ORIGINAL PAPER

Movement, site fidelity and connectivity in a top marine predator, the killer whale

Andrew D. Foote · Tiu Similä · Gísli A. Víkingsson · Peter T. Stevick

Abstract Movement, site fidelity and connectivity have important consequences for the evolution of population structure and therefore the conservation and management of a species. In this study photographs of naturally marked killer whales collected from sites across the Northeast Atlantic are used to estimate fidelity to sampling locations and movement between locations, expressed as transition probabilities, pt, using maximum likelihood methods. High transition probabilities suggest there is high inter-annual site fidelity to all locations, and large-scale movement between the spawning and wintering grounds of both Norwegian and Iceland stocks of Atlantic herring. There was no evidence of movement between the Norwegian herring grounds and Icelandic herring grounds, or between the mackerel fishing grounds and the herring fishing grounds. Thus the movement of predictable and abundant prey resources can lead to intrinsic isolation in this species We also find movement between the Northern Isles, Scotland and East Iceland. An association network indicates that killer whales predating seals around the Northern Isles, Scotland are linked to the community of killer whales that follow the Icelandic summer-spawning herring. This adds support to existing evidence of a broad niche width in some populations.

A. D. Foote (✉)
Institute of Biological and Environmental Sciences, University of Aberdeen, Lighthouse Field Station, Cromarty, Ross-shire IV11 8YJ, UK
e-mail: a.d.foote@abdn.ac.uk

T. Similä
Wild Idea, Box 181, 8465 Straumsjøen, Norway

G. A. Víkingsson
Marine Research Institute, Program for Whale Research, PO Box 1390, 121 Reykjavík, Iceland

P. T. Stevick
Hebridean Whale and Dolphin Trust, 28 Main Street, Tobermory, Isle of Mull PA75 6NU, UK

Introduction

Specialisation on a seasonally and spatially predictable prey resource can determine the movement patterns and site fidelity of, and connectivity between, predator populations (e.g. Musiani et al. 2007). The role of dispersal, movement and site fidelity in micro-evolutionary processes and their potential effect on population estimates makes them of great importance to the study of behavioral, conservation, evolutionary, and population ecology (e.g. Baker et al. 1990; Hestbeck et al. 1991; Palsbøll et al. 1995; Block et al. 2005; Bonfil et al. 2005; Shillinger et al. 2008).

Marine species are hindered by few extrinsic barriers to movement (Palumbi 1994, 2003), suffer a low energetic cost of movement (Tucker 1975; Williams et al. 1992; Williams 1999) and are known to travel large distances (Stone et al. 1990; Boustany et al. 2002; Block et al. 2005; Bonfil et al. 2005; Rasmussen et al. 2007; Shillinger et al. 2008). Yet molecular data on a large number of marine species indicate limited dispersal and provide evidence for intrinsic isolation (Palumbi 1994, 2003). Determinants of movement and site fidelity in marine species can include finding access to a suitable mate (Baker et al. 1990; Hendry et al. 2004) or breeding ground (Block et al. 2005; Rasmussen et al. 2007; Shillinger et al. 2008), or specialization on a seasonally and spatially predictable food resource (Palsbøll et al. 1995; Stevick et al. 2006).

Killer whales (*Orcinus orca*) are a cosmopolitan species found in all the world's oceans (Forney and Wade 2007). In high latitude areas with high levels of primary production, such as the North Pacific and Antarctica, killer whales appear to be foraging specialists (Ford et al. 1998; Pitman and Ensor 2003; Forney and Wade 2007). Foraging preference appears to have had a strong influence on the pattern of movement and population structure of this top marine predator in both the Antarctic and Pacific (Hoelzel et al. 2007; Andrews et al. 2008). Less is known about the movement, site fidelity and population linkages of North Atlantic killer whales. The most extensively studied population is found in waters around Norway (Stenersen and Similä 2004) and numbers ~1,000 individuals (Kuningas et al. 2007). Several methodological approaches have been utilized to study foraging behavior (Similä and Ugarte 1993; Similä 1997) and have identified the Norwegian spring-spawning (NSS) stock of Atlantic herring (*Clupea harengus*) as the main prey of this population. However, direct observation, stable isotope analysis and stomach contents indicate that individuals from this population also predate marine mammals and seabirds (Similä et al. 1996; Bisther and Vongraven 2001; Stenersen and Similä 2004; Foote et al. 2009). Satellite tagging of 6 individuals indicated they follow the migration of the NSS herring stock (Stenersen and Similä 2004). Systematic surveys during winter and summer months around the Lofoten and Vesterålen region of Northern Norway indicate that most pods are site faithful and re-sighted each year (Similä et al. 1996). Spring surveys in the NSS herring spawning grounds in the Møre region of Southern Norway (Bisther and Vongraven 1995) also re-identified individuals from the NSS herring wintering grounds in the North. There are no published studies using data on identified individuals from any other region of the Northeast Atlantic. Therefore, although it is known that killer whales are regularly seen feeding around trawlers in the northern North Sea (Luque et al. 2006), predating seals around the Northern Isles (Bolt et al. 2009) and feeding on herring around Iceland (Simon et al. 2007), we know nothing of the relationship among these groups of killer whales and movement among these sites.

Here we estimate the movement of naturally marked individual killer whales among locations across the Northeast Atlantic and the inter-annual site fidelity to these locations as transition probabilities using maximum likelihood methods (Hilborn 1990; Whitehead

2001; Stevick et al. 2006) and social network analysis (Scott 1988). Recent (40–45 years ago) dramatic shifts in fish stocks (e.g. Røttingen 1990; Jakobsson and Østvedt 1999) known to be prey of North Atlantic killer whales, e.g. the NSS and Icelandic summer-spawning (ISS) stocks of Atlantic herring (*Clupea harengus*), could lead to isolation of populations in a timescale not detectable by genetic analysis. Therefore contemporary movement data are a useful and complimentary tool to molecular techniques for identi-fying management units (Paetkau et al. 1999). We discuss our findings in terms of their broad implications for conservation and management of this wide ranging species and the potential drivers and evolutionary consequences of high site fidelity and limited dispersal.

Materials and methods

Study sites and data collection

Photo-identification data from across the Northeast Atlantic were collated as part of a collaborative study, the North Atlantic Killer Whale ID Project from the following loca-tions Vestmannaeyjar; East Iceland; the northern North Sea; Lofoten and Vesterålen; the Northern Isles and the Hebrides (Fig. 1).

Photo-identification data were collected around Iceland between 1981 and 2007. Around Iceland, killer whales are known to feed primarily on Atlantic herring (Sig-urjónsson et al. 1988; Simon et al. 2007), although there are also confirmed reports of killer whales predating seabirds, grey seals and a minke whale in this area (Víkingsson 2004). The Marine Research Institute (MRI), Reykjavík carried out dedicated killer whale photo-identification surveys in the wintering grounds of the ISS stock of Atlantic herring off the East coast of Iceland in October 1985 (see Lyrholm et al. 1987 for details) and around the entire coast in October–November 1986 (see Sigurjónsson et al. 1988 for details). During 1994–2000 the MRI also opportunistically collected photo-identification data in several
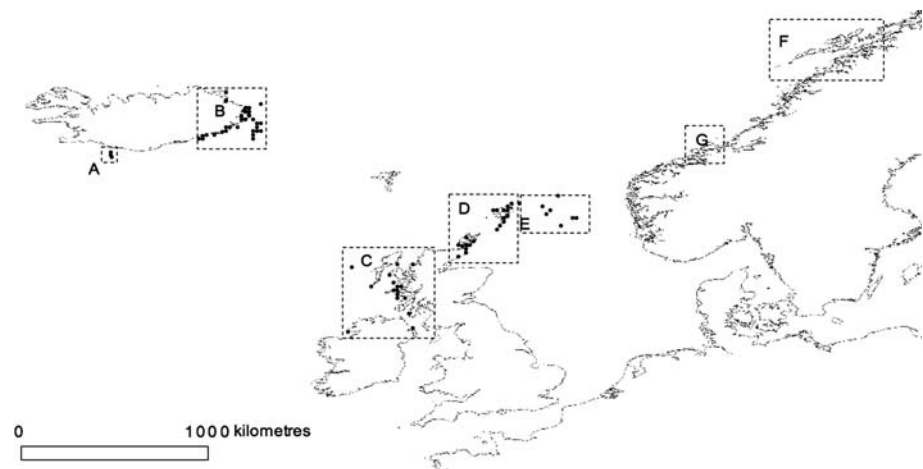
Fig. 1 Map of the Northeast Atlantic, showing the study locations and encounters (n = number of photographic encounters used in this study) *A* Vestmannaeyjar (n = 37); *B* East Iceland (n = 111); *C* the Hebrides (n = 33); *D* the Northern Isles (n = 64); *E* northern North Sea (n = 8); *F* Lofoten and Vesterålen; *G* Møre, Norway (see Similä et al. (1996) for details of Norwegian photo-identification encounters)

smaller scale surveys at the herring wintering grounds in autumn and during the summer around the island archipelago of Vestmannaeyjar, a summer-spawning ground of ISS herring. In addition the MRI collected photos in other non-killer whale focused research surveys between 1981 and 2006. Only left-side photographs were used in the MRI catalogue following the protocol of Bigg (1982). The Ocean Futures Society in collaboration with the MRI collected additional photo-identification data around the island archipelago of Vestmannaeyjar during the summer months of 2000, 2001 and 2002 (Simon et al. 2009). Lastly opportunistic photographs from Icelandic whale watching vessels and members of the public were also included for analysis.

Photo-identification data were collected between 1992 and 2008 around the west coast of Scotland by the Hebridean Whale and Dolphin Trust (HWDT) during dedicated boat-based cetacean surveys on the SV Silurian. HWDT also collected opportunistic photographs from the public and Scottish whale watching community through the establishment of a sightings network. Survey effort was limited to summer months and photographs from opportunistic encounters are also likely to be biased towards summer encounters when the weather is better and more recreational vessels are on the water.

Dedicated photo-identification work around Shetland was carried out during the summers of 2007–2008 and photographs from the Northern Isles and Pentland Firth taken between 1993 and 2008 were collected from the public. As above, there is likely to be a seasonal bias in opportunistic encounters. The occurrence of killer whales in this area is highly correlated with the harbor seal pupping season (Bolt et al. 2009) and observed predation events, group follows and collected prey remains suggest that the killer whales photo-identified in this area are predating frequently upon seals (Foote unpublished data).

Photo-identification in the northern North Sea, ten kilometers or more offshore of Shetland, between 60–61°N and 000°50′W-002°E was carried out during October 2007–2008 from the FV Adenia during pelagic mackerel trawling. Killer whales regularly feed on the discards from this fishery during October (Luque et al. 2006).

Photo-identification data were collected from 1983 to 2006 from the area around the Lofoten and Vesterålen region of Norway both between October–January where they feed on the over-wintering NSS herring and during dedicated summer surveys (see Similä et al. 1996; Kuningas et al. 2007). As above, only photographs of the left-sides were catalogued for ID purposes.

Photographic analyses

Photographs were graded on photographic quality and the distinctiveness of the individual. Photographs in which the fin and saddle filled less than 10% of the photograph, were not in focus, were poorly lit or in which the animal was not parallel to the camera were excluded. The best photograph of each individual from each encounter was then selected. Approximately 90% of encounters from dedicated survey work resulted in photographs in which all individuals were photo-identified and photographs were included in this study, ~60% of opportunistic encounters resulted in all or most individuals being photo-identified. Individuals were classified as 'well-marked' if they were sufficiently distinctive for re-identification without the risk of false positives or negatives, based on the presence of long-lasting markings such as fin-nicks, or scars or pigmentation on the saddle patch (see Similä and Lindblom 1993). The best photograph of each individual across all encounters within a study site for each year was selected for comparing with catalogues for other study areas.

Transition probabilities

Inter-annual site fidelity was estimated as a transition probability, pt, using maximum likelihood methods (see Hilborn 1990; Whitehead 2001; Stevick et al. 2006). These methods allow the number of identifications to be used as a measure of effort allowing the inclusion of all years with any individual identifications (Whitehead 2001). In a population of n individuals, the log-likelihood that m_{ij} (the number of observed re-sightings) of the n_i animals identified within a location in year i were also identified from n_j animals at this location in year j was given as the Poisson approximation (Whitehead 2001):

$$L = (m_{ij} \log(\hat{m}_{ij}) - \hat{m}_{ij}) + \text{constant}$$

Where the expected number of re-sightings is

$$\hat{m}_{ij} = \text{pt}_{ij} n_i (n_j/n)$$

The sum of the likelihoods for each combination of years was maximized over 10,000 transition probabilities drawn from a uniform distribution between 0 and 1 and a uniform range of values for n between 10 and 10,000.

Movement between each pair of locations was estimated using the same method to estimate a transition probability between location i and location j. Movement between Lofoten and Vesterålen and Møre was estimated from previously published mark-recapture data, based on the number of pods re-sighted between the two locations (Similä et al. 1996). As the Norwegian and Icelandic datasets consisted of photographs of left-sides all transition probabilities were calculated using photographs of left-sides only.

Social network analysis

Overlap in the range of individuals does not necessarily indicate they are part of the same population, e.g. across the Northeast Pacific there are a number of sympatric killer whale populations that are socially and reproductively isolated from one another (Hoelzel et al. 2007). To identify communities across and within multiple sites we constructed a social network diagram using Netdraw 2.043 (Borgatti 2002). In this diagram each individual is represented by a node, color coded to indicate which area(s) that individual has been identified in. Association between individuals was taken as 1 for all pairs of individuals being identified together within 10 meters of one another (Mann 1999), and individuals never seen together were given an association of 0. There was no attempt made to measure the strength of association, i.e. based on the number of times they have been seen in association with one another. Lines were drawn between nodes to represent an association between those individuals.

Results

Photo-identification of marked individuals

In total 896 marked individuals were catalogued from across the Northeast Atlantic. The number of marked individuals identified using left-sides from each location was 82 from Vestmannaeyjar (from years 1984, 1997, 1999, 2001, 2005–2007), 308 from the East Iceland (from years 1984–1988, 1990–1995, 1999), 10 from the Hebrides (from years

1992, 1994–1995, 1998, 2000–2001. 2004–2005, 2007–2008), 24 from the Northern Isles (from years 2005–2008), 21 from the North Sea (from years 2007–2008), and 469 from Lofoten and Vesterålen (from years 1986–2004).

Transition probabilities

Relatively high transition probabilities of individuals returning to the same site each year were found for all our study locations (Table 1). There was a high estimated rate of movement between the ISS herring spawning grounds of Vestmannaeyjar and the wintering grounds off East Iceland (Table 2). We also estimated a high rate of movement between the ISS herring wintering grounds off East Iceland and the Northern Isles where eight matched individuals were seen predating harbor seals (Table 2). The same individuals were photographed in a large group of over 25 killer whales over four consecutive days on the East Icelandic herring wintering ground during October 1999 from a vessel undertaking herring surveys. Four of these individuals had been photographed in previous encounters off East Iceland in October 1986, November 1986, October 1987, November 1988, November 1990 and November 1995. It should be noted that effort was seasonal during these years (see methods). All eight individuals were identified around the Northern Isles during the summer months in at least two different years between 2005 and 2008. The right-hand sides of 2 individuals from a group of 5 regularly photographed around the Northern Isles were photographed off St Kilda, of the Outer Hebrides, in May 2006. One of these 2 individuals has also been photographed off of East Iceland. This was the only match between the Northern Isles and the Hebridean and Western Isles from 91 encounters between 1992 and 2008. Ten days later the same group were photographed off the Northern Isles. The right-hand side of a group of four individuals were photographed off the Faeroe Islands in April 2009 while feeding on guillemots. These individuals had previously been photographed feeding on seals and eider ducks around the Northern Isles and one had been photographed on the herring grounds of East Iceland. St Kilda and Faeroe Islands are between Iceland and the Northern Isles and the encounters noted above occurred at the start of the seasonal peak in sightings around the Northern Isles (Bolt et al. 2009). These groups may therefore have been traveling between Iceland and the Northern Isles.

Photo-identification studies have also been carried out at the NSS herring spawning grounds in the Møre region of Southern Norway during spring months (Bisther and Vongraven 1995; Fig. 1). Individuals from seven different pods identified in the Lofoten

Table 1 Resightings (n_{ij}) of individuals within a location between years expressed as transition probabilities (pt)

Area	n	pt
Vestmannaeyjar	82	0.500
East Iceland	308	0.336
Hebrides	10	0.446
Northern Isles	24	0.701
Northern North Sea	21	0.855
Lofoten and Vesterålen	469	0.604

n Is the number of individuals identified at each location using photographs of left-sides. For full details of re-sights between years see electronic supplementary material online

Table 2 Resightings (n_{ij}) of individuals between locations expressed as transition probabilities (pt_{ij})

Area$_i$	Area$_j$	n_i	n_j	n_{ij}	pt_{ij}
Vestmannaeyjar	East Iceland	82	308	10	0.613
East Iceland	Northern Isles	308	24	8	0.420

n Is the number of individuals identified at each location using photographs of left-sides. No movement was detected using photographs of left-sides between all other pairs of locations

and Vesterålen region have been re-sighted in the Møre region (Similä et al. 1996), this movement can be expressed as a transition probability of $pt_{ij} = 0.434$.

Comparing photographs collected across all years, a period spanning 20 years (approximately one generation, Olesiuk et al. 1990) we found no matches of individuals from Norway and Iceland. There was also no movement between the Hebrides, the Northern Isles and North Sea based on left-side photos despite their proximity, however, as noted above there were matches of right sides between the Hebrides and Northern Isles. Additionally one individual with a severed dorsal fin was photographed in the northern North Sea during 2007 in a large aggregation feeding around pelagic mackerel fishing vessels was photographed on the right side from the shore off the Shetland mainland in 1991.

Social network analysis

The eight individuals sighted in both East Iceland and the Northern Isles represented nodes in a social network connecting the community following the ISS herring stock and the community predating on harbor seals around the Northeast of Scotland (Fig. 2a). The eight individuals seen in both locations traveled in at least four different sub-groups, all seen hunting seals, but these occasionally formed temporary multi-group associations and swapped group members, linking the identified Northern Isles individuals through direct association or through an intermediary.

The social structure of the Hebridean community appeared to be very fluid but all 10 individuals were linked by association (Fig. 2b). Five of these 10 individuals are adult males and no calves have been observed in association with any of the 5 adult females in photographs collected between 1992 and 2008 (mean inter-calf interval for killer whales is ∼5 years; Olesiuk et al. 1990; Kuningas et al. 2007), suggesting stochastic effects on demography may be impacting this community. Despite the occurrence of some individuals from the Northern Isles in the Hebrides these were not linked by association to this Hebridean community (Fig. 2). Phenotypic differences also suggest the two are isolated (Foote et al. 2009).

Discussion

Our results suggest a high degree of ecological spatial structuring in North Atlantic killer whales with high site fidelity by marked individuals to all locations and movement mostly limited to between locations that prey resources moved between e.g., the spawning and wintering grounds of the ISS and NSS herring stocks. The movement of an abundant and spatially predictable prey resource therefore appears to be a potential cause of delineation between North Atlantic killer whale communities, as has been found in some terrestrial
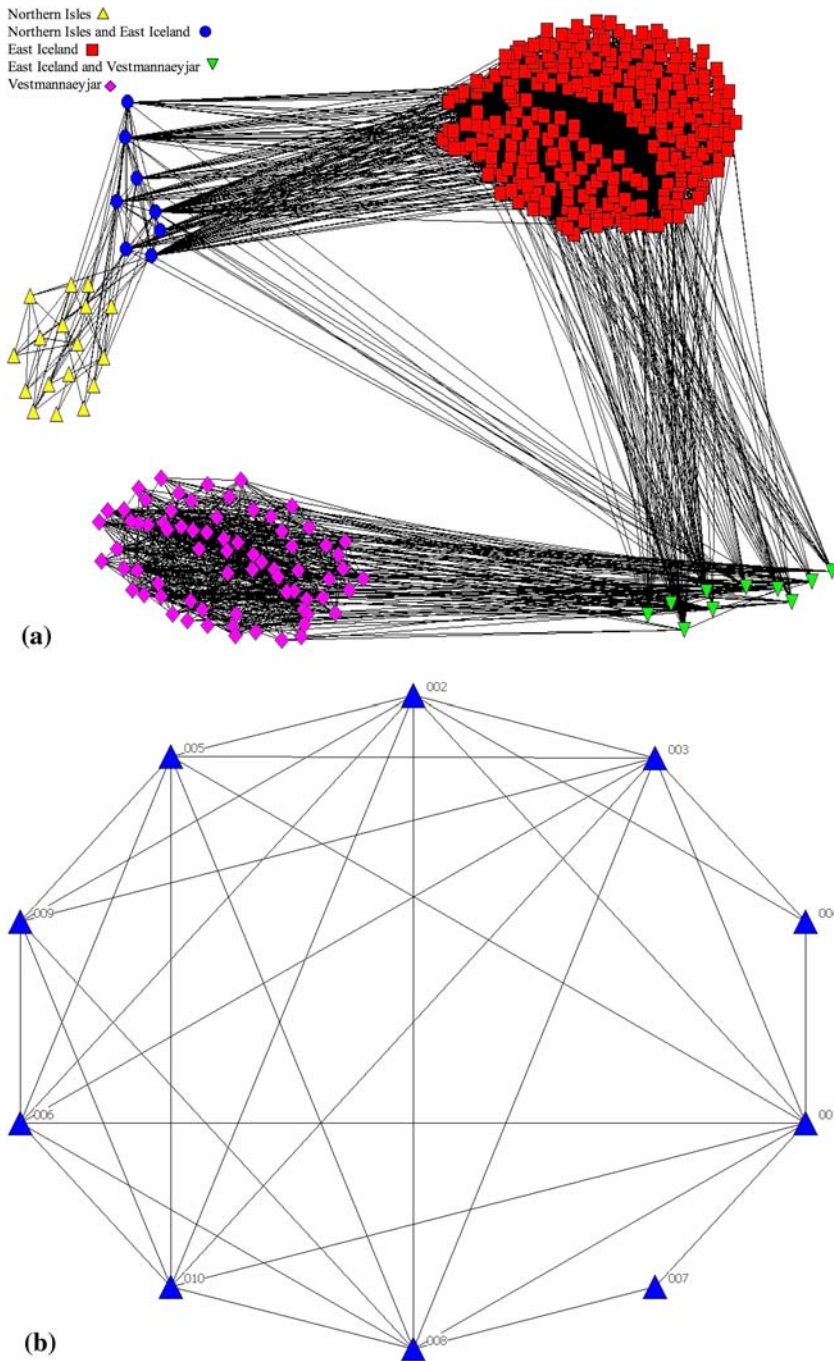
Fig. 2 **a** Social network diagram of Icelandic and Northern Isles killer whales. *Nodes* represent individual killer whales, *lines* between nodes represent that the individuals have been photographed associated together in a group or aggregation. The strength of association is not measured. **b** Social network diagram of the Hebridean killer whales

predators (e.g. Musiani et al. 2007). Some individuals were not associated with a single prey resource and moved between Icelandic herring grounds and the harbor seal pupping area of the Northern Isles, outside the distribution of the ISS herring stock (Jakobsson and Stefánsson 1999). This is consistent with stable isotope results, which suggest that subsets of individuals within the herring- and mackerel-eating populations also persistently forage on marine mammals (Foote et al. 2009). It also reflects earlier observations of identified individuals from the Norwegian herring-eating population predating seals (Bisther and Vongraven 2001; Stenersen and Similä 2004). Converse to the strict dietary specialization observed in North Pacific killer whales (Ford et al. 1998), it appears that some North Atlantic killer whale populations are generalists.

Movement data based on the capture-recapture of marked individuals can underestimate the level movement of individuals between distant sites (Koenig et al. 1996). So although a transition probability of 0 had the maximum likelihood between all pairs of location for which we found no matches, this should be interpreted as a minimum estimate of movement. However, it does suggest that there is no large-scale contemporary movement between these pairs of locations. For example our data suggest that there is no large-scale movement between the Icelandic and Norwegian herring grounds during the period covered by our photo-id data. Conversely, Strager (1995) found that a stereotyped call type was shared between Icelandic and Norwegian killer whales; the learnt nature of these call types (Foote et al. 2006) suggests contact between them. However, satellite tracking, which can be more effective at detecting long-range movement patterns (Koenig et al. 1996), also indicated that six tagged Norwegian killer whales followed the NSS herring stock and did not move to Iceland (Stenersen and Similä 2004).

It could be that mixing between Icelandic and Norwegian killer whales occurs outside of our study locations, for example we have shown that some Icelandic herring-eating killer whales move to the Northern Isles in the summer and some satellite-tagged Norwegian herring-eating killer whales were tracked close to the Northern Isles during the summer months (Stenersen and Similä 2004). Additionally our dataset covers only two decades, a period of a single killer whale generation (Olesiuk et al. 1990). Contact between Icelandic and Norwegian killer whales could be historic, as both the ISS and NSS herring stocks have undergone major migration changes during the twentieth century and both stocks over-wintered off the East coast of Iceland until the late 1960's (Røttingen 1990; Jakobsson and Østvedt 1999). High catches of the NSS herring stock have been taken off southeast Iceland during the 2008/2009 fishing season suggesting the delineation of this stock may be shifting back to its pre-1967 boundaries (Marine Research Institute 2009).

High site fidelity by North Atlantic killer whales could be driven by ecological, social and genetic advantages. (e.g. Weatherhead and Forbes 1994). For example site fidelity would increase knowledge of the local environment and allow the exploitation of predictable prey resources. It may also be advantageous in finding a suitable mate adapted to the appropriate conditions (Hendry et al. 2004) and facilitating non-random social encounters with kin (Wolf and Trillmich 2007).

The apparent intrinsic isolation of communities due to the resources they follow may have important conservation and management implications (Caughley 1994; Block et al. 2005). If populations are truly closed then local population dynamics (e.g. Kuningas et al. 2007) will primarily be driven by births and deaths. Local management agencies can then monitor these dynamics to detect any decline at an early stage. The high level of site fidelity in each location presents an opportunity to conservation and management agencies to monitor these populations (Shillinger et al. 2008).

References

Andrews RD, Pitman RL, Ballance LT (2008) Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. Polar Biol 31:1461–1468

Baker CS, Palumbi SR, Lambertsen RH, Weinrich MT, Calambokidis J, O'Brien J (1990) Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. Nature 344:238–240

Bigg MA (1982) An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. Rep Int Whaling Comm 32:655–666

Bisther A, Vongraven D (1995) Studies of the social ecology of Norwegian killer whales (*Orcinus orca*). In: Blix AS, Walloe L (eds) Whales, seals, fish and man. Elsevier, Amsterdam, pp 169–176

Bisther A, Vongraven D (2001) Killer whales feeding on both mammals and fish: A transient, resident or opportunistic type? Abstracts from society for marine mammalogy Biennial conference, Vancouver BC

Block BA, Teo SLH, Walli A, Boustany A, Stokesbury MJW, Farwell CJ, Weng KC, Dewar H, Williams TD (2005) Electronic tagging and population structure of Atlantic bluefin tuna. Nature 434:1121–1127

Bolt HE, Harvey PV, Mandelberg L, Thompson PM, Foote AD (2009) Occurrence of killer whales in Scottish inshore waters: temporal and spatial patterns relative to the distribution of declining harbour seal populations. Aquat Cons Mar Freshw Ecosys 19:671–675

Bonfil R, Meyer M, Scholl MC, Johnson R, O'Brien S, Oosthuizen H, Swanson S, Kotze D, Paterson M (2005) Transoceanic migration, spatial dynamics, and population linkages of white sharks. Science 310:100–103

Borgatti SP (2002) Netdraw: graph visualization software. Analytical Technologies, Harvard

Boustany AM, Davis SF, Pyle P, Anderson SD, Le Boeuf BJ, Block BA (2002) Expanded niche for white sharks. Nature 415:35–36

Caughley G (1994) Directions in conservation biology. J Anim Ecol 63:215–244

Foote AD, Griffin RM, Howitt D, Larsson L, Miller PJO, Hoelzel AR (2006) Killer whales are capable of vocal learning. Biol Lett 2:509–512

Foote AD, Newton J, Piertney SB, Willerslev E, Gilbert MT (2009) Ecological morphological and genetic divergence of sympatric North Atlantic killer whale populations. Mol Ecol (in press)

Ford JKB, Ellis GM, Barrett-Lennard LG, Morton AB, Palm RS, Balcomb KC (1998) Dietary specialisation in two sympatric populations of killer whale (*Orcinus orca*) in coastal British Columbia and adjacent waters. Can J Zool 76:1456–1471

Forney KA, Wade P (2007) Worldwide distribution and abundance of killer whales. In: Estes J (ed) Whales, whaling and ecosystems. University of California Press, California, pp 145–162

Hendry AP, Castric V, Kinnison MT, Quinn TP (2004) The evolution of philopatry and dispersal; homing versus straying in salmonids. In: Hendry AP (ed) Evolution illuminated: Salmon and their relatives. Oxford University Press, Oxford, pp 52–91

Hestbeck JB, Nichols JD, Malecki RA (1991) Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72:523–533

Hilborn R (1990) Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Can J Fish Aquat Sci 47:635–643

Hoelzel AR, Hey J, Dahlheim ME, Nicholson C, Burkanov V, Black N (2007) Evolution of population structure in a highly social top predator, the killer whale. Mol Biol Evol 24:1407–1415

Jakobsson J, Østvedt OJ (1999) A review of joint investigations on the distribution of herring in the Norwegian and Icelandic Seas 1950–1970. Rit Fisk 16:209–238

Jakobsson J, Stefánsson G (1999) Management of summer-spawning herring off Iceland. ICES J Mar Sci 56:827–833

Koenig WD, Vuren DV, Hooge PN (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends Ecol Evol 11:514–517

Kuningas S, Similä T, Hammond PS (2007) Population dynamics of killer whales (*Orcinus orca*) off Northern Norway. Report to Scientific Committee of the International Whaling Commission Anchorage, SC/59/SM13

Luque PL, Davis CG, Reid DG, Wang J, 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. Aquat Liv Res 19:403–410

Lyrholm T, Leatherwood S, Sigurjónsson J (1987) Photo-identification of killer whales (*Orcinus orca*) off Iceland, October 1985. Cetology 52:1–14

Mann J (1999) Behavioral sampling methods for cetaceans: a review and critique. Mar Mamm Sci 15:102–122

Marine Research Institute (2009) Status report 2009. Marine Research Institute, Reykjavík, Iceland. Available from http://www.hafro.is/Astand/2009/20-sild.PDF (accessed July 2009)

Musiani M, Leonard JA, Cluff HD, Gates CC, Mariani S, Paquet PC, Vilàs C, Wayne RK (2007) Differentiation of tundra/taiga and boreal coniferous forest wolves: genetics, coat colour and association with migratory caribou. Mol Ecol 16:4149–4170

Olesiuk PF, Bigg MA, Ellis GM (1990) Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep Int Whaling Comm Special Issue 12:209–243

Paetkau D, Amstrup SC, Born EW, Calvert W, Derocher AE, Garner GW, Messier F, Stirling I, Taylor MK, Wiig Ø, Strobeck C (1999) Genetic structure of the world's polar bear populations. Mol Ecol 8:1571–1584

Palsbøll P, Clapham PJ, Mattila DK, Larsen F, Sears R, Siegismund HR, Sigurjónsson J, Vasquez O, Arctander P (1995) Distribution of mtDNA haplotypes in North Atlantic humpback whales: the influence of behaviour on population structure. Mar Ecol Prog Ser 116:1–10

Palumbi SR (1994) Genetic divergence, reproductive isolation, and marine speciation. Annu Rev Ecol Syst 25:547–572

Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. Ecol Appl 13:S146–S158

Pitman RL, Ensor P (2003) Three forms of killer whales (*Orcinus orca*) in Antarctic waters. J Cetacean Res Manage 52:131–139

Rasmussen K, Palacios DM, Calambokidis J, Saborio MT, Dalla Rosa L, Secchi ER, Steiger GH, Allen JM, Stone GS (2007) Southern hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. Biol Lett 3:302–305

Røttingen I (1990) A review of the variability in the distribution and abundance of Norwegian spring spawning herring and Barents Sea capelin. Polar Res 8:33–42

Scott J (1988) Social network analysis. Sociology 22:109–127

Shillinger GL, Palacios DM, Bailey H, Bograd SJ, Swithenbank AM, Gaspar P, Wallace BP, Spotila JR, Paladino FV, Piedra R, Eckert SA, Block BA (2008) Persistent leatherback turtle migrations present opportunities for conservation. PLoS Biol 6:1408–1416

Sigurjónsson J, Lyrholm T, Leatherwood S, Jónsson E, Víkingsson G (1988) Photoidentification of killer whales off Iceland 1981 through 1986. Rit Fisk 11:99–114

Similä T (1997) Sonar observations of killer whales (*Orcinus orca*) feeding on herring schools. Aquat Mamm 23:119–126

Similä T, Lindblom L (1993) Persistence of natural markings on photographically identified killer whales (*Orcinus orca*). ICES C.M. 1993/N:11

Similä T, Ugarte F (1993) Surface and under-water observations of cooperatively feeding killer whales in northern Norway. Can J Zool 71:1494–1499

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. Can J Fish Aquat Sci 53:769–779

Simon M, McGregor PK, Ugarte F (2007) The relationship between the acoustic behaviour and surface activity of killer whales (*Orcinus orca*) that feed on herring (*Clupea harengus*). Acta ethol 10:47–53

Simon M, Hanson MB, Murrey L, Tougaard J, Ugarte F (2009) From captivity to the wild and back: an attempt to release Keiko the killer whale. Mar Mamm Sci 25:693–705

Stenersen J, Similä T (2004) Norwegian killer whales. Tringa Forlag

Stevick PT, Allen J, Clapham PJ, Katona SK, Larsen F, Lien J, Mattia DK, Palsbøll PJ, Sears R, Sigurjónsson J, Smith TD, Vikingsson G, Øien N, Hammond PS (2006) Population spatial structuring on the feeding grounds in North Atlantic humpback whales (*Megaptera novaeangliae*). J Zool 270:244–255

Stone GS, Flórez-Gonzalez L, Katona S (1990) Whale migration record. Nature 346:705

Strager H (1995) Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca*, in the waters of northern Norway. Can J Zool 73:1037–1047

Tucker VA (1975) The energetic cost of moving about. Am Scientist 63:413–419

Víkingsson GA (2004) Háhyrningur. In: Hersteinsson P (ed) Íslensk spendýr, Vaka-Helgafell, Reykjavík, pp 166–171

Weatherhead PJ, Forbes MRL (1994) Natal philopatry in passerine birds: genetic or ecological influences? Behav Ecol 5:426–433

Whitehead H (2001) Analysis of animal movement using opportunistic individual identifications: application to sperm whales. Ecology 82:1417–1432

Williams TM (1999) The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. Phil Trans R Soc B 354:193–201

Williams TM, Friedl WA, Fong ML, Yamada RM, Sedivy P, Haun JE (1992) Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. Nature 355:821–823

Wolf JBW, Trillmich F (2007) Beyond habitat requirements: individual fine-scale site fidelity in a colony of the Galapagos sea lion (*Zalophus wollebaeki*) creates conditions for social structuring. Oecologia 152:553–567