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ORIGINAL PAPER

Spatial and social connectivity of fish-eating "Resident" killer whales (*Orcinus orca*) in the northern North Pacific

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Abstract The productive North Pacific waters of the Gulf of Alaska, Aleutian Islands and Bering Sea support a high density of fish-eating "Resident" type killer whales (*Orcinus orca*), which overlap in distribution with commercial fisheries, producing both direct and indirect interactions. To provide a spatial context for these interactions, we analyzed a 10-year dataset of 3,058 whale photo-identifications from 331 encounters within a large (linear ~4,000 km) coastal study area to investigate the ranging and social patterns of 532 individually identifiable whales photographed in more than one encounter. Although capable of large-scale movements (maximum 1,443 km), we documented ranges generally <200 km, with high site fidelity across summer sampling intervals and also re-sightings during a winter survey. Bayesian analysis of pair-wise associations identified four defined clusters, likely representing groupings of stable matrilines, with distinct ranging patterns, that combined to form a large network of associated whales that ranged across most of the study area. This provides evidence of structure within the Alaska stock of Resident killer whales, important for evaluating ecosystem and fisheries impacts. This network included whales known to depredate groundfish from longline fisheries, and we suggest that such large-scale connectivity has facilitated the spread of depredation.

Introduction

Describing ranging and distribution patterns within wildlife populations is key to understanding population structure (Whitehead et al. 2008; Silva et al. 2008), identifying important habitat relationships (Tufto et al. 1996; Elwen and Best 2004; Friedlaender et al. 2006) and evaluating and

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mitigating conflicts due to shared resources with humans (Hoare 1999; Sigler et al. 2008; Mazur and Seher 2008; Whitehead 2010). In mammals, social organization may underlie ranging patterns, both by restricting movements and reflecting a response to a heterogeneous environment (Emlen and Oring 1977; Clutton-Brock and Harvey 1977; Packer et al. 1990; Wittemyer et al. 2005; Whitehead et al. 2008). Analysis of social affiliations between individuals can provide context for understanding individual movements, as well as the overall social structure of the population, and can further our understanding of the spatial ecology and resource requirements of a population.

The influence of social structure on the spatial partitioning of populations is likely to be particularly important in the marine environment (e.g., Lusseau et al. 2005), where there is an absence of major physical barriers to movement. It is therefore not unexpected that some of the most stable social structures among mammals are found in the marine environment, notably the matrilineally structured societies of killer whales (Bigg et al. 1990; Baird and Whitehead 2000; Parsons et al. 2009). Long-term studies in the eastern North Pacific have documented three genetically divergent, sympatric lineages (Stevens et al. 1989; Hoelzel and Dover 1991; Hoezel et al. 1998, 2002; Barrett-Lennard 2000) with differences in morphology (Baird and Stacey 1988; Ford et al. 2000), vocalizations (Ford 1989; Barrett-Lennard et al. 1996a, b; Deecke et al. 2005) and social structure (Bigg et al. 1990; Baird and Whitehead 2000). It has been suggested that the evolution of these lineages has been supported by cultural traditions, vertically transmitted across generations within stable family groupings (Baird 2000; Rendell and Whitehead 2001; Yurk et al. 2002), and has recently been proposed that they may represent different species (Morin et al. 2010). These lineages have distinct prey specializations (Ford et al. 1998; Saulitis et al. 2000), with "Resident" type killer whales feeding on fish, notably salmon in some areas (Ford and Ellis 2006), "Bigg's" killer whales (previously referred to as "transients," Ford 2011) feeding on marine mammals and "Offshores" thought to specialize on high trophic level fish (Herman et al. 2005; Krahn et al. 2007a; Dahlheim et al. 2008), notably sharks in recent observations (Ford et al. 2011). Consequently, these lineages are often referred to as "ecotypes" (Ford et al. 2000).

Killer whale social and population ecology is well documented for the coastal waters of the eastern North Pacific. However, relatively few data exist for the more remote waters of the northern North Pacific, despite the densities of killer whales in the Gulf of Alaska (GOA), Aleutian Islands and Bering Sea being among the highest in the world (Forney and Wade 2006). Recent work has shown that the dietary differences and ecotype classification of killer whales from the eastern North Pacific also extend to these more remote waters (Herman et al. 2005; Krahn et al. 2007a), and the fish-eating Residents are by far the most abundant (Zerbini et al. 2007; Matkin et al. 2007; Durban et al. 2010). This high density of Resident killer whales overlaps in distribution with the most lucrative commercial fisheries in US waters, producing both direct and indirect interactions between whales and fisheries (Braham and Dahlheim 1982; Yano and Dahlheim 1995; Dahlheim 1997). There is still considerable uncertainty about the diet of Residents that occur in this region (Herman et al. 2005; Krahn et al. 2007a), but observations have included whales feeding on commercially important species such as Atka mackerel (*Pleurogrammus monopterygius*), Pacific salmon (*Oncorhynchus* spp.) and Pacific halibut (*Hippoglossus stenolepis*) (Matkin et al. 2007; NMML, unpublished data). Additionally, Residents commonly depredate halibut, sablefish (*Anoplopoma fimbria*), arrowtooth flounder (*Atheresthes stomias*), Greenland turbot (*Reinhardtius hippoglossoides*) and Pacific cod (*Gadus macrocephalus*) from longline fisheries (Yano and Dahlheim 1995; Lunsford and Rutecki 2010; Peterson et al. 2013) and are frequently observed feeding on the discards of trawlers (Yano and Dahlheim 1995; Matkin et al. 2007). Killer whales are known to have high caloric requirements (Williams et al. 2004; Noren 2011) and the impact of this competition with fisheries may be considerable (Lunsford and Rutecki 2010; Peterson et al. 2013).

Assessment of the spatial extent, intensity and value of these interactions is required to develop mitigation strategies and account for this substantial natural mortality in ecosystem and fisheries assessments (Lunsford and Rutecki 2010; Peterson et al. 2013). This in turn requires data on the distribution and population structuring of killer whales in this region. Currently, all Resident killer whales in the GOA, Aleutian Islands and Bering Sea are managed as the "Eastern North Pacific Alaska Resident" stock (Allen and Angliss 2012), but there is new genetic evidence of structure at finer spatial scales (Parsons et al. 2013). In this study, we use 10 years of sighting surveys and photo-identifications of individual whales to explore the spatial connectivity of Resident killer whales in coastal waters from the western GOA to the western Aleutian Islands, including the Bering Sea shelf edge. We include a quantitative description of the social structure underlying individual movements. Notably, we examine the associations and movements of whales that have been observed to depredate longlines to understand their social and spatial relationship within the region.

Materials and methods

Study area and data collection

Photo-identification data were collected from 2001 to 2010, during sightings surveys conducted in coastal waters

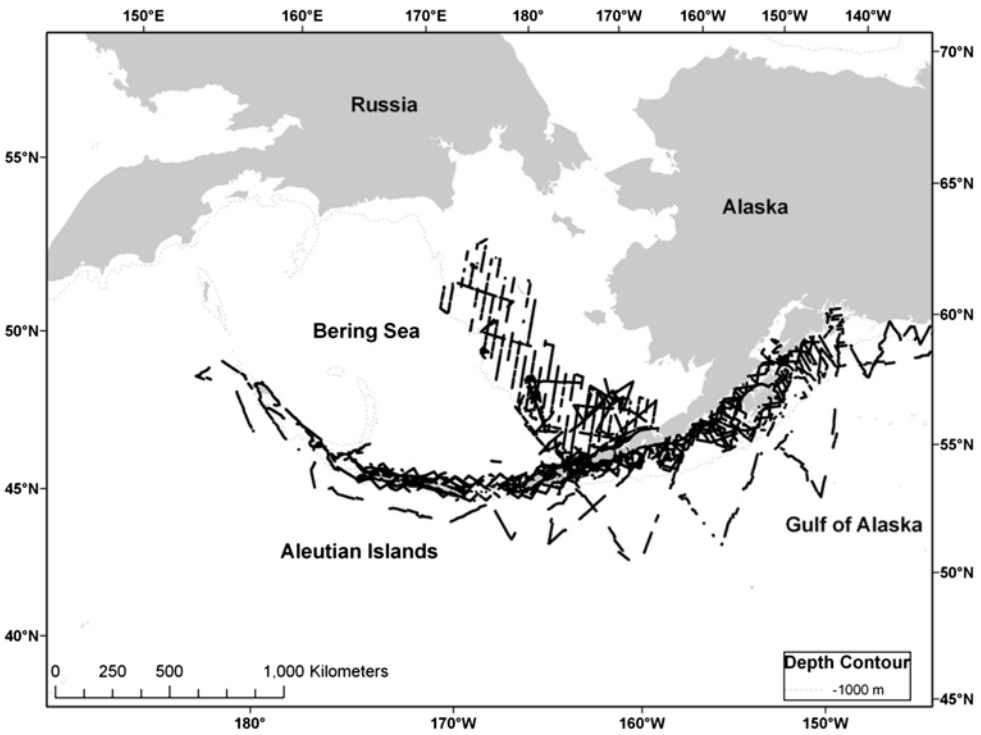

Fig. 1 Map showing vessel track lines (*solid lines*) during sightings surveys with photo-identification of killer whales, 2001–2010

ranging from the northern GOA (~60°N, 150°W) to the western extent of US waters in the western Aleutian Islands (~55°N, 175°E), including the waters of the continental shelf edge in the Bering Sea. The area surveyed covered a linear distance of ca. 4,000 km, generally including waters <30 km from shore or the shelf edge (Fig. 1). This large area is composed of a varied physical environment, ranging from continental shelf waters in the east to deep pelagic waters around the western Aleutian Islands, with highly productive passes between the Aleutian Islands (Hunt and Stabeno 2005; Ladd et al. 2005).

Sighting surveys consisted of a combination of directed surveys to search for killer whales, and surveys when killer whale sightings and photo-identification data were collected opportunistically from other platforms (Table 1). These surveys were primarily conducted in the summer months between May and September, but there was additional survey effort in late February and early March 2008. The directed surveys were designed to investigate the distribution and abundance of killer whales throughout the study area; line-transect methods were employed for random-area coverage from 2001 to 2003 (Zerbini et al. 2007), and surveys from 2004 to 2010 adopted a more focused approach to survey in areas known to be regularly used by killer whales. Large charter vessels (40–60 m) were used for these surveys, and observers searched for killer whales using handheld 7 × 50 binoculars or fixed-mount 25× magnification binoculars from heights of 5.5–10 m (e.g., Zerbini et al. 2007). Directed killer whale surveys were also conducted in a focused area of the eastern Aleutian Islands from 2001 to 2005 using smaller (10–14 m) charter fishing vessels (NGOS, Table 1; Matkin et al. 2007).

Data were also collected on an opportunistic basis from a number of platforms: during wide-scale sightings surveys for humpback whales (04MA, 05OD; Calambokidis et al. 2008) and right whales (02MA, 07OD, 08OL; LeDuc 2004; Clapham et al. 2009; Wade et al. 2011); cetacean surveys aboard walleye pollock (*Theragra chalcogramma*) trawl research surveys (02MF, 03MF, 04MF; Moore et al. 2002; Waite et al. 2002); and oceanographic surveys (01AH, 02AH; Sinclair et al. 2005) (Table 1). Photographs and geolocations of depredating killer whales were taken by observers during standardized longline fishing surveys in the summers of 2006–2010 (Lunsford and Rutecki 2010; Peterson et al. 2013), providing a sample of whales that were observed to be actively depredating on groundfish during longline fishing operations.

When killer whales were encountered during these surveys, identification photographs were taken from the ship platform or during closer approaches using a 6-m rigid hulled inflatable boat (RHIB). An attempt was always made to photograph as many different individuals within the encounter as possible. Encounters were stratified into apparently spatially contiguous aggregations of whales that were typically with 500 m of each other. During dedicated surveys, skin and blubber samples were also collected using remote biopsy techniques (e.g., Barrett-Lennard et al. 1996a, b). These samples were used in combination

Table 1 List of dedicated (D) killer whale sighting surveys and opportunistic (O) platforms from which killer whale photo-identification data were collected

Survey	Ship	Dates	Type	Areas	IDs
01AH	F/V Alpha Helix	04-Jun-01: 17-Jun-01	O: Oceanographic	1, 2, 4, 5, 8	98
01AM	F/V Aleutian Mariner	20-Jul-01: 25-Aug-01	D: Killer whale	1, 2, 3, 4, 5, 8	123
02AH	F/V Alpha Helix	21-May-02: 18-Jun-02	O: Oceanographic	1, 2 4, 5, 8	99
02CP	F/V Coastal Pilot	12-Jul-02: 20-Aug-02	D: Killer whale	1, 2, 3, 4, 5, 8	112
02MA	R/V MacArthur I	13-Jul-02: 29-Aug-02	O: Right whale	1, 2, 3, 4, 7, 8	14
02MF	R/V Miller Freeman	16-Jun-02: 28-Jul-02	O: Pollock trawl	2, 4, 7, 8	20
03CP	F/V Coastal Pilot	03-Jul-03: 14-Aug-03	D: Killer whale	1, 2, 3, 4, 5, 8	153
03MF	R/V Miller Freeman	27-Jun-03: 15-Jul-03	O: Pollock trawl	1, 2	4
04AE	F/V Alaskan Enterprise	21-Jul-04: 27-Aug-04	D: Killer whale	2, 3, 4, 5, 7, 8	58
04MA	R/V MacArthur II	29-Jun-04: 31-Oct-04	O: Humpback whale	1–8	100
04MF	R/V Miller Freeman	04-Jun-04: 04-Jul-04	O: Pollock trawl	2, 4, 7, 8	6
05AE	F/V Alaskan Enterprise	31-May-05: 11-Jul-05	D: Killer whale	2, 4, 5, 6, 7, 8	131
05OD	R/V Oscar Dyson	02-Aug-05: 28-Sep-05	O: Humpback whale	1, 2	20
06OL	F/V Ocean Olympic	31-May-06: 25-Jun-06	D: Killer whale	4, 5, 6, 7, 8	253
07OD	R/V Oscar Dyson	01-Aug-07: 28-Aug-07	O: Right whale	4, 8	16
07OL	F/V Ocean Olympic	30-May-07: 16-Jun-07	D: Killer whale	4, 8	9
08DA	R/V Oscar Dyson	15-Feb-08: 03-Mar-08	O: Pollock trawl	4, 5	15
08OL	F/V Ocean Olympic	02-Aug-08: 12-Sep-08	O: Right whale	2, 4, 8	5
09AQ	F/V Aquila	21-Jun-09: 14-Jul-09	D: Killer whale	4, 5, 7, 8	79
10AE	F/V Alaskan Enterprise	24-Jun-10: 12-Jul-10	D: Killer whale	4, 5, 6	197
LL	F/V Alaskan Leader	May–Sep 06–10	O: Longline	2, 3, 4, 5, 7, 8	41
NGOS	Various	May–Sep 01–05	D: Killer whale	4, 8	288

"Areas" lists the 5° latitude by 10° longitude areas that were covered by each survey area (see Fig. 2), and IDs is the total number of distinct "Resident" type killer whales identified from high-quality photographs on each survey

with the photographs to confirm lineage. Lineage assignment was made using the criteria established in previous studies in this region (Matkin et al. 2007; Zerbini et al. 2007; Durban et al. 2010; Parsons et al. 2013), based on a combination of molecular genetic analysis from skin samples (Parsons et al. 2013) to corroborate assignments based primarily on morphological characteristics of the photographed whales. Resident killer whales are by far the most frequently encountered in this region (Zerbini et al. 2007) and can be readily distinguished from Bigg's and Offshore killer whales in photographs by experienced observers (Durban et al. 2010). Specifically, there are key morphological differences in dorsal fin shape and saddle patch pigmentation that have been long established as diagnostic features to distinguish these lineages (Baird and Stacey 1988; Ford et al. 2000). In this study, all photographic assignments were conducted by at least two of the authors, who independently analyzed all photographs collected in each encounter, extending previous assessments of lineage in earlier examinations of this growing dataset (Zerbini et al. 2007; Matkin et al. 2007; Durban et al. 2010). Where available, genetic analysis of biopsy samples was used to directly confirm the ecotype identity of whales in a sampled encounter and to indirectly assign whales in additional encounters through association with individuals from a biopsied encounter (e.g., Zerbini et al. 2007; Matkin et al. 2007; Durban et al. 2010; Parsons et al. 2013). This approach is validated by an absence of association between killer whales of different lineages in the North Pacific, including our study area, despite decades of previous observations (Ford et al. 1998, 2000; Matkin et al. 2007; Zerbini et al. 2007; Durban et al. 2010; Parsons et al. 2013).

Photo analysis

Photo-identification images were taken with either 35-mm SLR cameras, shooting Fuji Neopan 1600 ISO black and white film (2000–2003), or with digital SLR cameras with a minimum resolution of 6 MP (2004–2010). All 35-mm photo-identification images were digitized using a slide copy adaptor to capture 6 MP tagged image format files with a Nikon Coolpix digital camera. Once all images were in digital format, the best photograph of each whale, in each encounter (the best-in-encounter photograph), was selected.

Each best-in-encounter photograph was then compared to a master photo-identification catalog of individuals. If a match was found, the whale was linked with the corresponding identification number. If no match was found, a new number was assigned. Although unique identification numbers were assigned to every whale that could be differentiated during an encounter, permanent numbers were only assigned to whales that were deemed to be distinctly marked so that they could be matched between encounters

and across years. Temporary numbers were assigned to whales that could only be distinguished within the encounter and were not sufficiently distinct to track over time. Distinctiveness was based on a combination of features of the dorsal fin (e.g., distinctive shape, the presence of notches) and the adjacent saddle patch (distinctive pigmentation, scarring patterns) following Durban et al. (2010), with the distinctiveness of features being determined by the expert opinion of two of the authors (H.F., D.E.). Only distinctive whales were used in the subsequent analysis. In addition, all best-in-encounter photographs were assigned quality grades (Q = 1–3) for exposure, amount of fin and saddle captured, clarity and angle, and only high-quality photographs ($Q > 1$ for all categories) were included in the subsequent analysis.

Data analysis

Ranging patterns were examined for all distinctly marked individuals that were identified two or more times. We used ARCGIS 9.2 (www.esri.com) with Hawth's analysis tools (http://www.spatialecology.com/htools/tooldesc.php) to map encounter locations for each individual and summarized two ranging parameters: maximum extent of movement and maximum longitudinal range using the great circle distance calculation. Spatial ranging was further summarized by examining the overlap of individual encounter locations relative to eight areas of dimension 5° latitude by 10° longitude (Fig. 2).

Associations between individuals were evaluated using the half-weight index (HWI, Cairns and Schwager 1987), also known as Dice's index (Dice 1945). We assumed that any two whales identified in the same encounter were associated, and the half-weight index of association was calculated for each pair of whales as $\mathrm{HWI} = 2X/(A + B)$, where X = the total number of times that individuals A and B were observed together and $A + B$ represents the total number of times individuals A and B were observed (Cairns and Schwager 1987). The HWI, therefore, ranged from 0, when two individuals were never seen in the same encounter, to 1, if two individuals were always seen together.

To characterize population structure, we adopted a Bayesian approach to fitting a social network model to identify significant clusters of associates from the repeated pair-wise association measures. Specifically, we used the Latentnet package from the statistical software program R (R Development Core Team 2011) to fit latent position and cluster models to these association indices (Krivitsky and Handcock 2008). This approach assumes the existence of a latent (unknown) space of sociality of the individuals, where the probability of a relationship between two individuals is modeled as a function of an estimated distance between two individuals in a two-dimensional Euclidean "social space" (e.g., Hoff et al. 2002). Latentnet provides a way of assessing the significance of social relationships (distances) between individuals by assigning cluster membership for each individual based on their position in Euclidean space (Krivitsky and Handcock 2008). This Bayesian inference is probabilistic, estimating the probability of each whale belonging to each cluster, which is desirable given sparse observational data with limited numbers of re-sightings across this large study area. The package performs estimation using a Markov Chain Monte Carlo (MCMC) algorithm and provides a way of assessing how many clusters there are by identifying the model (number of clusters) with the lowest Bayesian information criterion (BIC). As with other model selection methods, this criterion achieves a compromise between the goodness-of-fit and a penalty for the number of free parameters in the model; the model with the smallest BIC value was estimated to be the model that best fit the data. We fit the social network models to two datasets, to assess the sensitivity of inference to the selected number of sightings that qualified individuals for inclusion in the analysis. One dataset comprised association indices between all whales that were seen on two or more occasions and another restricted the dataset to whales that were seen on three or more occasions.

Results

Data samples

A total of 331 encounters with Resident killer whales were included in analyses (Fig. 2), based on assignment to the Resident type. Ecotype identification based on defining morphological characteristics was congruent at all times between the two photo analysts and was also consistent with previous assessments of earlier subsets of these data (Zerbini et al. 2007; Matkin et al. 2007; Durban et al. 2010). There were no disparities between the morphological assessments and the genetic assignments, when available (Parsons et al. 2013). Ecotype identification was directly corroborated by genetic sequence data for 90 of these encounters from which biopsy samples were also obtained from at least one whale and for an additional 205 encounters through individual associations to biopsied whales at other times, for a total of 295 (89 %) of all encounters. Most of the encounters occurred around the central and eastern Aleutian Islands, largely reflecting the increased survey effort in this central area, although Resident killer whales were encountered throughout the study area, ranging from the northern GOA to the western Aleutians and into the Bering Sea. Residents were always encountered in aggregations, ranging in size from 3 to 120 whales (median = 15).

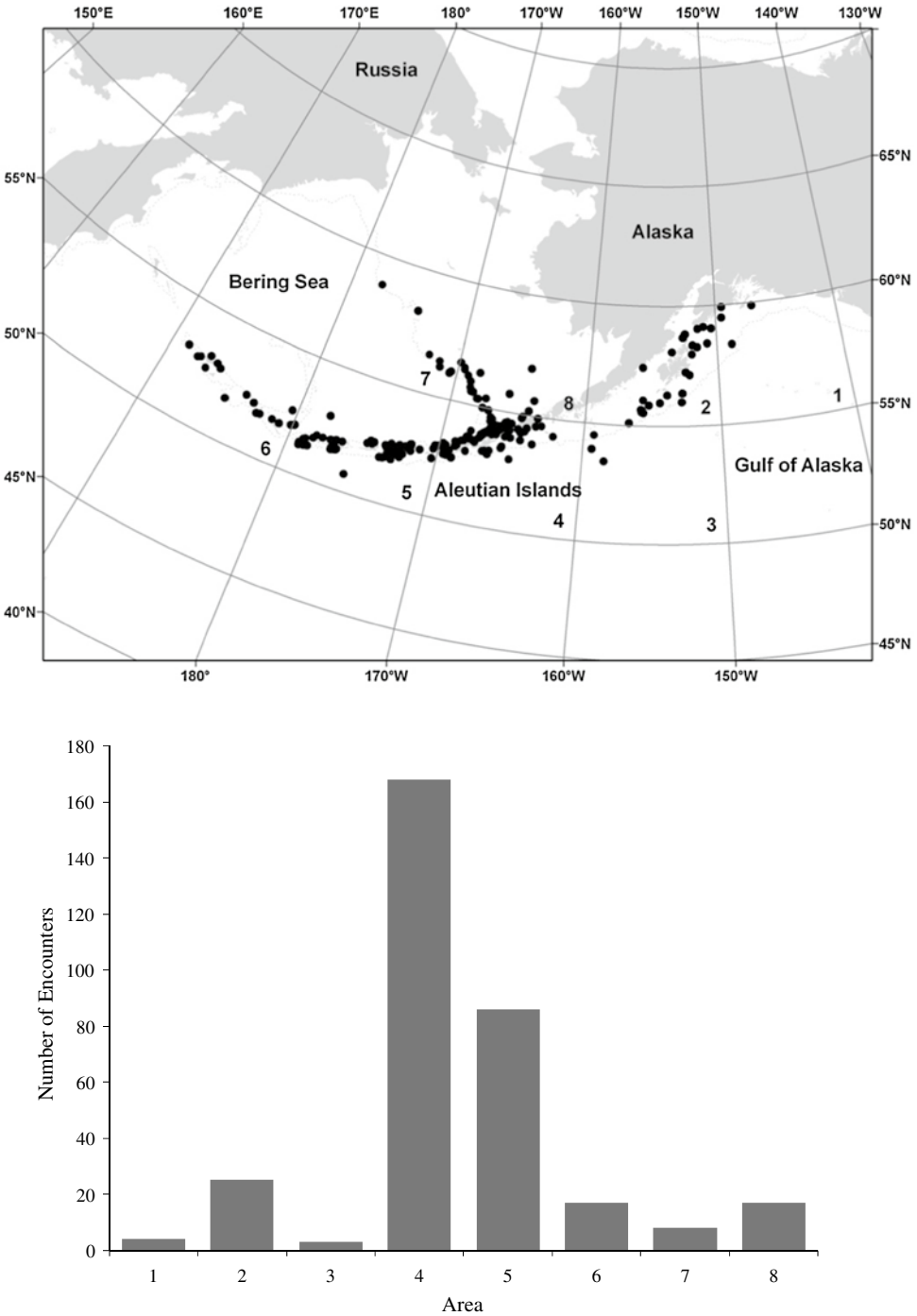

Fig. 2 *Top* map of the study area showing all encounters with "Resident" type fish-eating killer whales from 2001 to 2010 ($n = 331$), *bottom* the number of encounters in each of eight spatial areas of dimension 5° latitude by 10° longitude (see *top*)

In total, 77,815 photographs of Resident killer whales were taken, resulting in 3,058 unique whale-by-encounter identifications and 1,220 distinct individuals. The majority (2,705) of these unique identifications were judged to be of sufficiently reliable photographic quality, comprising 1,186 distinct individuals. The re-sighting frequency varied for these individuals, with a median of 1 encounter per individual, a range of 1–7 encounters, and 417 whales were seen in more than one calendar year (median = 1 year, range 1–6 different years). Most (1,002) of these distinct whales were only seen in a single spatial area, with the highest number seen in the eastern and central Aleutians areas (Fig. 2; areas 4 and 5), with re-sightings in the same area up to 10 years apart. However, 169 whales were photographed in two areas, and 2 whales were documented in three areas. These spatial re-sightings were not solely in adjacent areas, indicating some relatively long-distance movements (Table 2).

Table 2 Table of the total number of distinct individual "Resident" type killer whales that were identified in each of eight spatial areas (diagonal cells) of dimension 5° latitude by 10° longitude (Fig. 2) and overlap of individuals between areas (non-diagonal cells)

	Area 1	Area 2	Area 3	Area 4	Area 5	Area 6	Area 7	Area 8
Area 1	**6**	10	0	0	0	0	0	0
Area 2		**158**	1	21	0	0	0	0
Area 3			**3**	0	0	0	0	0
Area 4				**373**	35	1	7	64
Area 5					**352**	31	0	0
Area 6						**95**	0	1
Area 7							**1**	4
Area 8								**14**

The bold values represent the total number of distinct individual "Resident" type killer whales that were identified in each of eight spatial areas

Examination of re-sighting locations of whales identified during the winter survey (08DA) provided an initial indication of year-round site fidelity. Of the 15 distinct whales identified in area 5 during February 2008, three whales were re-sighted in the summer months, all in area 5. Two of these whales were seen during our surveys (02AH and 06OL), and the third whale (an adult male with distinctly white pigmentation) was photographed 8 years prior to the winter sighting (Renner and Bell 2008).

The 41 whales observed depredating groundfish were seen at survey stations in 5 areas (2, 3, 4, 5 and 7), but were not observed in areas 1, 6 and 8 (Fig. 3a), supporting the widespread practice of depredation in the eastern and central Aleutian Islands, Bering Sea shelf edge and the western GOA, and apparent absence in the GOA waters east of Kodiak Island (Lunsford and Rutecki 2010; Peterson et al. 2013). Most (33/41) of these whales were also seen during other surveys, typically in the same or adjacent areas up to 9 years apart: 19 were observed depredating in two different areas and also re-sighted in the same areas during other surveys; 14 whales were only seen in a single area both while depredating and during surveys. Whales observed depredating in the eastern Aleutians ranged across areas 4 and 5, with two whales moving between area 4 and area 7, along the Bering Sea shelf edge, and one whale re-sighted only within area 5 (Fig. 3a).

Movements

Movement analysis was conducted for all whales seen on more than one occasion ($n = 532$). Examination of the longitudinal ranges of these whales (Fig. 4) indicated limited east–west movements, and most (335/532) of these whales were observed in the same area in different years, indicating long-term site fidelity. Furthermore, the median "range" indicated by the maximum distance between repeated encounter locations was only 196.5 km (interquartile range = 88.5–304.5 km, maximum = 1,443 km). The vast majority (469) of these whales had a maximum extent of their movement being <500 km, although long-distance movements (500–1,450 km) were documented for 63 whales. Of these, 21 whales moved between 750 and 1,000 km and four whales moved more than 1,000 km (Fig. 5).

Maps of these typically short movements (Fig. 3b) illustrate significant spatial structuring, with movements primarily restricted within three regions: the northern GOA (areas 1 and 2), the eastern Aleutian Islands and Bering Sea shelf edge (areas 4, 7 and 8), and the central Aleutian Islands (areas 5 and 6). The relatively rare longer distance movements (Fig. 3c) do show some overlap between the central Aleutian Islands and the eastern Aleutians/Bering Sea shelf edge, and between the eastern Aleutian Islands and western GOA waters west of Kodiak Island (areas 1, 2 and 3).

Association network

Analysis of the associations between $n = 532$ whales seen on more than one occasion revealed one large network of 441 (83 %) connected individuals, and some peripheral groupings comprising 91 individuals that were unconnected to the large network. Of the 41 whales seen depredating longline fisheries, 33 were seen more than once and were therefore included in the association analysis; 30 of these whales fell within the connected network, and 3 were in the unconnected groupings.

The distribution of association values for all pairs of whales within the connected network was generally low (M = 0.02, SD = 0.11), with a large number of unassociated pairs (only 5 % nonzero values). However, Bayesian cluster analysis revealed that the associations were not randomly distributed across the network. Bayesian measures of model fit indicated 4 distinct clusters of whales within this network (Fig. 6), with the lowest BIC = 5,639 for the 4-cluster model, compared to a next best fit of BIC = 5,647 for the 5-cluster model. Although there was some uncertainty over the cluster assignment of some whales under the

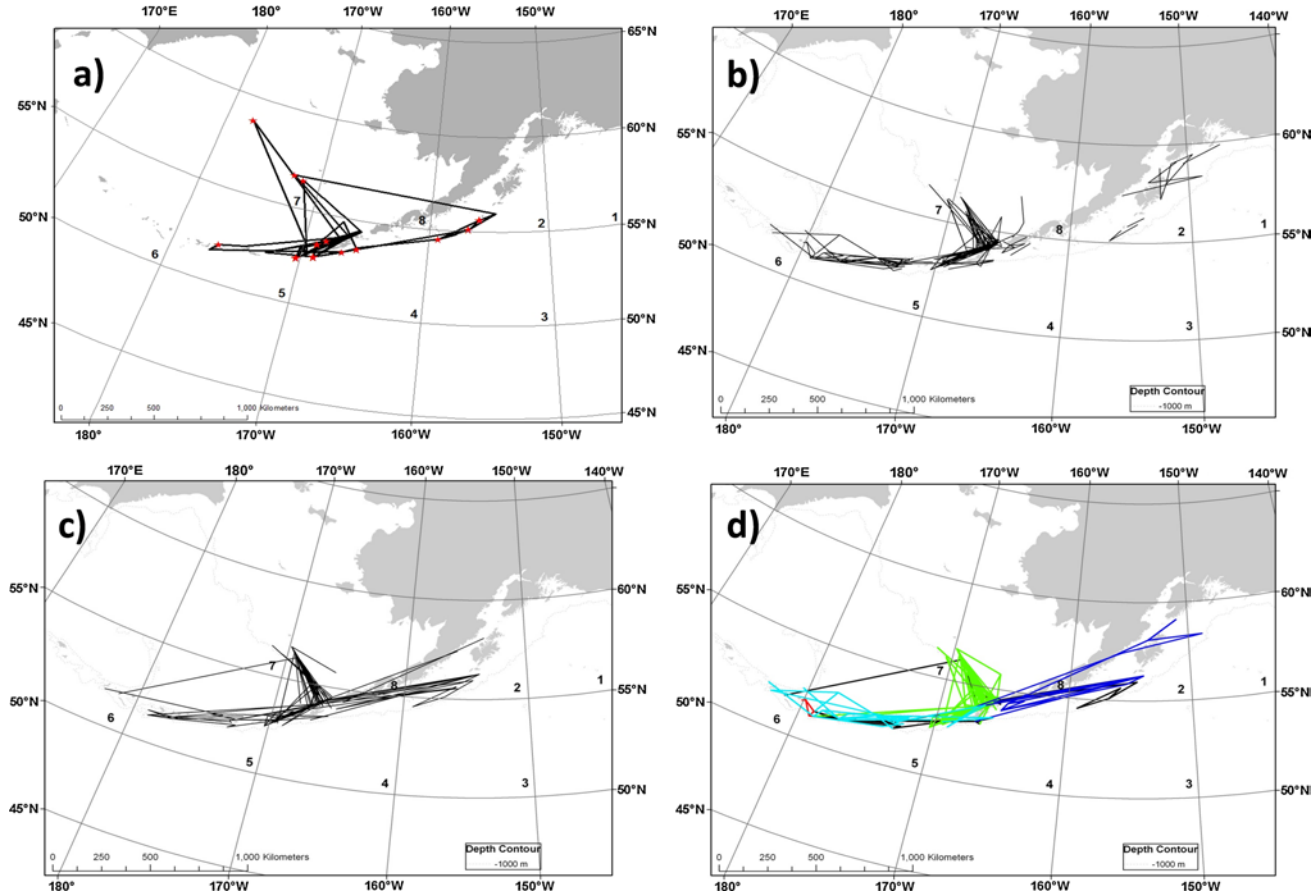

Fig. 3 Maps displaying. **a** Encounter locations for $n = 41$ "Resident" type fish-eating killer whales that have been observed depredating longline fisheries. *Red stars* depict locations where whales were observed depredating and black lines connect repeated encounters, **b** connections of repeated encounter locations of "Resident" type fish-eating killer whales with maximum ranges <500 km ($n = 469$), **c** connections of repeated encounter locations of "Resident" type fish-eating killer whales with maximum ranges more than 500 km ($n = 63$), **d** straight line distance between the repeated encounter locations for $n = 441$ "Resident" type fish-eating killer whales within the large connected social network. *Line color* represents distinct cluster membership of whales assigned with high probability ($p \geq 0.75$) as per Fig. 6; *cluster 1 red*, $n = 31$ whales; *cluster 2 green*, $n = 169$ whales; *cluster 3 blue*, $n = 33$ whales; *cluster 4 turquoise*, $n = 94$ whales, *black lines* depict whales within the network that could not be assigned to a specific cluster with high probability

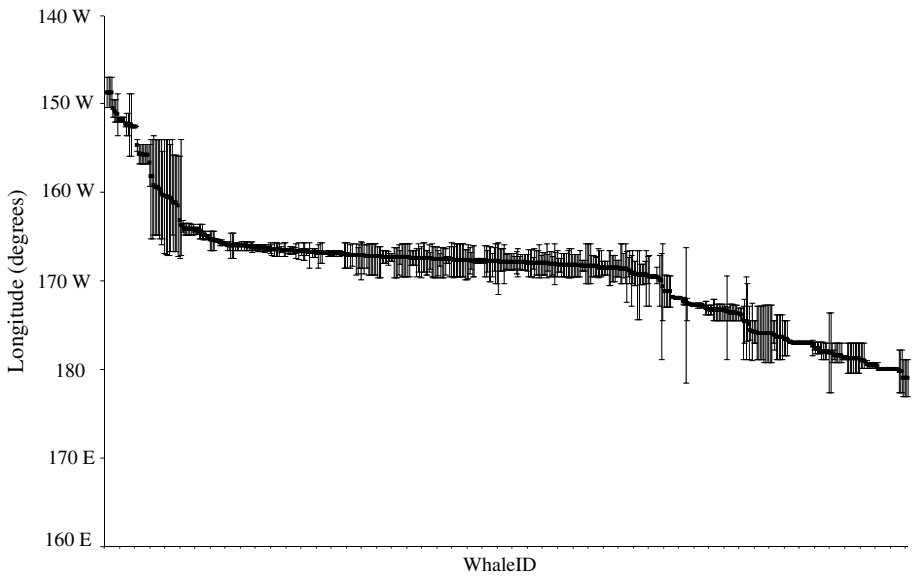

Fig. 4 Maximum longitudinal extent (*vertical lines*) of movement for $n = 532$ "Resident" type fish-eating killer whales identified in more than one encounter. Individuals are ordered based on mean longitude at which they were encountered (*solid line*)

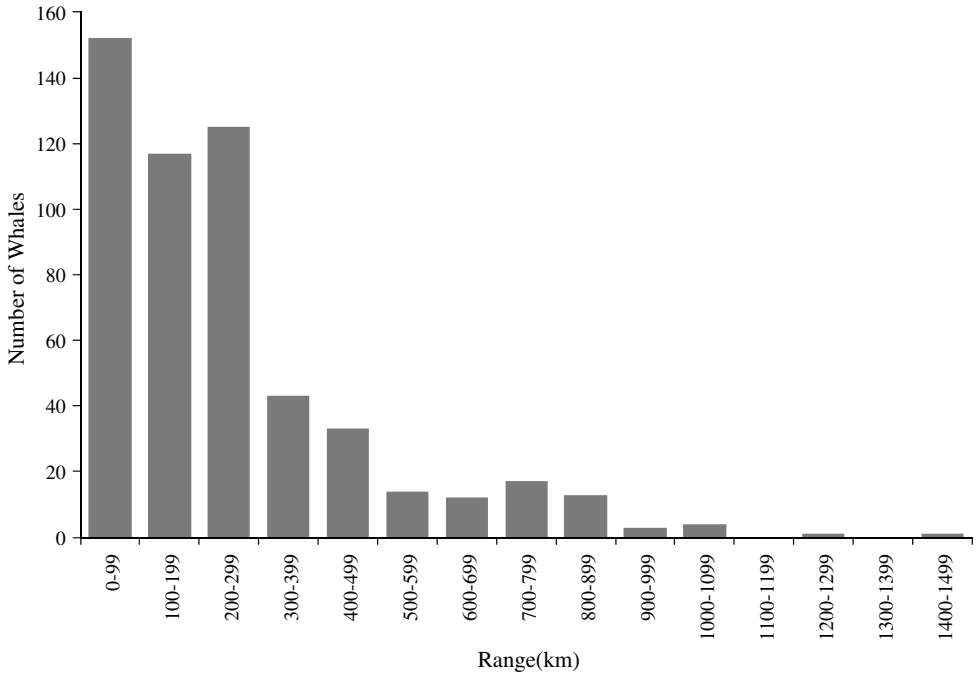

Fig. 5 The range indicated by the maximum distance between re-sighting locations for $n = 532$ "Resident" type fish-eating killer whales identified in more than one encounter

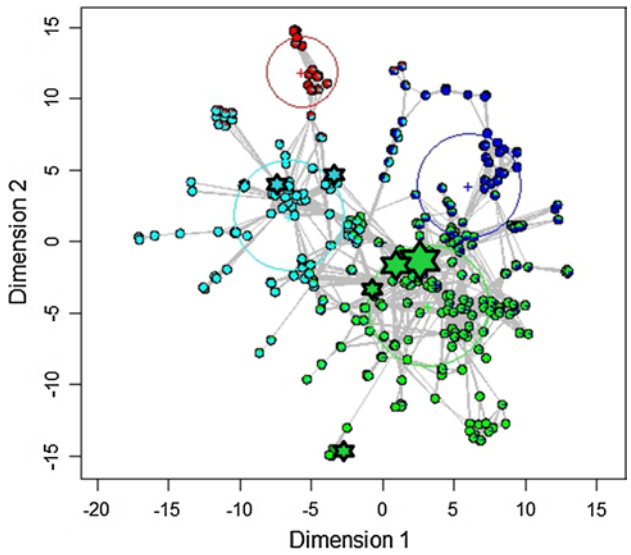

Fig. 6 Cluster assignment in 2-D social space of $n = 441$ "Resident" type fish-eating killer whales encountered more than once that were part of a connected network. Direct associations (seen together at least once) are indicated by *solid lines*, social positions for each whale (*circular pie symbols*) were estimated from association indices between each pair of whales: The *color* of the pie reflects the cluster assignment of each whale, with the proportion composed of each *color* representing the probability of that whale being assigned to each cluster. *Cluster 1 red*, $n = 31$ whales; *cluster 2 green*, $n = 169$ whales; *cluster 3 blue*, $n = 33$ whales; *cluster 4 turquoise*, $n = 94$ whales. *Cross symbols* indicate the mean social space of each cluster, *open circles* represent the estimated the standard deviation of the intra-cluster variances and *stars* represent the estimated social position of whales that have been observed depredating, with *star* size proportional to number of whales (range 1–10)

4-cluster model, 327/441 whales could be assigned to a distinct cluster with high probability ($p \geq 0.75$; cluster 1 = 31 whales; cluster 2 = 169 whales; cluster 3 = 33 whales; cluster 4 = 94 whales). The 114 remaining whales could not be assigned with such high confidence to a specific cluster, although probability of cluster membership fell between 0.50 and 0.74 for 103 of these whales. Notably, of the 30 depredating whales included in the social network, 17 whales were assigned to social cluster 2, 3 whales were assigned to social cluster 4 and 10 whales could not be assigned to a specific social cluster with high probability.

Similar inference (84 % of individuals connected and four estimated clusters) was obtained when fitting the social network model to a dataset constrained to include only individuals seen on three or more occasions ($n = 209$). This indicated that the inference was not sensitive to the selection of the number of sightings that qualified individuals for inclusion in the social network analysis. As such, we based inference on the dataset including individuals seen on two or more occasions, with more individuals ($n = 532$) providing greater population coverage.

The levels of association between whales differed within these defined clusters, with mean association values of 0.36 (SD = 0.37, nonzero values = 56.1 %), 0.07 (SD = 0.17, nonzero values = 18.9 %), 0.23 (SD = 0.29, nonzero values = 42.2 %) and 0.09 (SD = 0.22, nonzero values = 18.1 %) for clusters 1, 2, 3 and 4, respectively. Notably, all four clusters contained some highly associated whales, with 53, 84, 20 and 100 pair-wise association indices equaling a value of 1, where two whales were always

seen together. These consistent associations persisted for up to 10 years (maximum duration of the study).

This connected social network was composed of whales with a combined range spanning more than half of the study area, covering a linear distance of almost 3,000 km (Fig. 3d). The distinct social clusters of whales within this network also showed relatively distinct ranging patterns, with limited spatial overlap between clusters. Whales in cluster 3 ranged most widely (median range 430 km, range 54–903 km), covering waters from the GOA to the eastern Aleutians (areas 1, 2, 4 and 8), followed by whales in cluster 2 (median range 236 km, range 6–1,061 km), that predominantly used the waters of the eastern Aleutian Islands, with north/south movements along the Bering Sea shelf edge (areas 4, 7 and 8). However, whales in this cluster also undertook east/west movements to the central Aleutians (5). Whales in cluster 4 (median range 162 km, range 1–988 km) predominantly used the waters of the central Aleutian Islands (areas 5), but also ranged into the eastern Aleutians (4) and the western Aleutian Islands (6). Finally, whales in cluster 1 were encountered over more restricted ranges (median range 91 km, range 17–245 km) near Amchitka Pass, on the boundary of the central and eastern Aleutian Islands (area 5).

Discussion

Quantitative analysis of photographs from 331 killer whale encounters revealed significant social and spatial structuring with within the Eastern North Pacific Alaska Resident stock of killer whales between the northern GOA and the western Aleutian Islands. Although some long-distance movements (up to 1,443 km) were documented, most whales had maximum observed ranges <200 km, with high site fidelity across years. The extent of this movement is much less than reported for other North Pacific ecotypes (e.g., maximum range of 2,660 km for Bigg's killer whales, Goley and Straley 1994; 4435 km for "Offshores," Dahlheim et al. 2008), but is comparable to the summer range of other populations of Resident killer whales (e.g., Matkin et al. 1997; Ford et al. 2000). Because our photo-identification sample was largely collected during summer months, we cannot rule out longer, unobserved, seasonal movements: "southern resident" killer whales in the eastern North Pacific demonstrate a high degree of site fidelity to the inshore waters around southern Vancouver Island during summer months, but some groups range more 2,000 km during winter (Krahn et al. 2007b). However, our small sample of winter Resident type identifications documented whales that were also seen in the same area in summer. Movements in mammalian populations are generally related to resource acquisition (Wrangham 1986; Wrangham and Rubenstein 1986), and the restricted range of these Resident killer whales may reflect the highly productive environment, particularly around the Aleutian passes (Sinclair et al. 2005), reducing the need to move long distances.

The movements we documented were primarily restricted within three regions: the northern GOA, the eastern Aleutian Islands and Bering Sea shelf edge, and the central Aleutian Islands. This is consistent with both dietary differences (Krahn et al. 2007a) and spatial patterns of genetic variability, indicating population structuring (Parsons et al. 2013). However, the relatively rare longer distance movements did suggest spatial connectivity between neighboring regions, specifically between the central Aleutian Islands and the eastern Aleutians/Bering Sea shelf edge, and between the eastern Aleutian Islands and western GOA waters west of Kodiak Island. There were no direct movements of whales between the northern GOA waters east of Kodiak Island and the Aleutian Islands, or between the far western Aleutian Islands and areas to the east. These could be edge effects, resulting from sparser photo-identification data at the far eastern and western extents of our study area. However, the limited exchange of whales between these areas and the core of our study area nonetheless suggests a lack of social connectivity and supports genetic hypotheses of population boundaries (Parsons et al. 2013). Our analysis of social connectivity suggested that this spatial structuring was mediated by social affiliations. Pair-wise associations were distributed into four distinct clusters, the largest three of which defined whales ranging in each of our three connected regions, respectively. The fourth, smaller, cluster consisted of whales was encountered exclusively at the boundary of the central and western Aleutian Islands, and it is likely that we have not sampled sufficiently to resolve the social and spatial connectivity of whales further west, with only three surveys in the western Aleutians to date.

Within these clusters, there were some very strong associations. Between 20 and 100 pairs of whales per cluster had an association index (HWI) of 1 that persisted across multiple years (up to the 10-year study duration), indicating highly stable social groupings. This is consistent with the stable matrilineal groupings described in Resident-type killer whales over four decades of study in the eastern North Pacific (Bigg et al. 1990; Matkin et al. 1999; Ford et al. 2000; Parsons et al. 2009). Matrilines of females and their descendants in these well-studied populations have remained stable for generations, with no dispersal from the natal groups (Parsons et al. 2009). However, clusters of matrilines have associated to varying degrees, sometimes comprising "pods," with dynamic associations coincident with changes in prey availability (Parsons et al. 2009; Ford et al. 2009). We suggest that the social clusters

we defined represent preferred but temporary groupings of multiple stable matrilines, based on both strong and weak associations within each connected cluster. Future genetic work will help resolve the relatedness within and between clusters.

Many mammalian populations occur in social systems where changes in group membership are observed as individuals form temporary groups that fuse together and then break apart (Kummer 1971; Struhsaker and Leland 1979). The fission–fusion dynamics of populations that occur in a variable environment are likely to be less cohesive and are comprised of a few, large connected components, each consisting of highly associated "cliques" (Rubenstein et al. 2007; Aureli et al. 2008). In this case, our clusters of preferentially associating groups appear to align with key ecological variability: Specifically, an ecological gradient that shifts from the continental shelf in the nearshore waters of GOA to shelf edge waters in the eastern Aleutian Islands/Bering Sea shelf and finally to more pelagic waters off the shelf in the central Aleutian Islands (Fig. 1; Krahn et al. 2007a). Chemical analyses of skin biopsies from these Resident killer whales revealed a similar gradient in skin stable isotope profiles (Krahn et al. 2007a) that supports an east–west shift away from prey found in shallower waters on the continental shelf. Resident killer whales in the GOA consume salmon as a substantial part of their diet (Saulitis et al. 2000), but it is likely that whales in the eastern Aleutian Islands consume salmon to a lesser extent (Wade et al. 2006) and those in the central Aleutian Islands likely consume alternative locally available prey in deeper waters (Krahn et al. 2007a). The socially mediated spatial structure we have documented supports consistent use of different foraging areas by these clusters, helping to explain these spatial differences in dietary signals.

At a larger scale, the four defined clusters were linked by occasional associations to form a single large connected network, with an expansive longitudinal range (ca. 3,000 km), including most (83 %) of the photo-identified whales that were seen on more than one occasion. Due to limited sample sizes, we cannot assess the significance of the outliers: It is possible that they were simply not observed sufficiently often to be seen associating within the network. However, it is interesting to note that the percentage of whales included in the network remained similar, regardless of whether individuals qualified with a criterion of being seen on more than one or more than two occasions. This tends to imply that it may not be sampling variability alone that led to their exclusion, and there may be further structure to be detected in this region. For example, we may not have fully sampled the clusters ranging at the western extent of our study area or along the Bering Sea shelf edge, due to more limited survey effort in these regions. Nonetheless, the large connected network may facilitate the spread of information throughout the population by cultural transmission, likely enhancing success in resource acquisition (Lusseau and Newman 2004; Rubenstein et al. 2007; Allen et al. 2013) and fitness (Whitehead and Rendell 2004; Whitehead et al. 2004; Whitehead 2010). In this case, large-scale social connectivity may facilitate the widespread practice of depredation of longline fisheries, despite relatively restricted movements of some whales.

Depredation of longlines by killer whales in Alaskan waters has been observed for several decades (Dahlheim 1988; Yano and Dahlheim 1995; Matkin et al. 1997), but the incidence of depredation has been increasing in recent years (Lunsford and Rutecki 2010; Peterson et al. 2013). Whales that were photographed while depredating longlines in several areas throughout our study area were members of the two largest social clusters primarily using the eastern Aleutian Islands/Bering Sea and central Aleutian Islands, respectively. This aligns with widespread depredation by killer whales along the Aleutian chain and into the Bering Sea (Yano and Dahlheim 1995; Lunsford and Rutecki 2010; Peterson et al. 2013). Although our sample size is small, we did not confirm any depredation by whales assigned to the cluster that ranged into the Northern GOA waters east of Kodiak Island, coinciding with a negligible occurrence of killer whale depredation in this region (Yano and Dahlheim 1995; Lunsford and Rutecki 2010; Peterson et al. 2013), despite frequent depredation by sperm whales (*Physeter macrocephalus*, Sigler et al. 2008). This supports previous suggestions (Whitehead and Rendell 2004; Whitehead 2010) that a social mechanism may be responsible for the spread of depredation, through the vertical and horizontal cultural transmission of learned behaviors between associated individuals (Whitehead and Rendell 2004; Rubenstein et al. 2007; Aureli et al. 2008; Whitehead 2010; Allen et al. 2013).

We hypothesize that depredation behavior is likely first spread within groups of consistent associates (likely matrilines) and then spread to associating groups that may witness depredation during these associations. During this study, we observed large aggregations of whales (max encounter group size = 120) likely composed of multiple matrilines traveling and feeding together (median encounter group size = 15, consistent with a single matriline; see Matkin et al. 1999; Ford et al. 2000). Other killer whale populations are known to form ephemeral aggregations during feeding. Pack-ice (type B) killer whales in Antarctica feed predominantly on ice seals and stable groups have been observed joining to engage in cooperative feeding (Pitman and Durban 2012) and Resident killer whales in eastern North Pacific form larger social clusters, comprising multiple matrilines, in years with a higher abundance of their Chinook salmon (*Oncorynchus tshawytscha*) prey

(Parsons et al. 2009). It is plausible therefore that such feeding aggregations also offer opportunities for social learning among a larger number of associating whales. Although there was some depredation observed by apparently unconnected individuals in the western GOA, it is possible that their connections to the network were undetected in our data sample. Recent observations have documented the long-distance movement of known depredating whales over more than 1,200 km between the eastern Aleutians and western GOA (CBSFA Final Report 2012), aligning with a recent increase in depredation by killer whales in the western GOA, west of Kodiak Island (Peterson et al. 2013). Further collection of movement and association data will help to resolve the finer details of the association network and further examine the likely social basis for the spread of depredation.

The spatial structuring we have documented within killer whales in the coastal waters between the northern GOA and the western Aleutian Islands needs to be considered when evaluating the ecosystem impact of these top predators (e.g., Guenette et al. 2006) and the extent of competition with fisheries (e.g., Lunsford and Rutecki 2010; Peterson et al. 2013). Killer whales are known to have high caloric requirements (Williams et al. 2004; Noren 2011), and the density of Resident killer whales in these productive waters is considered to be among the highest in the world (Forney and Wade 2006; Zerbini et al. 2007). Their impact in this region is therefore undoubtedly considerable, but likely underestimated (Lunsford and Rutecki 2010). Future assessments of the importance of killer whale predation are needed and should incorporate area-specific abundance estimates, guided by the clustered space-use patterns we have reported.

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