progress made on understanding the ecology and biology of North Atlantic killer whales, and based on the discussions held at the workshop suggest pressing research questions for the future, in particular highlighting how new methodologies can build upon existing work.

TWENTY-FIVE YEARS OF PROGRESS

The 2012 North Atlantic killer whale workshop marked the 25th anniversary of a previous workshop on this topic held in Provincetown, MA, USA. At this time, research on killer whales in the waters of British Columbia, Canada and Washington state, USA had made substantial progress. This was largely due to the pioneering work by the late Dr Michael Bigg, who developed the use of photographs of the dorsal fin and saddle patches to identify individuals, allowing for the first time an annual census and the subsequent analyses of population dynamics, insights into social structure, life history and analyses of site fidelity and movement (Bigg, 1982; Bigg *et al*., 1987, 1990; Olesiuk *et al*., 1990). Dr John Ford, was also reporting the first evidence of a complex pattern of group and population specific call dialects in North Pacific killer whales (Ford & Fisher, 1982, 1983). Inspired by this progress of studies in Pacific waters, the aims of the North Atlantic killer whale workshop in 1987 were to see if by building collaborations between researchers and critically reviewing existing data they could provide a synthesis that would describe distribution, movement, numbers, population structure and ecology of killer whales in the North Atlantic.

Many of the studies presented at the 1987 workshop were published in a special issue of the journal of the Marine Research Institute, Reykjavík, the *Rit Fiskideildar* (Sigurjónsson & Leatherwood, 1988). The majority of these early studies were preliminary investigations of the distribution of killer whales in North Atlantic waters based on sighting data, whaling catch statistics or stranding data (e.g. Christensen, 1988; Evans, 1988; Hammond & Lockyer, 1988; Øien, 1988). Whilst subject to the biases of occurrence data uncorrected for effort, these reviews identified potential hotspots and seasonality in occurrence and therefore provided the foundations, which subsequent dedicated research could build upon. They also identified some of the major prey resources that killer whales appeared to be tracking in the North Atlantic, which included the Icelandic summer-spawning (ISS) and Norwegian spring-spawning (NSS) stocks of Atlantic herring (*Clupea harengus*) (Christensen, 1988; Øien, 1988; Sigurjónsson *et al*., 1988).

INSIGHTS FROM PHOTO-IDENTIFICATION

At the time of the 1987 workshop, Thomas Lyrholm and colleagues had initiated the first photo-identification studies of

Corresponding author:
A.D. Foote
Email: footead@gmail.com

killer whales in Norwegian and Icelandic waters. Lyrholm (1988) photographically recaptured a small number of naturally marked individual killer whales between years on the NSS herring wintering grounds in the Lofoten region of Northern Norway, and between Lofoten and the spawning grounds of the NSS herring in the Möre region of Southern Norway. In subsequent years, Dr Tiu Similä and colleagues have built upon this earlier work and expanded the photo-identification catalogue to include close to 600 individuals. They have further demonstrated the association between the movement and site fidelity of killer whales and the migration of the NSS herring stock (Similä *et al.*, 1996). By 1987, Sigurjónsson *et al.* (1988) had also photographically recaptured individuals between years on the wintering grounds of the ISS stock of Atlantic herring. Further work carried out by the Marine Research Institute, Reykjavík and others, has found that killer whale groups are also associated with, and to some extent follow the ISS herring stock (Sigurjónsson *et al.*, 1988; Foote *et al.*, 2010; Samarra *et al.*, 2012). Killer whales were later also reported feeding on the North Sea stock of Atlantic herring, off the coast of Shetland (Deecke *et al.*, 2011), although in much smaller aggregations. Over 1000 individual killer whales have now been photo-identified across the north-east Atlantic and collaboration among institutions has allowed comparisons of photo-identification catalogues over greater spatial and temporal scales. A general pattern is emerging of site fidelity and association with a particular prey resource at several locations across the north-east Atlantic (Foote *et al.*, 2010). However, some groups may switch between different prey resources depending on their seasonal availability (Foote *et al.*, 2010; Vester & Hammerschmidt, 2013; Vongraven & Bisther, 2014).

Photo-identification studies in some areas of the North Atlantic arguably face greater logistical challenges than those faced by colleagues working during the summer months in the relatively sheltered nearshore waters of British Columbia and Washington State. The densest occurrences of North Atlantic killer whales during the 1980s and 1990s were in the fjords of the Lofoten region of northern Norway and off eastern Iceland where the NSS and ISS herring stocks over-wintered. During winter, at these high latitudes, there are few hours of daylight in which photography could successfully capture the scars and nicks on the saddle patch and dorsal fin of killer whales necessary to identify them. Additionally, the sheer numbers of killer whales aggregated on the herring wintering grounds meant that only a proportion of them could be photo-identified within a season, in contrast to the almost complete annual census of all individuals being conducted on some Pacific killer whale populations. However, by applying mark–recapture models that account for the potential biases in such a dataset, a study presented in this special section has been able to use the long-term photo-identification dataset from northern Norway to estimate population size, survival and reproductive rates and compare these parameters with populations in the North Pacific and a population from the Crozet Archipelago in the southern Indian Ocean (Kuningas *et al.*, 2014). Similarly, off Iceland, distance-sampling methods were used across a large survey area, which also estimated large numbers of killer whales in these waters (Gunnlaugsson & Sigurjónsson, 1989; Sigurjónsson *et al.*, 1991).

INSIGHTS FROM BEHAVIOURAL STUDIES

These logistical difficulties meant that the research on Norwegian killer whales to some extent shifted focus during the 1990s to the behavioural techniques used by the killer whales when foraging for herring. Arguably for the first time, the North Atlantic researchers became the pioneers of new approaches to study killer whales. Dr Tiu Similä and colleagues used underwater cameras and sonar, multi-hydrophone arrays and custom-built multi-sensor acoustic tags to record the movement and behaviour of killer whales during what has become known as carousel feeding (Similä & Ugarte, 1993; Similä, 1997; Nøttestad & Axelsen, 1999; Simon *et al.*, 2005; Shapiro, 2008). During carousel feeding the killer whales appear to work as a coordinated group, encircling a ball of herring whilst flashing their white undersides and releasing bubbles to herd a ball of herring from the school before tail slapping the ball to stun and then eat individual herring (Similä & Ugarte, 1993).

INSIGHTS FROM ACOUSTIC RECORDINGS

It is during feeding on herring that killer whales in the waters of Norway, Iceland and Shetland are most vocally active (van Opzeeland *et al.*, 2005; Simon *et al.*, 2007; Deecke *et al.*, 2011). Killer whales feeding on herring off Iceland and Shetland produce a distinctive low frequency pulsed call just prior to tail slapping the herring (Simon *et al.*, 2006; Deecke *et al.*, 2011). The low frequency of the call may resonate the herring's swim bladder and therefore help herd the herring (Simon *et al.*, 2006). This 'herding' call has not been recorded off Norway to date. However, distinctive ultrasonic whistles have been recorded from killer whales feeding on herring around Iceland, Shetland and Norway (Samarra *et al.*, 2010a). These recent findings on the acoustic behaviour build on earlier work published in the *Rit Fiskideildar* special issue (Sigurjónsson & Leatherwood, 1988). Those early studies provided the first descriptions of Norwegian and Icelandic killer whale call repertoires and found preliminary evidence of group-specific repertoires, but only tentative evidence for some call sharing between Iceland and Norway (Moore *et al.*, 1988; Strager, 1995). Since then, considerably larger acoustic datasets have been gathered and work is currently underway to conduct a broader geographical comparison of the call repertoire of north-east Atlantic killer whales (Samarra, Deecke and Miller, unpublished data).

INSIGHTS FROM GENETIC DATA

Further light has been shed on the relationship between Icelandic and Norwegian herring-eating killer whales by genetic investigations. Early genetic studies typically used DNA from captive Icelandic killer whales as outgroups for studies focused on North Pacific killer whales (e.g. Stevens *et al.*, 1989). Only recently, have studies used larger sample sizes from across the North Atlantic using both mitochondrial and nuclear genetic markers. Allele frequencies of 17 polymorphic microsatellite loci indicated individuals from the Norwegian and Icelandic herring grounds were a single panmictic population; however, there was significant differentiation between the two regions based on mitochondrial DNA (Foote *et al.*, 2011). Stable isotope ratios differed significantly between Icelandic and Norwegian killer whales assigned to this panmictic population, suggesting some differences in ecology, such as spatial distribution or trophic position (Foote *et al.*, 2012). A synthesis of these investigations highlights the benefits of a multi-disciplinary approach, especially when different markers give a signal of differentiation or connectivity over different timescales. The emerging picture, based on multiple markers (e.g. acoustic, genetic, isotope and photographic markers), is that the killer whales that forage for herring around Iceland, Shetland and Norway originate from a recent common ancestral lineage, which diverged to follow different stocks of Atlantic herring, but that male-mediated gene flow still occurs among killer whale lineages when these herring stocks spatially and temporally overlap (Foote *et al.*, 2011).

Genetic studies have also provided evidence of recent trans-oceanic and trans-equatorial migration, with mitogenome haplotypes that cluster with the North Pacific 'offshore' ecotype being found off Newfoundland and haplotypes related to Antarctic 'type A' killer whales found off the coasts of Scotland, the Gulf of Mexico, and the Canary Islands (Morin *et al.*, 2010; Foote *et al.*, 2011).

OPPORTUNISTIC RESEARCH

While the predictable seasonal aggregations close to shore in some parts of the north-east Atlantic have enabled dedicated fieldwork and the set-up of long-term studies, in other parts of the North Atlantic sightings are sparse and sporadic and a more opportunistic approach to data collection is often required. Reeves & Mitchell (1988a) identified areas across the North Atlantic where killer whale sightings and takes by American pelagic whalers were high. Many localized studies are now conducted on a variety of cetaceans within the pelagic waters of this region, e.g. the Azores, the Canary Islands, Strait of Gibraltar, West Africa, Bahamas and Caribbean, and local researchers collect data on killer whales when they encounter them (Weir *et al.*, 2010; Dunn & Claridge, 2014; Esteban *et al.*, 2014). Photo-identification data and even the first biopsy samples are being collected across the mid-Atlantic. Several groups conducting these studies were present at the 2012 Galway workshop and presented their sightings data. The workshop provided a platform for them to form a working group and share photo-identification data to facilitate matching between study sites. Many of the killer whales photographed in the mid-Atlantic have distinctive cookie cutter shark (*Isistius brasiliensis*) bite marks on the dorsal fin and saddle patch and *Xenobalanus* barnacles trailing from the dorsal fin. Given that cookie cutter sharks and *Xenobalanus* barnacles are warm water species and neither shark bites nor barnacles have been reported on whales north of the Iberian Peninsula suggests there may be groups resident in the lower latitude waters of the North Atlantic. An interesting study on killer whales in the Bahamas presents a valuable long-term data set of observations suggesting some localized site fidelity and even foraging preferences (Dunn & Claridge, 2014). Populations in more northerly pelagic waters are also becoming accessible for behavioural observations, photo-identification and even biopsy sampling due to increased collaboration with the pelagic fishing industry and the use of these opportunistic platforms for research (Luque *et al.*, 2006; Foote *et al.*, 2010, 2011).

THE NORTH-WEST ATLANTIC AND CANADIAN ARCTIC

Whilst studies of the north-west Atlantic and Canadian Arctic were well represented in the 1988 special issue of the *Rit Fiskideildar* on North Atlantic killer whales (Lien *et al.*, 1988; Mitchell & Reeves, 1988; Reeves & Mitchell, 1988b), subsequent research in these waters lagged behind the progress made in the north-east Atlantic until the relatively recent work by Steve Ferguson and colleagues. They have employed the use of tried and tested methods, in addition to developing novel and highly innovative approaches to investigate the ecology of killer whales in the rapidly changing ecosystem of the Canadian Arctic (e.g. Higdon *et al.*, 2014). As global temperatures rise and the Arctic sea ice retreats, many former 'choke points' are opening up and allowing killer whales to enter the bays and inlets of the Canadian Arctic; resulting in a significant increase in recent sightings (Higdon & Ferguson, 2009). Interviews with local Inuit hunters suggest that marine mammals are the main prey of killer whales in the Canadian Arctic (Ferguson *et al.*, 2012; Higdon *et al.*, 2014). Killer whales are known to be able to have a population level effect on prey populations due to top down effects, and therefore have the potential to significantly shape this rapidly changing Arctic ecosystem (Higdon & Ferguson, 2009; Higdon *et al.*, 2014). An important question that needs to be addressed to better understand the potential impact of killer whale predation is how persistent it is over time. Satellite tracks of a tagged killer whale found that it moved between areas with known aggregations of marine mammals before heading out in to the open North Atlantic in late autumn as the sea ice increased in concentration in the inlets (Matthews *et al.*, 2011). Therefore, predation on Arctic marine mammals may be seasonal; in this special issue, Matthews and colleagues shed further light on the diet of Canadian Arctic killer whales using stable isotope from tooth growth layer groups which suggest individuals in this region may be associated with different food webs (Matthews & Ferguson, 2014). This special section also contains the first in-depth review of killer whale ecology in the north-west Atlantic for 25 years (Lawson & Stevens, 2014), and some useful clues that humpback whale *Megaptera novaeangliae* calves may be more regularly on the menu of killer whales in the north-west than in the north-east Atlantic (McCordic *et al.*, 2014).

DATA SHARING AND COLLABORATIVE MULTI-DISCIPLINARY RESEARCH

This brief summary of the past 25 years of research on North Atlantic killer whales shows how much has been learned about these animals, despite the logistical difficulties in studying them (Figure 1; Table 1). In many cases the success of the research hinged on multi-national and institutional collaborations and data sharing. As noted above, one of the aims of the

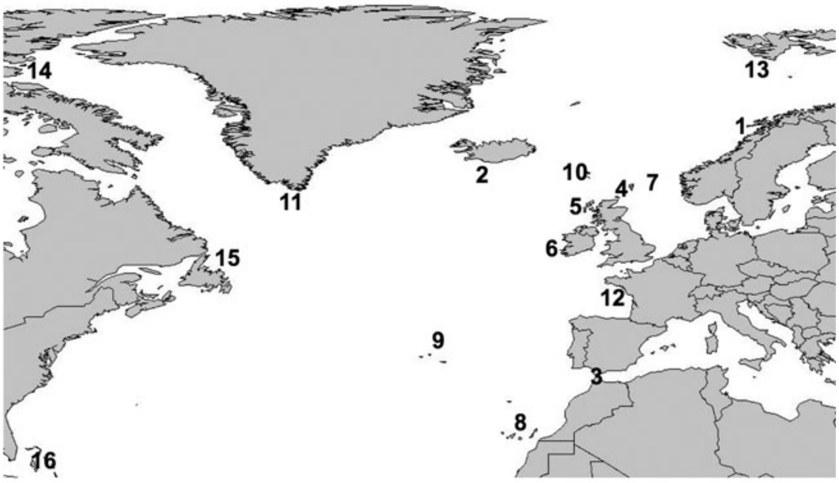

Fig. 1. Locations of dedicated and opportunistic research conducted on North Atlantic killer whales. Further details are given in Table 1.

North Atlantic killer whale workshop in Galway 2012, was to facilitate the sharing of data and build upon existing collaborations. Initial efforts on sharing of data had begun with the creation of a North Atlantic Killer Whale ID Project, however this was still limited to only partial datasets from a few areas in the north-east Atlantic. In this digital age it is much easier to store, copy and share photographic images and sound recordings. It also facilitates the use of opportunistic data collection, for example the use of photographs collected by members of the public (Beck *et al.*, 2014) and we anticipate an increase in this so-called 'Citizen Science' (Tweddle *et al.*, 2012) as a monitoring tool for killer whales. We strongly recommend digitization of past photographic and acoustic data and that this should be archived at a suitable institute or online database. Similarly, genetic data should be stored on publicly accessible databases such as GenBank and the National Science Foundation-sponsored Dryad archive at http://datadryad.org (Whitlock *et al.*, 2010). This ensures that data remain available after the initial study is complete.

The effectiveness of these large shared datasets was recently demonstrated in an unusual scenario, when a young killer whale became stranded off the coast of The Netherlands. No photo-identification matches were made, but sequencing of informative regions of the mitochondrial genome suggested that the whale belonged to the lineages that follow the NSS herring. This was then further supported by the matching of several stereotyped call types produced by the whale and those recorded by groups feeding on herring in northern Norway (Samarra *et al.*, 2010b). Whilst the completeness of photo-identification, genetic and acoustic repertoire sampling of North Atlantic killer whales still lags behind the North Pacific, this case study demonstrates that it has come a remarkably long way in the past 25 years. The data collected over the past 25 years also provide important insights into conservation priorities at the population level. The different markers (e.g. photo-identification, acoustics, genetics, morphology and stable isotopes) provide a basis for delineating 'management units', i.e. populations that are demographically isolated and so population size depends upon births and deaths rather than immigration (e.g. Beck *et al.*, 2014; Kuningas *et al.*, 2014). The long-term and ongoing collection of photo-identification data then allows us to quantify these population parameters within each management unit (e.g. Kuningas *et al.*, 2014) and to detect trends such as declines (e.g. Beck *et al.*, 2014). Lastly, the behavioural and dietary studies allow us to better understand the ecology of each population and therefore better determine which population-level threats they might be exposed to. A good example of this is the IUCN-listed threatened population of killer whales in the Strait of Gibraltar (Cañadas & de Stephanis, 2006). Over a decade of dedicated research by the organization CIRCE has identified a population decline concurrent with a decrease in the blue fin tuna (*Thunnus thynnus*) stock, which they have also identified as the killer whale population's main prey resource (Esteban-Pavo, 2008). The threatened status of the killer whale population in the Strait of Gibraltar was discussed during the 2012 workshop and conservation measures recommended by CIRCE were endorsed by the workshop attendees.

ANTICIPATED PROGRESS DURING THE NEXT 25 YEARS?

We look forward with eager anticipation to the next 25 years of research on North Atlantic killer whales. We predict that the recent methodological advances in DNA sequencing technology, which have already been harnessed to sequence a dataset of complete mitochondrial genomes for North Atlantic killer whales (Morin *et al.*, 2010; Foote *et al.*, 2011), will be further applied to produce a complementary nuclear genomic dataset. The first high coverage marine mammal genomes have now been sequenced and the data made publicly available and these include a North Atlantic killer whale. This genomic data will allow the comparisons of natural selection upon the genome among populations. The large acoustic datasets that have been collected for the past 25 years have allowed us to better understand the acoustic behaviour of north-east Atlantic killer whales. We anticipate that work currently undertaken will allow for broader geographical comparisons as well as better understanding of the function of different signals, such as the still little understood high-frequency whistles. In addition, recent projects deploying state-of-the-art multi-sensor tags in different locations in the north-east Atlantic promise to allow for detailed comparisons of behavioural parameters. We

Table 1. Description of studies conducted on North Atlantic killer whales by location. The table includes the nature of the study, type of data collected, duration of data collection and example publications arising from each location. Sampling locations ('Map Point') refer to Figure 1. This list is by no means exhaustive. References: 1. Christensen (1988); 2. Lyrholm (1988); 3. Øien, (1988); 4. Similä & Ugarte (1993); 5. Strager (1995); 6. Similä *et al.* (1996); 7. Similä (1997); 8. Kuningas *et al.* (2014); 9. Moore *et al.* (1988); 10. Sigurjónsson *et al.* (1988); 11. Simon *et al.* (2006); 12. Samarra *et al.* (2010a); 13. Hoelzel *et al.* (2002); 14. Cañadas & de Stephanis (2006); 15. Esteban-Pavo (2008); 16. Esteban *et al.* (2014); 17. Bolt *et al.* (2009); 18. Foote *et al.* (2010); 19. Deecke *et al.* (2011); 20. Beck *et al.* (2012); 21. Beck *et al.* (2014); 22. Reid *et al.* (2003); 23. Luque *et al.* (2006); 24. Foote *et al.* (2011); 25. Bloch & Lockyer (1988); 26. Heide-Jørgensen (1988); 27. Hammond & Lockyer (1988); 28. Lien *et al.* (1988); 29. Mitchell & Reeves (1988); 30. Reeves & Mitchell (1988b); 31. Higdon & Ferguson (2009); 32. Matthews *et al.* (2011); 33. Ferguson *et al.* (2012); 34. Higdon *et al.* (2014); 35. Matthews & Ferguson (2014); 36. Lawson & Stevens (2014); 37. Dunn & Claridge (2014).

Map point	Location	Type of study	Photo-ID	Genetic sampling	Dietary sampling	Satellite tagging	Acoustics recording	Sightings reports	Duration	Example publications
1	NSS herring grounds	Dedicated	x	x	x	x	x	x	1980s–present	1–8
2	ISS herring grounds	Dedicated	x	x	x		x		1980s–present	9–13
3	The Strait of Gibraltar	Dedicated	x	x	x	x	x	x	2000s–present	14–16
4	Caithness, Orkney and Shetland (north-east Scotland)	Dedicated/opportunistic	x	x	x		x	x	2000s–present	17–20
5	The Hebrides (west Scotland)	Opportunistic	x					x	1990s–present	18, 21
6	Ireland	Opportunistic	x					x	1990s–present	22
7	The North Sea	Dedicated/opportunistic	x	x					1990s–present	18, 22–24
8	The Canary Islands	Opportunistic	x	x	x		x		2000s–present	24
9	The Azores	Opportunistic	x						2000s–present	
10	The Faroe Islands	Opportunistic	x					x	1980s–present	25
11	Greenland	Opportunistic	x	x	x			x	1980s–present	26
12	The Bay of Biscay	Opportunistic	x	x				x	1980s–present	27
13	Svalbard, Bering Sea	Opportunistic	x					x		
14	The Canadian Arctic	Dedicated/opportunistic	x	x	x	x		x	2000s–present	28–35
15	Labrador and Newfoundland	Dedicated/opportunistic	x					x		28,36
16	The Bahamas	Opportunistic	x					x	2000s–present	37

expect that together these developments will improve our understanding of the biology, behaviour and ecology of killer whales in the North Atlantic.

Finally, the past 25 years have seen global temperatures rise, including in the North Atlantic (Lyman *et al.*, 2010), and these changes have had biological consequences across a range of taxa (Hughes, 2000). As noted above, diminishing sea ice has led to a significant increase in killer whale sightings in the Canadian Arctic during this period. There have also been natural shifts in the distribution of prey resources, e.g. the NSS and ISS herring stocks and north-east Atlantic mackerel stock, and subsequently the killer whale lineages that follow them (Kuningas *et al.*, 2013). The next 25 years will likely lead to further and more rapid changes in climate, particularly in the Arctic as the sea ice melts (Screen & Simmonds, 2010). We therefore predict that the prey resources exploited by North Atlantic killer whales will shift their distribution and may undergo declines or increases as a result. Additionally, new prey resources may become available to North Atlantic killer whales. Although our understanding of killer whale ecology and evolution has come a long way in the last 25 years, there are still many gaps in our knowledge of the extent of geographical movements and consequently connectivity between different locations, the prey preferences and diet composition, the population viability and status of killer whales in different locations in the North Atlantic. Without such information it is impossible to completely critically assess the threats faced by killer whales in these locations and their conservation status. Collaboration between researchers and long-term consistent monitoring effort will be critical to effectively assess these issues. The ecosystems of the North Atlantic are likely to be highly dynamic during the next 25 years, and both North Atlantic killer whales and the researchers that investigate them will need to adapt to these ongoing changes and challenges.

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Correspondence should be addressed to:
A.D. Foote
Centre for GeoGenetics
Natural History Museum of Denmark
University of Copenhagen
Øster Volgade 5-7,
DK-1350 Copenhagen, Denmark
email: footead@gmail.com