Vol. 564: 199–210, 2017
doi: 10.3354/meps11998

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 3

# Intra-population variation in isotopic niche in herring-eating killer whales off Iceland

**Filipa I. P. Samarra[1,*], Morgana Vighi[2], Alex Aguilar[2], Gísli A. Víkingsson[1]**

[1]Marine and Freshwater Research Institute, Skúlagata 4, 101 Reykjavík, Iceland

[2]Biodiversity Research Institute (IRBio) and Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, University of Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain

ABSTRACT: Among-individual variation in dietary preferences can impact community dynamics and be a driving force for evolutionary divergence, although it can be difficult to assess in free-ranging marine mammal populations. In this study, we investigate the existence of variation in isotopic niche within a population of putative herring-specialist killer whales. Isotopic ratios of carbon and nitrogen were measured in 67 skin biopsy samples from 56 individual killer whales, sampled in herring overwintering (winter) grounds and spawning (summer) grounds in Iceland when the whales were presumably feeding on herring. Whales that appeared to follow herring year round (n = 31) had lower $\delta^{15}N$ values, consistent with a diet predominantly composed of herring. This supports the existence of herring specialists in the population. In contrast, whales that were only photo-identified either in winter or in summer (n = 25) had larger variation in $\delta^{15}N$ values. A discriminant function analysis clearly distinguished between putative herring specialists and whales seasonally travelling to Scotland in summer (n = 3), which exhibited distinctly larger $\delta^{15}N$ values indicative of a diet including higher trophic level prey. This study shows that herring-eating killer whales in Iceland exhibit intra-population ecological variation, whereby individuals or groups differ in the proportional contribution of different prey items to their diet. This variation occurs in the absence of social and, potentially, reproductive isolation. Although further information will be required to assess the degree of structuring within the population, such heterogeneity should be taken into account in future conservation and management plans.

KEY WORDS: Niche width · Prey specialisation · Stable isotopes · Foraging · Orca

*Resale or republication not permitted without written consent of the publisher*

## INTRODUCTION

Ecological variation, in the form of diversity in resource use, has long been recognised as a potential driving force for evolutionary divergence potentially leading to sympatric speciation (e.g. Mayr 1947, Smith & Skúlason 1996, Rundle & Nosil 2005). However, traditional studies of resource use have often treated individuals within a population as equivalent. The niche variation hypothesis proposed by Van Valen (1965) suggests that generalist populations are more variable than those that specialise in a resource and that such variation may be achieved by higher among-individual heterogeneity. This hypothesis has gained recent support as apparently generalist populations have been shown to be ecologically heterogeneous, where individuals differ in their use of a common resource pool (Bolnick et al. 2003, 2007, Araújo et al. 2011), which could have significant effects on population and community dynamics (Bolnick et al. 2011). Highly mobile apex predator populations composed of individual specialists can affect ecosystem dynamics by linking separate food chains (Araújo et al. 2011). Long-lived top predators such as marine

*Corresponding author: fipsamarra@gmail.com

© Inter-Research 2017 · www.int-res.com

mammals are of particular interest since possible cultural transmission of their foraging behaviours could be an important mechanism underlying among-individual variation in resource use and its maintenance over generations (Estes et al. 2003, Sargeant et al. 2005, Torres & Read 2009). However, obtaining the necessary long-term data to assess the existence of individual preferences and possible genetic isolation in free-ranging marine mammal populations is difficult.

Measuring tissue chemical tracers in a predator acquired through prey offers an integrated measure of all prey assimilated over a period of days to years, thus providing a long-term overview of prey preferences (Michener & Schell 1994). The tracers most commonly used for dietary studies are stable isotope ratios, especially those of nitrogen ($^{15}N/^{14}N$, denoted as $\delta^{15}N$) and carbon ($^{13}C/^{12}C$, denoted as $\delta^{13}C$). Both are enriched in a predictable manner in consumers relative to their prey, although the enrichment of $\delta^{15}N$ is more pronounced than that of $\delta^{13}C$, providing a good estimate of a species' trophic position (DeNiro & Epstein 1981, Hobson & Welch 1992). $\delta^{13}C$ can provide information on predator foraging areas as it generally varies with latitude and, in the marine environment, presents clear differences between offshore vs. inshore or benthic vs. pelagic food sources (e.g. Cherel & Hobson 2007). As a result of these well-defined patterns of variation, variance in isotopic ratios can be used to infer trophic niche width (Bearhop et al. 2004) as well as to reliably identify individual-level variation in foraging preferences (Newsome et al. 2009a).

The killer whale *Orcinus orca* is a marine top predator with a cosmopolitan distribution (Forney & Wade 2006) that is as a species considered to be a generalist (Hoyt 1984, Jefferson et al. 1991). However, some populations appear to specialise in specific prey types, such as fish or marine mammals (reviewed in de Bruyn et al. 2013), or even particular prey species, such as Chinook salmon *Oncorhynchus tshawytscha* (Ford et al. 1998, 2016, Ford & Ellis 2006, Hanson et al. 2010). Ecotypes differing in diet, morphology, genetics and behaviour have been recognised in the North Pacific and Antarctica (e.g. Ford et al. 1998, 2011, Barrett-Lennard 2000, Pitman & Ensor 2003, Pitman et al. 2007, 2011, LeDuc et al. 2008, Pitman & Durban 2010, 2012). Dietary differences between these ecotypes and prey specialisation have been supported by visual observation of feeding events (e.g. Ford et al. 1998, 2011, Saulitis et al. 2000, Pitman & Ensor 2003, Burdin et al. 2004, Ford & Ellis 2006, Dahlheim et al. 2008, Pitman & Durban 2010, 2012), analysis of stomach contents or faecal material (Ford et al. 1998, 2016) and stable isotope analysis (Herman et al. 2005, Krahn et al. 2007a,b, Newsome et al. 2009b, Durban et al. 2017). Specialised resource use appears to be culturally transmitted through generations within matrilineal social units (Riesch et al. 2012, Ford & Ellis 2014). The existence of ecological divergence and the transmission of resource use patterns through generations may be a mechanism that maintains social and reproductive isolation and, over long time scales, leads to the formation of separate ecotypes in sympatry (Moura et al. 2014, Foote et al. 2016).

The degree of dietary specialisation in killer whales has been proposed to relate to habitat productivity and availability of high-quality prey (Baird et al. 2006). Observations in tropical regions support a broad dietary range (Baird et al. 2006, Weir et al. 2010, Bolaños-Jiménez et al. 2014). Nevertheless, killer whales with an apparently mixed diet, i.e. including fish and marine mammals, have also been reported in high-latitude, productive regions both in the southern and northern hemispheres (Argentina: Iñiguez et al. 2002; Chilean Patagonia: Capella et al. 2014; Crozet Islands: Guinet 1992, Tixier et al. 2015; Marion Island: Reisinger et al. 2016; Norway: Vongraven & Bisther 2014; and South Africa: Best et al. 2010). Although prey specialisation is extensively documented in some well-studied populations and this has allowed clear ecotype assignment, the lack of long-term ecological data in other areas has impeded clarification of whether prey specialisation is a universal trait of the species (de Bruyn et al. 2013). Dietary studies providing long-term ecological data are, thus, crucial to understand the extent of ecological diversity within and between extant populations and to assess the role such variation may play in eventual ecotype formation in these long-lived top predators.

In Iceland and Norway, the occurrence of large aggregations of killer whales feeding on herring *Clupea harengus* has prompted suggestions of the existence of coastal communities or populations specialising on this prey (Sigurjónsson et al. 1988, Similä et al. 1996). Stable isotope analyses of the skin of individuals sampled in herring overwintering grounds in Norway supported at least seasonal herring specialisation in this location (Foote et al. 2012). These whales share the same complex feeding strategy (Similä & Ugarte 1993, Simon et al. 2007, Samarra & Miller 2015), suggesting similar ecology. However, observations of small subsets of killer whales switching prey in Norway (Vongraven & Bisther 2014) and

seasonally travelling away from the known herring stock distribution areas in Iceland (Samarra & Foote 2015) suggest the existence of ecological variation within herring-eating killer whales, whereby individuals may differ in the proportional contribution of different prey types to their diets, as proposed for Type 1 killer whales in the North Atlantic (Foote et al. 2009). Yet, the lack of foraging observations combined with isotopic analyses from known individuals has limited our understanding of the extent of prey specialisation in putative herring-specialist killer whales.

Here, we combine measurements of variation in $\delta^{13}C$ and $\delta^{15}N$ values in skin samples of free-ranging killer whales in Iceland with individual information, including sex, sighting frequency and movement patterns, to test the hypothesis that this population exhibits diet specialisation on herring. To do this, we sampled killer whales while they were observed presumably feeding on herring in the overwintering and spawning grounds of the Icelandic summer-spawning (ISS) herring during winter and summer, respectively. We hypothesised that if killer whales were herring specialists, following the herring year round between overwintering, feeding and spawning grounds, their trophic niche would be narrow and variance in their stable isotope ratio values would be low. This study contributes towards our understanding of the foraging ecology of Northeast Atlantic herring-eating killer whales and to what extent prey specialisation may be a generalised trait of this species.

## MATERIALS AND METHODS

### Sample and data collection

Killer whale biopsy samples were collected in winter and summer from ISS herring overwintering and spawning grounds, respectively, where killer whales are frequently seen feeding on herring. Sample collection in winter took place in February and March in 2013 and 2014 in Grundarfjörður and Kolgrafafjörður (West Iceland), 2 fjords that at the time formed part of the overwintering grounds of ISS herring (Fig. 1A, ICES 2014). Effort varied primarily due to weather and research priorities. In 2013, 2 out of 26 d with killer whale encounters were dedicated to biopsy sampling, while in 2014 there were 23 d with killer whale encounters and attempted biopsy collection. Sample collection in summer occurred in July 2014 in Vestmannaeyjar (South Iceland, 15 d with killer whale encounters), a spawning ground of ISS herring (Fig. 1B, Jakobsson & Stefánsson 1999). In both locations, killer whales aggregated seasonally coinciding with the migration of herring into the area.

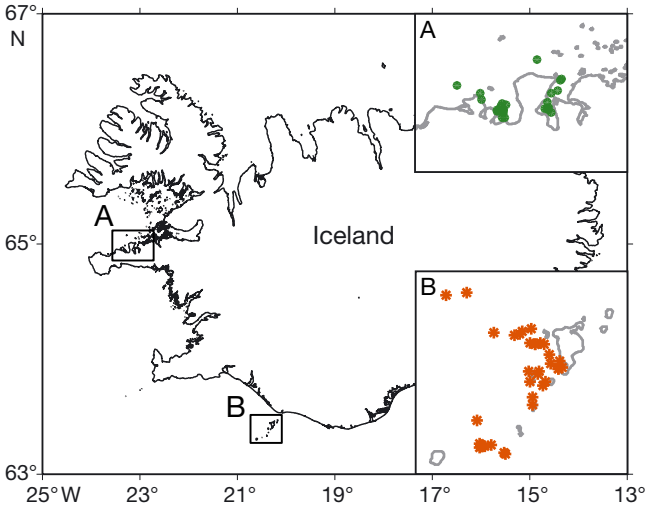


Fig. 1. Locations of killer whale biopsy sample collection in (A) overwintering grounds in winter and (B) spawning grounds in summer of Icelandic summer-spawning herring stock

Biopsy samples of skin and blubber were collected using a pneumatic rifle with 35 or 40 mm biopsy tips in 2013 and an ARTS pneumatic darting system (Kvadsheim et al. 2009) and stainless steel 25 mm biopsy tips in 2014. Biopsy tips were sterilised before use and stored in clean plastic bags. Samples were generally collected from the mid-lateral region of the body, below the dorsal fin. The whole layer of skin was used in subsequent analyses. Skin biopsy samples collected in 2013 were stored in ethanol (n = 8), while skin samples collected in 2014 were stored frozen (n = 51, Table S1 in the Supplement at www.int-res.com/articles/suppl/m564p199_supp.pdf). While freezing is not considered to cause changes in the stable isotope values of tissues, in cetacean skin samples, ethanol preservation slightly depletes $\delta^{13}C$ values but has no significant effect on $\delta^{15}N$ values (Kiszka et al. 2014). We tested for potential differences between the 2 preservation methods and found no difference in $\delta^{15}N$ (Wilcoxon rank sum test: W = 82, p = 0.77) or $\delta^{13}C$ values (*t*-test: *t*-value = 1.91, df = 12.48, p = 0.08). Given these results, we combined the 2 sets of data. The turnover time of skin, that is, the time lapse during which the stable isotopic signal of a given type of diet remains in skin, is a few weeks in odontocete cetaceans (Browning et al. 2014, Giménez et al. 2016) unlike other tissues, such as teeth, which can

provide a lifelong sequential record of dietary preferences (Foote et al. 2009, Newsome et al. 2009b, Matthews & Ferguson 2014).

All sampled individuals were photographically identified (Bigg 1982) to try to avoid within-season repeated sampling of the same individual. Differences between repeated within-season samples from the same whale yielded $\delta^{13}C$ and $\delta^{15}N$ values within limits of analytical error and therefore were averaged. Sex was assigned based on genetic analysis. No calves or young juveniles were sampled, but each sex class may include subadult or adult individuals. Each individual's encounter history was based on a photographic database collected between 2008–2010 and 2013–2015 in Vestmannaeyjar and between 2013 and 2015 in Grundarfjörður and Kolgrafafjörður (F. I. P. Samarra unpubl. data). This included the individual's sighting frequency, corresponding to the total number of days with sightings in the database, and a movement pattern, classified as following herring year round (Group A) if photographed in both herring overwintering and spawning grounds or seen only in summer or winter (Group B). Of those individuals sighted only in summer or winter, seasonal movement patterns are only known for a few individuals that have been seen to move between Iceland in winter and Scotland in summer (Group C; Samarra & Foote 2015), away from the known distribution of ISS herring. All other individuals were only seen either in the summer or in the winter, and their year-round movements are unknown. There are more ISS herring overwintering and spawning grounds than those sampled in this study (Jakobsson & Stefánsson 1999, ICES 2014). Consequently, Group B may include individuals that do follow herring year round but to unknown grounds or individuals that seasonally move to other unknown areas.

### Stable isotope analysis

All samples were dried at 60°C for 48 h and then powdered with a mortar and pestle. Lipid extraction was performed using a 2:1 solution of chloroform and methanol, and samples were then dried again at 60°C for 48 h to remove any remaining solution. Approximately 0.3 mg of powdered samples was weighed into tin capsules and then automatically loaded and combusted at 1000°C in a continuous-flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA; Thermo-Finnigan). All analyses were undertaken at the Centres Científics i Tecnològics of the University of Barcelona (CCiT-UB). Standards for $^{13}C$ and $^{15}N$ were Vienna Pee Dee Belemnite (V-PDB) and atmospheric nitrogen, respectively. International isotope secondary standards of known $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in relation to V-PDB and air, respectively, were used for calibration of $\delta^{13}C$ and $\delta^{15}N$, including polyethylene (IAEA-CH-7, $\delta^{13}C$ = –31.8‰), sucrose (IAEA-CH-6, $\delta^{13}C$ = –10.4‰), ammonium sulfate (IAEA-N-1, $\delta^{15}N$ = +0.4‰; IAEA-N-2, $\delta^{15}N$ = +20.3‰), potassium nitrate (IAEA-NO-3, $\delta^{15}N$ = +4.7‰) and L-glutamic acid (USGS40, $\delta^{13}C$ = –26.2‰ and $\delta^{15}N$ = –4.6‰). All reference materials used are distributed by the International Atomic Energy Agency (IAEA). Standards were included after every 10 samples. Results were expressed as per mille (‰) following the delta (δ) notation. Replicate measurements of internal laboratory standards indicate measurement errors of 0.28 ± 0.15‰ for $\delta^{13}C$ and 0.34 ± 0.16‰ for $\delta^{15}N$.

### Statistical analysis

We tested the effects of sex (Male vs. Female), season (Winter vs. Summer), sighting frequency and movement pattern (Group A vs. Group B) on the $\delta^{13}C$ and $\delta^{15}N$ values of killer whale skin samples using either a generalised linear model or a combination of Wilcoxon rank sum tests and Spearman's rank correlation, depending on whether the data followed a normal distribution or not, respectively. A Bonferroni correction was used when applicable to adjust the significance level to account for multiple comparisons. All analyses were conducted in R 3.2.2 for Mac OS X (R Core Team 2015).

Isotopic niche width of individuals that moved between herring grounds year round (Group A) or were seen in only 1 season (Group B) was estimated in a Bayesian framework based on multivariate ellipse-based metrics, which allowed for sampling error to propagate to generated estimates, providing robust statistical comparisons between samples (Jackson et al. 2011). Standard ellipses corrected for sample size ($SEA_C$), which are less influenced by extreme values and are equivalent to standard deviation in univariate cases, were generated using the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al. 2011). The area of a $SEA_C$ contains approximately 40% of the data, regardless of sample size. Differences in $SEA_C$ between groups were statistically tested by comparing the probability distributions of standard ellipse areas for both groups generated as the outcome of $10^6$ resampling runs (Jackson et al. 2011).

To test for fine-scale differences in stable isotopic signatures of whales with different movement patterns (Group A, B or C), we also input the stable isotope measurements into a multivariate discriminant function analysis (DFA), where movement pattern was used as the grouping variable and the cross-validation performed through a jackknife technique implemented in the *lda* function of the MASS package version 7.3-16 (Venables & Ripley 2002) in R. The overall proportion of correct classifications and the proportion of correct classifications by location were calculated and compared to the proportion of by-chance accuracy, which was assumed to be equal (~33%) for all movement patterns.

### Diet composition

All killer whale skin samples used were collected in known herring grounds, where the whales were observed feeding on herring. Although killer whales in Iceland have also been observed predating seabirds, seals and minke whales (Víkingsson 2004), such observations have generally not been accompanied by identifications of the whales. Therefore, separate ecotype assignment of these latter whales could not be made. Throughout several field seasons in the herring overwintering and spawning grounds, our observations have only identified herring as a major prey item. The only 2 interactions with other prey observed were of a whale with a lumpfish *Cyclopterus lumpus* in its mouth and whales throwing a salmon *Salmo salar* in the air.

When killer whales were observed feeding, herring stunned by killer whale underwater tail slaps could be seen at the surface and were often caught by seabirds flying above feeding whales. In many cases, the research vessel was not close enough to collect the herring, but when possible, stunned fish were opportunistically collected and stored frozen. Samples of approximately 1 × 3 cm of herring muscle (including skin) were taken from each fish. Herring samples were processed following the same procedures for stable isotope analysis as detailed for killer whale skin samples (see 'Materials and methods: Stable isotope analysis).

To understand if herring could be a major component of the diet, we estimated the isotopic values of killer whales that would be based on a diet exclusively composed of herring. We calculated killer whale expected $\delta^{15}N$ and $\delta^{13}C$ values ($\delta^{15}N_{expected}$ and $\delta^{13}C_{expected}$, respectively) by adding skin isotopic enrichment per trophic level values to the average prey isotopic values (following equations in Herman et al. 2005).

Skin isotopic enrichment values per trophic level for nitrogen and carbon were +1.3 and +1.35, respectively, derived from a controlled diet experiment (García-Tiscar 2009). We used these values following the methodology of García-Tiscar (2009); however, the author pointed out that these values varied considerably between and within individuals examined (García-Tiscar 2009). Although the enrichment factor for nitrogen is below the 2 to 5‰ range found in other marine mammals (Newsome et al. 2010, Borrell et al. 2012), this value is consistent with the lower discrimination factors for killer whale blood and plasma measured from controlled diet experiments (García-Tiscar 2009, Caut et al. 2011) and agrees with the diet-predator enrichment expected from skin biopsies of free-ranging whales feeding on herring in Norway (Foote et al. 2012). The expected values were then directly compared to the measured mean $\delta^{15}N$ and $\delta^{13}C$ results of each group.

## RESULTS

We collected 67 skin samples from 56 individual killer whales; 15 of them were repeated samples of the same individual killer whales within the same season and, thus, were averaged; 3 were repeated samples across different seasons and were kept as separate samples (Table S1 in the Supplement). This resulted in 59 measurements in total, 17 females and 42 males; 32 were collected in summer and 27 in winter (Table S1). Of the 59 measurements, 34 were whales that presumably followed herring year round (Group A), while the remaining 25 were whales only seen in 1 season (Group B), 3 of which were whales seen seasonally travelling to Scotland (Group C, Table S1). Killer whale skin sample $\delta^{15}N$ values ranged between 12.5 and 15.1‰ (mean ± SD: 13.2 ± 0.6‰, n = 59), and $\delta^{13}C$ values ranged between −18.5 and −16.9‰ (mean ± SD: −17.8 ± 0.3‰, n = 59, Table S1, Fig. 2).

### Stable isotope analysis

The $\delta^{13}C$ data followed a normal distribution (Shapiro-Wilks test: W = 0.98, p = 0.43). A generalised linear model was fitted assuming a normal distribution with identity link and with sex (Male vs. Female), season (Winter vs. Summer), movement pattern (Group A vs. Group B) and sighting frequency as explanatory variables. There was a significant effect of sex on $\delta^{13}C$ values, with males having slightly higher values than females (Male vs. Female:

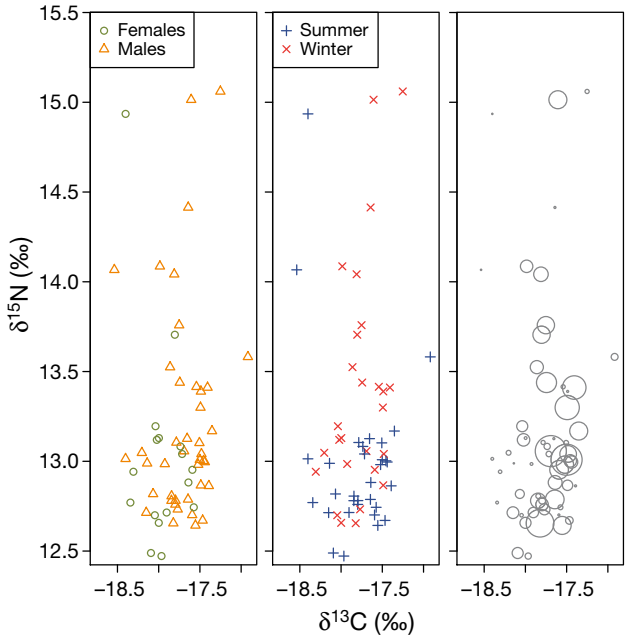


Fig. 2. Variation in killer whale stable isotopes with sex (left panel), season (center panel) and sighting frequency (right panel: circle diameter increases with sighting frequency)

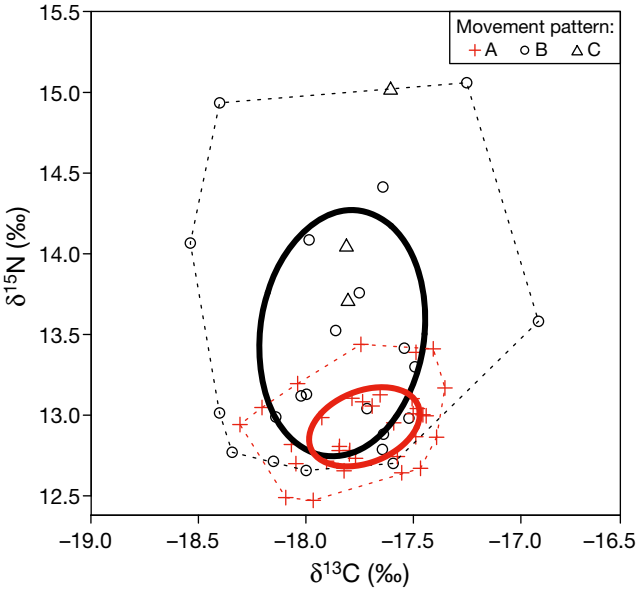


Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ values of skin samples from killer whales seen in herring grounds year round (Group A) and whales that are only seen seasonally (Groups B and C). Solid lines represent the standard ellipses corrected for sample size (SEAc), while dashed lines represent the convex hull area. Whales seen in Iceland only in winter that travel to Scotland in summer (Group C) are represented as triangles

coefficient estimate = 0.22, *t*-value = 2.56, df = 54, p = 0.01), but no other variable was significantly different (Fig. 2). Because the $\delta^{15}N$ data did not follow a normal distribution (Shapiro-Wilks test: W = 0.80, p < 0.001), Wilcoxon rank sum tests and a Spearman's rank correlation test were used instead. There was no significant effect of sex on $\delta^{15}N$ (Wilcoxon rank sum test: p > 0.1). There was no relationship between sighting frequency and $\delta^{15}N$ (Spearman's rank correlation: $r_S$ = −0.02, S = 34 759, p = 0.91, Fig. 2). However, there was a significant effect of season (Wilcoxon rank sum test: W = 631, p = 0.002, Fig. 2) and movement pattern (Fig. 3). Although the range of values for summer and winter was similar, killer whales sampled in summer were more likely to have lower $\delta^{15}N$ values. Only 9% of whales sighted in summer in comparison to 30% of whales in winter had $\delta^{15}N$ values >13.5‰, a threshold based on the largest value of the convex hull area encompassing putative herring specialists (see Fig. 3).

Whales that followed herring year round (Group A) had a significantly lower $\delta^{15}N$ than whales only seen in 1 season (Group B; Wilcoxon rank sum test: W = 220, p = 0.001, Fig. 3). In addition, whales that followed herring year round (Group A) had a smaller convex hull total area than whales seen only in 1 season (Group A vs. Group B: total area = 0.63 vs. 3.01‰$^2$, Fig. 3) as well as a significantly lower $SEA_C$ (Group A vs. Group B: 0.19 vs. 0.92‰$^2$, p = 0, Figs. 3 & 4), indicating a narrower isotopic niche width. Three individuals that followed herring year round were sampled in both winter and summer (Table S1). The mean ± SD difference between samples from winter and summer of each individual was 0.12 ± 0.12‰ for $\delta^{15}N$ and 0.35 ± 0.30‰ for $\delta^{13}C$.

A multivariate DFA showed high stable isotopic variation between whales that follow herring year round (Group A) and whales that travel between Iceland and Scotland (Group C), with the first discriminant function accounting for 98% of the variability. The loadings of the first discriminant function revealed that $\delta^{15}N$ was the main discriminating predictor (loadings: $\delta^{15}N$ = −2.06, $\delta^{13}C$ = 0.44). The cross-validated classification showed an overall correct classification of 64% of samples to the correct movement pattern, compared to a by-chance proportion of 33%. The largest correct classification score was 85% for Group A, followed by 67% for Group C. None of the misclassifications for Group A were assigned to Group C, and none of the misclassifications of Group C were assigned to Group A, supporting a good separation between these groups (Fig. 3). Whales only seen in 1 location (Group B) had a correct classification score of 32%. Misclassifications were assigned to the other 2 movement types, reflecting less discrimination between whales seen in

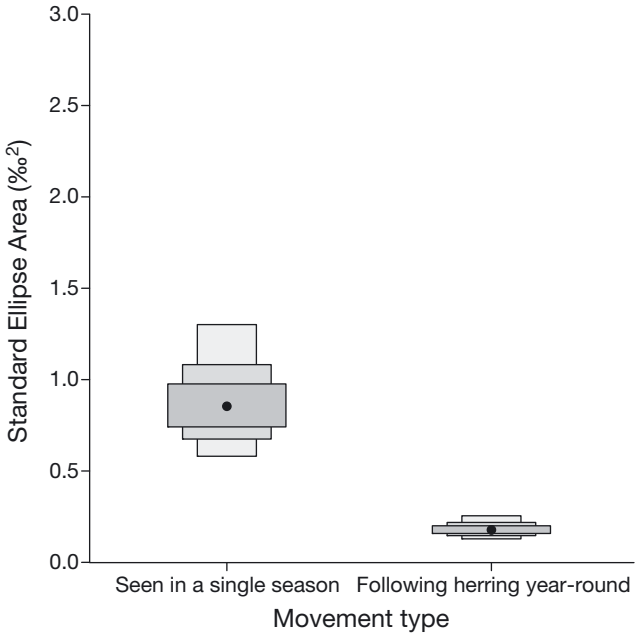


Fig. 4. Distribution in the standard ellipse area (‰$^2$) estimates based on $10^6$ resampling runs for whales with different movement types. Left: whales seen seasonally (Group B); right: whales seen in herring grounds year round (Group A). Black dots represent the mode, and the shaded boxes represent the 50, 75 and 95% credible intervals from dark to light grey. Note that the lack of overlap between both distributions indicates a significantly different isotopic niche width between whales following herring year round and those only seen seasonally

one location (Group B) relative to putative herring specialists (Group A) or whales that move to Scotland (Group C, Fig. 3).

### Diet composition

We sampled 12 herring collected in summer and winter fieldwork sites during killer whale feeding events. Herring had a mean ± SD of 11.78 ± 0.50‰ for $\delta^{15}N$ and −19.13 ± 0.47‰ for $\delta^{13}C$; there was no statistically significant difference between samples collected in winter and summer (Wilcoxon rank sum test: W = 26, p = 0.24 for $\delta^{15}N$ and W = 23, p = 0.48 for $\delta^{13}C$). The assumption of a diet exclusively composed of herring resulted in a $\delta^{15}N_{expected}$ of 13.08‰ and a $\delta^{13}C_{expected}$ of −17.78‰. The modelled herring diet isotopic ratios ($\delta^{15}N_{expected}$ and $\delta^{13}C_{expected}$) were very close to the mean and within the range of values (shown as [minimum; maximum]) for killer whales following herring year round (group A, 12.93 [12.47; 13.44]‰ for $\delta^{15}N$ and −17.73 [−18.31; −17.35]‰ for $\delta^{13}C$). Similarly, the modelled herring diet isotopic ratios ($\delta^{15}N_{expected}$ and $\delta^{13}C_{expected}$) were also close to the mean and within the range of whales only seen in 1 season (group B, 13.4 [12.66; 15.06]‰ for $\delta^{15}N$ and −17.84 [−18.54; −16.92]‰ for $\delta^{13}C$) but considerably lower than the most extreme $\delta^{15}N$ values within this group, which had larger variation than group A. In comparison to whales seen travelling between Iceland and Scotland (group C), the modelled herring diet isotopic ratios ($\delta^{15}N_{expected}$ and $\delta^{13}C_{expected}$) were lower than the mean and outside the range for $\delta^{15}N$ values (14.25 [13.71; 15.02]‰) but not for $\delta^{13}C$ values (−17.74 [−17.81; −17.61]‰).

## DISCUSSION

Killer whale ecotypes in the Northeast Pacific have become an important study system of ecological diversification due to their discrete diet based on either fish or mammals, which is in turn linked to behavioral differences and social and genetic segregation (Riesch et al. 2012). In contrast, this study on a population of Northeast Atlantic killer whales previously presumed to be herring specialists (Sigurjónsson et al. 1988, Simon et al. 2007) provides isotopic evidence for fine-scale within-population niche variation. The variation in $\delta^{15}N$ values spanned ~2.5‰, a value consistent with over 1 trophic level of niche width, assuming estimates of discrimination factors in killer whale skin of around ~1.3‰ (García-Tiscar 2009). When the stable isotopic values are examined in the light of individual sighting history information, variation in $\delta^{15}N$ values correlated with season and movement patterns. This indicates that while many individuals appeared to specialise on herring, not all individuals within the population were equivalent. A few individuals had stable isotope values indicative of a broader diet, which could include seasonal or opportunistic targeting of herring.

### Variation in isotopic niche with movement pattern

Whales that appeared to follow herring year round had overall lower $\delta^{15}N$ than whales seen in only one season as well as a significantly narrower trophic niche width. A diet composed exclusively of herring was consistent with the stable isotopic values of these whales, and year-round specialisation on herring was supported by a very low difference in repeated samples collected from the same individuals across seasons. Among whales only seen in one season, there was increased variation in $\delta^{15}N$ values, with

some whales grouping well with whales following herring but others having higher $\delta^{15}N$ values indicative of incorporation of higher trophic level prey in their diet. This increased variation was evident in the low rate of discrimination between this and the other groups in the DFA. The individuals seen in only one season but with $\delta^{15}N$ values similar to those following herring year round also grouped well with a diet consisting mainly of herring, indicating that some whales may follow herring year round but to unknown locations.

There was particularly good discrimination in $\delta^{15}N$ values between whales following herring year round and whales travelling seasonally to Scotland. For some of the whales seen in only one season, and particularly those known to travel seasonally between Iceland and Scotland, $\delta^{15}N$ values were higher than expected based on a diet consisting exclusively of herring. While they may seasonally aggregate in herring grounds to exploit this prey, the diet of these individuals appears to also include higher trophic level prey. Indeed, two of the biopsy-sampled individuals included in this study that are seen seasonally travelling between Iceland and Scotland (IS172 and 997, Table S1 in the Supplement) have been confirmed attacking and consuming grey seals *Halychoerus grypus* in summer in Scotland (Fig. S1 in the Supplement). Nevertheless, the presence of individuals with presumably mixed diets was not related with sighting frequency. Indeed, the individuals sighted moving between Iceland and Scotland are sighted frequently in the herring overwintering grounds (Samarra & Foote 2015), despite their higher $\delta^{15}N$ values. Thus, although we lack sufficient information in this study to elucidate what other high trophic level prey may compose their diet in Iceland or other locations where these whales may travel to, at least some individuals within the population have a broader niche width and do not specialise exclusively on fish. Complementary analysis on other chemical tracers (e.g. Herman et al. 2005) and genetic markers should provide a better understanding of the level of dietary and demographic structuring in this population.

### Intra-population diversity in prey specialisation

In killer whales, the occurrence of a mixed diet, including high and low trophic level prey, has been visually observed in several locations and shown based on stable isotope analysis (Foote et al. 2009, 2013, Reisinger et al. 2016). In the North Atlantic, analysis of stranded and museum specimens showed the existence of an ecotype including individual-level variation in the proportional contribution of fish and marine mammal prey to the diet (Foote et al. 2009), a finding supported by a few observations in Norway of a group of killer whales switching between the 2 prey types (Vongraven & Bisther 2014). In Icelandic waters, sympatric killer whales appear to divide into different movement patterns that correlate with their use of resources, with apparent seasonal overlap in targeted resources. While some whales appear to specialise on herring year round, others target both herring and other higher trophic level prey and appear to maintain such preferences over time. This indicates a generalist population, but one in which isotopic niche width is primarily driven by among-individual or group variation rather than by all individuals consuming the same wide range of prey, as it has been reported to occur in other taxa (Bolnick et al. 2003, 2007, Araújo et al. 2011).

Ecological variation and divergence appears to be an important factor promoting genetic divergence in marine top predators (e.g. Louis et al. 2014), including killer whales (Foote et al. 2016). Unlike sympatric killer whale populations of different ecotypes described in other areas that are ecologically, socially and genetically isolated (e.g. Ford et al. 1998, 2011), in Iceland ecological specialisation does not appear to occur at the population level. Instead, groups within the population appear to share part of their ecological niche at least seasonally. This shared niche, together with temporary social associations (Tavares et al. 2016), may mean that there is no genetic divergence between the different groups described here and, thus, that different movement patterns and foraging traditions may be maintained without genetic divergence. This would agree with observations of the maintenance of among-individual ecological variation in North Atlantic killer whales across thousands of years without leading to sympatric speciation (Foote et al. 2013); however, genetic analyses will be required to assess whether the observed ecological diversity maps to different lineages.

Our study was composed, in most cases, of only one measurement per individual, which precluded us from evaluating within-individual variation, except for 3 individuals that showed very low variation in stable isotopic values between seasons, supporting specialisation on herring year round. Together with movement patterns that appear to be maintained over several years (Foote et al. 2010, Samarra & Foote

2015), the analysis in this study suggests that foraging traditions may be kept in the long term. Such persistent variation in foraging behaviour is in agreement with the large variance in $\delta^{15}N$ values, indicative of a wide ecological niche, found in long-term dietary markers (tooth and bone) for Type 1 killer whales in the North Atlantic (Foote et al. 2009). Assessing the long-term stability of dietary preferences for herring-eating killer whales, by combining repeated feeding observations and isotopic measurements of identified individuals, would be important in the future, particularly if potential changes in stable isotope baselines are concurrently monitored.

Our study strongly supports the existence of herring-specialist killer whales that target this prey year round and follow its migration. Specialisation allows individuals to develop and refine foraging techniques and makes them more efficient hunters. Indeed, herring-eating killer whales are known to employ a complex group-coordinated feeding strategy to target herring (Similä & Ugarte 1993). In highly specialised killer whale populations, low prey abundance can severely impact population demography (Ward et al. 2009, Ford et al. 2010, Esteban et al. 2016) and social connectivity (Foster et al. 2012). Herring is a prey known to change migration routes and to be subject to severe changes in abundance (Jakobsson & Stefánsson 1999, Óskarsson et al. 2009), and as a consequence, whenever its abundance falls below certain levels, it is likely to impact the demography and social connectivity of herring-specialist killer whales. Consequently, assessing the degree of dependence on herring as well as determining the proportion of specialised individuals within the killer whale population and their level of foraging flexibility is of utmost relevance to investigate the effects of this top marine predator in the ecosystem and its resilience to environmental changes. Assessing the long-term variation in prey specialisation within this population will also increase our understanding of the role such variation may play in eventual ecotype formation in these long-lived top predators.

*Acknowledgements*. We sincerely thank all the people involved in the fieldwork for their help in collecting the data as well as Láki Tours, particularly Gísli Ólafsson, in Grundarfjörður and the Vestmannaeyjar Research Centre, particularly Dr. Páll Jónsson, in Vestmannaeyjar for logistical support. We thank Tryggvi Sveinsson for help in collecting killer whale biopsy samples in 2013 and Dr. Patrick Miller for providing the ARTS biopsy system in 2014. We thank Wouter Jan Strietman and Wim en Viv for providing pictures of the whale with a lumpfish in its mouth and Guðmundur Óskarsson and Jón Sólmundsson for help in identifying the species, as well as Leticiaà Legat for additional pictures of the feeding event involving a salmon and Benóný Jónsson for help in identifying the species. Thank you to the Fair Isle Bird Observatory, particularly Sam Hood and David Parnaby, for kindly providing photographs and information on the seal predation event observed off Fair Isle. We also thank Sara Tavares for help in processing individual photo-identifications and for providing the genetic results for sex determination, as well as Andy Foote for commenting on an earlier version of the manuscript. The stable isotope analyses were conducted at CCiT-UB, where we thank Pilar Rubio for support during laboratory work. Biopsy sampling methods were approved by the School of Biology Ethics Committee of the University of St. Andrews. Funding was provided by an Icelandic Research Fund (i. Rannsóknasjó ur) START Postdoctoral Fellowship (grant number 120248042) to F.I.P.S. All research and sample collection was carried out in compliance with local regulations and under an institutional permit for the Marine Research Institute, Reykjavík.

## LITERATURE CITED

Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. Ecol Lett 14:948–958

Baird RW, McSweeney DJ, Bane C, Barlow J and others (2006) Killer whales in Hawaiian waters: information on population identity and feeding habits. Pac Sci 60:523–530

Barrett-Lennard LG (2000) Population structure and mating patterns of killer whales (*Orcinus orca*) as revealed by DNA analysis. PhD dissertation, University of British Columbia, Vancouver, BC

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73: 1007–1012

Best PB, Meÿer MA, Lockyer C (2010) Killer whales in South African waters — a review of their biology. Afr J Mar Sci 32:171–186

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

Bolaños-Jiménez J, Mignucci-Giannoni AA, Blumenthal J, Bogomolni A and others (2014) Distribution, feeding habits and morphology of killer whales *Orcinus orca* in the Caribbean Sea. Mammal Rev 44:177–189

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, David JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28

Bolnick DI, Svanbäck R, Araújo MS, Persson L (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proc Natl Acad Sci USA 104:10075–10079

Bolnick DI, Amarasekare P, Araújo MS, Bürger R and others (2011) Why intraspecific trait variation matters in community ecology. Trends Ecol Evol 26:183–192

Borrell A, Abad-Oliva N, Gómez-Campos E, Giménez J, Aguilar A (2012) Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. Rapid Commun Mass Spectrom 26:1596–1602

Browning NE, Dold C, I-Fan J, Worthy, GAJ (2014) Isotope turnover rates and diet–tissue discrimination in skin of *ex situ* bottlenose dolphins (*Tursiops truncatus*). J Exp Biol 217:214–221

Burdin AM, Hoyt E, Sato H, Tarasyan K, Filatova O (2004) Resident and transient-type killer whales, *Orcinus orca*, in southeast Kamchatka, Russia. Rep Sci Comm Int Whal Comm SC/56/SM15:1–3

Capella JJ, Abramson JZ, Vilina YA, Gibbons J (2014) Observations of killer whales (*Orcinus orca*) in the fjords of Chilean Patagonia. Polar Biol 37:1533–1539

Caut S, Laran S, Garcia-Hartmann E, Das K (2011) Stable isotopes of captive cetaceans (killer whales and bottlenose dolphins). J Exp Biol 214:538–545

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281–287

Dahlheim ME, Schulman-Janiger A, Black N, Ternullo R, Ellifrit D, Balcomb KC (2008) Eastern temperate North Pacific offshore killer whales (*Orcinus orca*): occurrence, movements, and insights into feeding ecology. Mar Mamm Sci 24:719–729

de Bruyn PJN, Tosh CA, Terauds A (2013) Killer whale ecotypes: Is there a global model? Biol Rev Camb Philos Soc 88:62–80

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochim Cosmochim Acta 45:345–351

Durban JW, Fearnbach H, Burrows DG, Ylitalo GM, Pitman RL (2017) Morphological and ecological evidence for two sympatric forms of Type B killer whale around the Antarctic Peninsula. Polar Biol 40:231–236

Esteban R, Verborgh P, Gauffier P, Giménez J, Foote AD, de Stephanis R (2016) Maternal kinship and fisheries interaction influence killer whale social structure. Behav Ecol Sociobiol 70:111–122

Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE (2003) Individual variation in prey selection by sea otters: patterns, causes and implications. J Anim Ecol 72: 144–155

Foote AD, Newton J, Piertney SB, Willerslev E, Gilbert MTP (2009) Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. Mol Ecol 18:5207–5217

Foote AD, Similä T, Víkingsson GA, Stevick PT (2010) Movement, site fidelity and connectivity in a top marine predator, the killer whale. Evol Ecol 24:803–814

Foote AD, Vester H, Víkingsson GA, Newton J (2012) Dietary variation within and between populations of northeast Atlantic killer whales, *Orcinus orca*, inferred from $\delta^{13}C$ and $\delta^{15}N$ analyses. Mar Mamm Sci 28: E472–E485

Foote AD, Newton J, Ávila-Arcos MC, Kampmann ML and others (2013) Tracking niche variation over millennial timescales in sympatric killer whale lineages. Proc R Soc B 280:20131481

Foote AD, Vijay N, Ávila-Arcos MC, Baird RW and others (2016) Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. Nat Commun 7: 11693

Ford JKB, Ellis GM (2006) Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. Mar Ecol Prog Ser 316:185–199

Ford JKB, Ellis GM (2014) You are what you eat: foraging specializations and their influence on the social organization and behavior of killer whales. In: Yamagiwa J, Karczmarski L (eds) Primates and cetaceans: field research and conservation of complex mammalian societies. Primatology Monographs, Springer, Tokyo, p 75–98

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

Ford JKB, Ellis GM, Olesiuk PF, Balcomb KC (2010) Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? Biol Lett 6:139–142

Ford JKB, Ellis GM, Matkin CO, Wetklo MH, Barrett-Lennard LG, Withler RE (2011) Shark predation and tooth wear in a population of northeastern Pacific killer whales. Aquat Biol 11:213–224

Ford MJ, Hempelmann J, Hanson MB, Ayres KL and others (2016) Estimation of a killer whale (*Orcinus orca*) population's diet using sequencing analysis of DNA from feces. PLOS ONE 11:e0144956

Forney KA, Wade P (2006) Worldwide distribution and abundance of killer whales. In: Estes JA, Brownell RL, DeMaster DP, Doak DF, Williams TM (eds), Whales, whaling, and ecosystems. University of California Press, Berkeley, CA, p 145–162

Foster EA, Franks DW, Mazzi S, Darden SK, Balcomb KC, Ford JKB, Croft DP (2012) Adaptive prolonged postreproductive life span in killer whales. Science 337:1313

García-Tiscar S (2009) Interacciones entre delfines mulares (*Tursiops truncatus*), orcas (*Orcinus orca*), y pesquerías en el mar de Alborán y Estrecho de Gibraltar. PhD dissertation, Universidad Autónoma de Madrid

Giménez J, Ramírez F, Almunia J, Forero M, de Stephanis R (2016) From the pool to the sea: applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (*Tursiops truncatus*). J Exp Mar Biol Ecol 475:54–61

Guinet C (1992) Predation behavior of killer whales around Crozet Islands. Can J Zool 70:1656–1667

Hanson MB, Baird RW, Ford JKB, Hempelmann-Halos J and others (2010) Species and stock identification of prey consumed by endangered southern resident killer whales in their summer range. Mar Ecol Prog Ser 11: 69–82

Herman DP, Burrows DG, Wade PR, Durban JW and others (2005) Feeding ecology of eastern North Pacific killer whales *Orcinus orca* from fatty acid, stable isotope, and organochlorine analyses of blubber biopsies. Mar Ecol Prog Ser 302:275–291

Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar Ecol Prog Ser 84:9–18

Hoyt E (1984) Orca, the whale called killer. Camden House Publishing, Camden East, Ontario

ICES (International Council for the Exploration of the Sea) (2014) Report of the North-Western Working Group (NWWG), 24 April–1 May 2014. ICES CM 2014/ACOM: 07, ICES, Copenhagen

Iñiguez MA, Tossenberger VP, Gasparrou C (2002) Cooperative hunting and prey handling of killer whales in Punta Norte, Patagonia, Argentina. In: Proc 4th Int Orca Symp Workshops, Villiers en Bois, 23–28 September 2002. CEBC-CNRS, Villiers en Bois, p 85

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602

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

Jefferson TA, Stacey PJ, Baird RW (1991) A review of killer whale interactions with other marine mammals: predation to co-existence. Mammal Rev 21:151–180

Kiszka J, Lesage V, Ridoux V (2014) Effect of ethanol preservation on stable carbon and nitrogen isotope values in cetacean epidermis: implication for using archived biopsy samples. Mar Mamm Sci 30:788–795

Krahn MM, Hanson MB, Baird RW, Boyer RH and others (2007a) Persistent organic pollutants and stable isotopes in biopsy samples (2004/2006) from southern resident killer whales. Mar Pollut Bull 54:1903–1911

Krahn MM, Herman DP, Matkin CO, Durban JW and others (2007b) Use of chemical tracers in assessing the diet and foraging regions of eastern North Pacific killer whales. Mar Environ Res 63:91–114

Kvadsheim PH, Lam FPA, Miller PJO, Alves AC and others (2009) Cetaceans and naval sonar—the 3S-2009 cruise report. FFI-rapport 2009/01140, Forsvarets Forskningsintitutt/Norwegian Defence Research Establishment, Kjeller

LeDuc RG, Robertson KM, Pitman RL (2008) Mitochondrial sequence divergence among Antarctic killer whale ecotypes is consistent with multiple species. Biol Lett 4: 426–429

Louis M, Fontaine MC, Spitz J, Schlund E and others (2014) Ecological opportunities and specializations shaped genetic divergence in a highly mobile marine top predator. Proc R Soc B 281:20141558

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. J Mar Biol Assoc UK 94:1343–1355

Mayr E (1947) Ecological factors in speciation. Evolution 1: 263–288

Michener RH, Schell DM (1994) Stable isotope ratios as tracers in marine aquatic food webs. In: Lajtha K, Michener RH (eds) Stable isotopes in ecology and environmental science. Blackwell, Oxford, p 138–157

Moura AE, Kenny JG, Chaudhuri R, Hughes MA and others (2014) Population genomics of the killer whale indicates ecotype evolution in sympatry involving both selection and drift. Mol Ecol 23:5179–5192

Newsome SD, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML, Estes JA (2009a) Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). Ecology 90:961–974

Newsome SD, Etnier MA, Monson DH, Fogel ML (2009b) Retrospective characterization of ontogenic shifts in killer whale diets via $\delta^{13}C$ and $\delta^{15}N$ analysis of teeth. Mar Ecol Prog Ser 374:229–242

Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mamm Sci 26:509–572

Óskarsson GJ, Gudmundsdottir A, Sigurdsson T (2009) Variation in spatial distribution and migration of Icelandic summer-spawning herring. ICES J Mar Sci 66: 1762–1767

Pitman RL, Durban JW (2010) Killer whale predation on penguins in Antarctica. Polar Biol 33:1589–1594

Pitman RL, Durban JW (2012) Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. Mar Mamm Sci 28:16–36

Pitman RL, Ensor P (2003) Three forms of killer whales (*Orcinus orca*) in Antarctic waters. J Cetacean Res Manag 5:131–139

Pitman RL, Perryman WL, LeRoi D, Eilers E (2007) A dwarf form of killer whale in Antarctica. J Mammal 88:43–48

Pitman RL, Durban JW, Greenfelder M, Guinet C and others (2011) Observations of a distinctive morphotype of killer whale (*Orcinus orca*), type D, from subantarctic waters. Polar Biol 34:303–306

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reisinger RR, Gröcke DR, Lübcker N, McClymont EL, Hoelzel AR, de Bruyn PJN (2016) Variation in the diet of killer whales *Orcinus orca* at Marion Island, Southern Ocean. Mar Ecol Prog Ser 549:263–274

Riesch R, Barrett-Lennard LG, Ellis GM, Ford JKB, Deecke VB (2012) Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? Biol J Linn Soc 106:1–17

Rundle HD, Nosil P (2005) Ecological speciation. Ecol Lett 8: 336–352

Samarra FIP, Foote AD (2015) Seasonal movements of killer whales between Iceland and Scotland. Aquat Biol 24: 75–79

Samarra FIP, Miller PJO (2015) Prey-induced behavioural plasticity of herring-eating killer whales. Mar Biol 162: 809–821

Sargeant BL, Mann J, Berggren P, Krützen M (2005) Specialisation and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). Can J Zool 83:1400–1410

Saulitis E, Matkin C, Barrett-Lennard L, Heise K, Ellis G (2000) Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. Mar Mamm Sci 16:94–109

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

Similä T, Ugarte F (1993) Surface and underwater 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

Smith TB, Skúlason S (1996) Evolutionary significance of resource polymorphism in fishes, amphibians, and birds. Annu Rev Ecol Syst 27:111–133

Tavares SB, Samarra FIP, Miller PJO (2016) A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. Behav Ecol arw 179. https://doi.org/10.1093beheco/arw179

Tixier P, Authier M, Gasco N, Guinet C (2015) Influence of artificial food provisioning from fisheries on killer whale reproductive output. Anim Conserv 18:207–218

Torres LG, Read AJ (2009) Where to catch a fish? The influ-

ence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. Mar Mamm Sci 25:797–815

Van Valen L (1965) Morphological variation and width of ecological niche. Am Nat 99:377–390

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York, NY

Víkingsson GA (2004) Háhyrningur (killer whale). In: Hersteinsson P (ed) Íslensk spendýr (Mammals of Iceland). Vaka-Helgafell, Reykjavík, p 166–171

Vongraven D, Bisther A (2014) Prey switching by killer whales in the north-east Atlantic: observational evidence and experimental insights. J Mar Biol Assoc UK 94:1357–1365

Ward EJ, Holmes EE, Balcomb KC (2009) Quantifying the effects of prey abundance on killer whale reproduction. J Appl Ecol 46:632–640

Weir CR, Collins T, Carvalho I, Rosenbaum HC (2010) Killer whales (*Orcinus orca*) in Angolan and Gulf of Guinea waters, tropical West Africa. J Mar Biol Assoc UK 90: 1601–1611

*Editorial responsibility: Yves Cherel, Villiers-en-Bois, France*

*Submitted: August 29, 2016; Accepted: November 23, 2016*
*Proofs received from author(s): January 16, 2017*