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ORIGINAL ARTICLE

Sexual segregation when foraging in an extremely social killer whale population

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Abstract Resident, fish-eating killer whales in the northeastern Pacific Ocean live in multi-generational matrilines containing both sexes. The degree of maternal fidelity and natal philopatry in this killer whale society is extreme even by the standards of lions, elephants or any highly social mammal. Benefits of group living include cooperative foraging and alloparental care, but few studies have explored how killer whales avoid within-group competition for prey. This study measured focal animal behaviour from one population in its legally designated critical habitat. Adult males and females overlapped spatially whilst resting, travelling and socialising, but during feeding bouts, females foraged nearshore in shallower waters, whilst adult males distributed foraging effort throughout the study area, with no statistically significant depth preference. We postulate that sex-biased dispersal in foraging ecology reflects physiological capacity for deeper diving in males than females, which may be either a driver or consequence of extreme sexual dimorphism in the species; alternative interpretations exist. Killer whales appear to be a cosmopolitan species complex including populations that range widely in body size and diet. Our physiological limitation theory could be tested with other ecotypes. For the northern resident killer whale population we studied, we postulate that our finding may indicate a mechanism to avoid or reduce competition for food within the family unit whilst ensuring group cohesion. Investigating sex differences in foraging habitat informs area-based management and conservation of this threatened population, but studies on other ecotypes are needed to improve our understanding of the evolution of sociality in this species.

Keywords Foraging ecology · Killer whale · Marine mammal · Niche partitioning · Sexual segregation · Intra-specific competition

Introduction

Killer whales (*Orcinus orca*) are highly social animals that live in hierarchical groups. Resident fish-eating killer whales, found in the waters of British Columbia (BC, Canada) and Washington State (USA), live in matrilineal family groups that consist of sexually dimorphic adults, juveniles, and dependent calves. Although animals in the same group differ in reproductive status and body size, offspring of both sexes spend their entire lives with their mother's social unit (Ford et al. 2000). The reason why these strongly bonded, mixed-sex groups can occur is poorly understood. Maintaining group cohesion is only possible if the group members synchronise their activities, such as travelling, foraging and resting (Jarman 1974). Several costs and benefits may result from group living. Across many taxa, including mammals, birds, fishes and invertebrates, it has been observed that living in a group can benefit individuals by increasing foraging success (e.g. Pitcher et al. 1982; Rypstra and Tirey 1991; Krause and Ruxton 2002; Dechmann et al. 2009; Beauchamp 2014). For example, shoaling in fishes allows individual fish to increase

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search efficiency (i.e. reduce search time) and spend more time feeding rather than avoiding predators (Pitcher et al. 1982). Dechmann et al. (2009) showed that groups of female bats foraged together, so information about prey resources could be transferred via echolocation calls to achieve more effective group foraging. Killer whales have no natural predators (Ford et al. 2010). For individual killer whales, benefits arising from group living could include a higher overall prey encounter rate due to cooperative foraging, an increase in offspring survival through food provisioning or alloparental care, but also opportunities for kin selection (Baird 2000; Ralls and Mesnick 2002; Johnstone and Cant 2010; Foster et al. 2012a). Cooperative foraging is known to play a role in the foraging ecology of resident killer whales; adult females share resources with juveniles, but prey sharing is not seen in adult male resident killer whales (Ford and Ellis 2006). This is in marked contrast to transient (also known as Bigg's or mammal-eating) killer whales in the same region, which are known to hunt cooperatively and share prey amongst all age-sex classes within a social unit (Ford et al. 1998; Baird 2000). The disadvantages of group living with respect to the costs of group foraging may include increase in competition for resources, overlap in search areas between group members and an increase in detectability by prey and/or predators (Clark and Mangel 1986; Krause and Ruxton 2002; Beauchamp 2012). An increase in group size may result in an increase in competition for mutually preferred resources when these are in limited supply (Wrangham et al. 1993; Grand and Dill 1999). Mechanisms to reduce within-group competition in large group sizes may include exploiting large food patches or increasing foraging effort (Clark and Mangel 1986; Janson 1988). Another aspect of group living to consider is that synchronisation over long time periods can involve ecological trade-offs at an individual level. Sexual size dimorphism in killer whales results in sex-based differences in energy requirements and/or physiological capabilities, such as swimming speeds or diving capabilities (Williams and Noren 2009; Williams et al. 2011). Individual group members may have to compromise their own optimal activity budgets whilst synchronising their activities with those of other group members (Conradt and Roper 2000, 2005). At an individual level, group living in some cases may therefore not be optimal and probably be even less optimal when living in groups consisting of different classes of individuals (McNamara et al. 1987; Conradt 1998; Ruckstuhl 1999; Conradt and Roper 2000, 2005). Resource partitioning through diet, temporal and/or habitat differentiation are other mechanisms seen for sympatric cetacean species to reduce competition for resources and in this way enable coexistence (Friedlaender et al. 2009; Fernández et al. 2013; Browning et al. 2014). Evidence of resource partitioning has also been seen in many other taxa, including fish (Alanärä et al. 2001), reptiles (Pearson et al. 2002), bats (Senior et al. 2005) and ungulates (McCullough et al. 1989), and therefore may be expected in resident, fish-eating killer whale populations. If resource partitioning is occurring in this killer whale population that never disperses from its natal unit, the effect must be a subtle one. The functional significance of sexual dimorphism in body size in killer whales warrants further investigation. The marked sexual size dimorphism in this species may have evolved as a result of sexual selection favouring larger males and/or may reflect ecological differences between the sexes (Slatkin 1984; Hedrick and Temeles 1989). In size dimorphic species, differences in morphology, energetic requirements and/or physiological capabilities may require the sexes to use different foraging strategies or different habitats (Beck et al. 2007; Ruckstuhl 2007; Staniland and Robinson 2008). Spatial and habitat segregation and differences in behaviour between the sexes have been described for several seal species that show a marked sexual dimorphism in size (Le Boeuf et al. 2000; Breed et al. 2006; Staniland and Robinson 2008; McIntyre et al. 2010; Leung et al. 2012). For example, resource partitioning and habitat segregation between the sexes have been described for elephant seals (*Mirounga* sp.; Le Boeuf et al. 2000; McIntyre et al. 2010). This behaviour is thought to be the result of differences in prey selection and might be a strategy to avoid inter-sexual competition (McIntyre et al. 2010). In the case of grey seals (*Halichoerus grypus*), researchers believe that the mating system and reproductive roles of each sex, associated with sexual size dimorphism, result in inter-sexual competition and niche separation that in turn cause sexual segregation (Breed et al. 2006). The potential for habitat partitioning to reduce intra-specific competition must be constrained in resident killer whales, given that they spend their entire lives together. For resident killer whales, Bain (1989) hypothesised (but did not demonstrate) that they may avoid or reduce intra-matriline competition whilst keeping group cohesion by adopting sex-specific foraging strategies. Few studies have tested this hypothesis. Amongst southern resident killer whales, males were found to dive deeper more frequently than females, which could be a strategy to mitigate competition for food (Baird et al. 2005). Besides these observations of segregation in the vertical dimension, adult male resident killer whales may follow another strategy that reduces intra-matriline competition. Several studies describe field observations of short temporal male dispersal (Felleman et al. 1991; Hoelzel 1993; Ford and Ellis 2006). Although members of matrilines stay together most of the time, when adult males are foraging, they often take up peripheral positions in the group and separate temporarily in order to forage in small subgroups or as individuals further offshore over deeper water. According to Bain (1989), the difference in foraging location between male and female killer whales may reflect differences in diving behaviour due to body size differences. In this study, we tested for sex-based habitat partitioning in the group-living northern resident killer whales, taking into account the impact that a change in food availability may have on the occurrence of male dispersal. Subsequently, we discuss what implications any such differences may have for conservation strategies. First, since the social organisation of resident killer whales is based on matrilines that spend their entire lives together, we expected no spatial separation between males and females when animals were engaged in travelling, resting or socialising activities. We hypothesised that the sexes would disperse during feeding activities, with females and calves using nearshore habitats and males foraging mid-strait over deeper waters. Second, resource availability (abundance and distribution of prey) may be an important determinant of seasonal distribution, population dynamics and structure and connectivity of the killer whale social network (Lusseau et al. 2004; Ford and Ellis 2006; Parsons et al. 2009; Foster et al. 2012b). For instance, inter-annual variability in abundance of their preferred prey, Chinook salmon (*Oncorhynchus tshawytscha*), affected the critical size of foraging groups of northern resident killer whales (Lusseau et al. 2004), whilst the social network of the parapatric southern resident killer whales became more connected in years of high prey abundance than in years when prey were scarce (Foster et al. 2012b). Therefore, we hypothesize that if males disperse as a strategy to mitigate intra-matriline competition for food, changes in prey availability may have an influence on the occurrence of segregation. Finally, the northern resident killer whale population is listed as 'threatened' in Canada due to its small population size, the reliance on specific populations of salmon and their sensitivity to human activities (COSEWIC 2008). Given that human activities seem to affect feeding behaviour more than other activities (Williams et al. 2006), sex-based differences in foraging habitat would need to be considered in conservation activities (Ashe et al. 2010).

Material and methods

The study area covered the western end of Johnstone Strait, BC, Canada (Fig. 1). The study area has been designated as part of the population's critical habitat under Canada's Species at Risk Act. Northern resident killer whales appear in the strait during summer but are found throughout the year ranging from central Vancouver Island to southeastern Alaska (Ford et al. 2000).

Theodolite tracking of killer whales

Using a land-based theodolite (a surveying tool), the movement paths and activity states of individual killer whales were recorded from an observation point on West Cracroft Island (50° 30′ N, 126° 30′ W; Williams et al. 2002a). Blind data recording was not possible because this study involved focal animals in the field. For each theodolite tracking session, an individual killer whale was selected from a group according to the selection criteria and activity state definitions described in Williams et al. (2002a, b). Tracking sessions varied in duration but were at least 15 min. Focal animals were identified comparing distinctive natural markings to published photo-identification catalogues containing as well information about the focal animal's age, sex and pod affiliation (Ford et al. 1994, 2000).

Data compilation–plotting presence and movement data and generating pseudo-absence data

Theodolite data (spatially and temporally explicit data on killer whale presence) were imported into ESRI ArcMap 10. In order to fit a model with a binary response of killer whale presence and absence in the study area, we generated pseudo-absence data (see Supporting Material for R code). Pseudo-absence data were generated to serve as a contrast for each presence location. Information on bearing and distance was extracted from the recorded tracks in order to have movements similar to the recorded tracks and to include biological constraints imposed by the physiology of the animals. Furthermore, the overall mean of distances between successive locations calculated for all recorded tracks was used to include information on the physiological capabilities of the animals to move certain distances between breaths. The direction of the bearing change (±) was set to be equal, and the mean change was small (mean±SD 1.62±7.5), so although circular tracks were theoretically possible, they were unlikely and the simulated tracks were comparable to the recorded tracks.

The movement parameters were

- The starting position for each contrasting track was randomly selected within the area that encompassed the recorded surfacing locations (Fig. 1).
- Size of bearing change from a location towards the next location was simulated from a normal distribution using the overall mean and standard deviation from the recorded tracks.
- The direction of bearing (±) was derived from a binomial distribution with equal probability of each sign.
- Successive location distances were simulated from a normal distribution, characterised by the overall mean and standard deviation found for distances of successive locations of the recorded tracks.

Once the pseudo-absence locations were generated, each pseudo-absence location received the same demographic and genealogical variables (sex, age and pod), temporal variable (year) and activity state (resting, travelling or foraging) as the contrasting surfacing location. The activity state categories

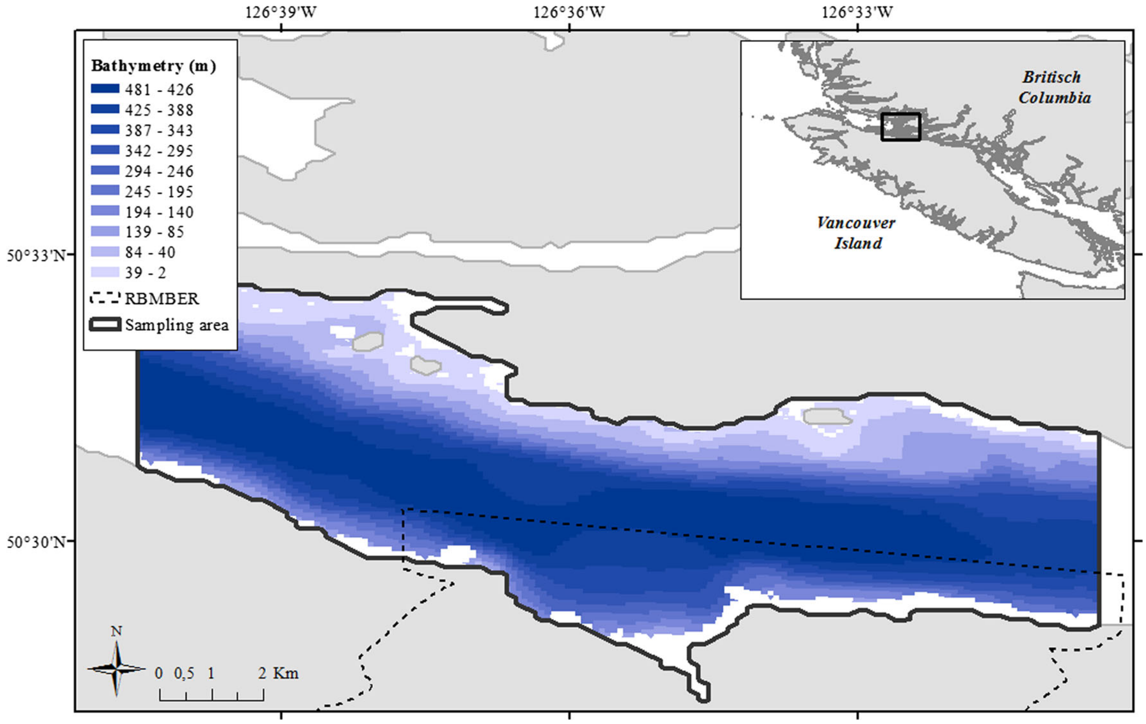

Fig. 1 Study area, Johnstone Strait, BC, Canada, indicating the bathymetry (provided by Natural Resources Canada (NRC), Robert Kung, NRC, Robert.Kung@nrcan-rncan.gc.ca, on September 2, 2009, personal communication); the sampling area used for pseudo-absence data generation; the boundaries of the Robson Bight Michael Bigg Ecological Reserve (RBMBER); and coastlines (Wessel and Smith 1996) Coordinate System NAD 1983

selected in the analysis were resting, travelling and foraging (Table 1). The definitions were adapted from earlier studies (Lusseau et al. 2009; Williams et al. 2006) and were designed to be mutually exclusive and cumulative, encompassing the entire repertoire of the activity budget of the whales in the area. (Note that due to rarity of observation, socializing and beach-rubbing activities were not included in the analyses.) The physiographic variable, depth, at each location (presence and pseudo-absence) was derived from a bathymetric layer (75 × 75-m resolution, provided by Natural Resources Canada (NRC), Robert Kung, NRC, Robert.Kung@nrcan-rncan.gc.ca, on September 2, 2009, personal communication). Water depths in the study area ranged from 2 to 481 m (depth mean = 271 m, SD = 153 m, median = 310 m).

Statistical analysis

We analysed data from 6 years (1995–1998, 2002 and 2004), covering the months of July and August (Williams et al. 2002a, b, 2006; Williams and Ashe 2007). During the period, Chinook salmon catch per unit effort in the study area was six times higher in the highest year than in the lowest year (Lusseau et al. 2004). A sixfold range in prey density is large relative to the threefold variability in one Chinook salmon index observed coastwide from 1973 to 2005 (Ford et al. 2010), so we consider "year" to be a good proxy for inter-annual variability in prey density and the study site to be a good snapshot of what the population experienced in terms of prey variability over biologically meaningful time scales. All tracking sessions were included; thus, no selection was made according to differences in duration between the sessions. Logistic generalized estimating equations (GEEs), which account for autocorrelation between successive locations along the tracks, were used to model the probability of killer whale occurrence in the area as a function of explanatory variables (demographic, temporal, activity and physical). An autoregressive correlation structure (AR1) was chosen to model the non-independence, as it was assumed that dependence between surfacing locations decreased as they became further apart in time and space. Variables included in the starting model were (1) main effects of water depth, killer whale activity state, sex, age and pod affiliation, and year (as factor); (2) two-way interactions between depth and activity state and between activity state and sex; and (3) the three-way interaction between water depth, activity state and sex. The three-way interaction was included in the model to test the specific hypothesis that killer whales partitioned their foraging habitat between the sexes. Pod affiliation, groups formed by related matrilines that travel more than 50 % of the time (Ford and Ellis 2002), was also included. Explanatory variables were selected by a manual stepwise both ways selection process, in order to select the combination of terms that provided the best fit to the data, with the quasi-Akaike information criterion (QIC) score (Pan 2001) penalising the addition of

Table 1 Definitions and frequency of occurrence for field classification of four coarse activity states of focal killer whale group *Orcinus orca*

Definition	Function
Slow swimming with predictable sequences of several short (30 s) dives followed by 3–5-min dives and characterized by the absence of surface active behaviour (e.g. breaching or tail-slapping)	Rest
Dive independently with entire group heading in the same general direction. Individual dive sequences characterized by pattern of several short dives followed by one long dive	Travel/forage
Individuals spread out, diving independently in irregular sequences of long and short dives; display fast, non-directional surfacing	Feed
Tight groups with tactile contact amongst individuals; irregular surfacing, speeds and high rates of surface active behaviour	Socialize

Adapted from Ashe et al. (2010)

unnecessary terms. In addition, Wald chi-squared tests (ANOVA function in the geepack library) were performed on the full model to determine whether the model terms were required in the model. Non-significant (where $p>0.05$) terms were removed from the model subject to the constraint that the contributory factors to all significant interaction terms were retained, after which the model was re-run. Both methods resulted in the same optimal model. All statistical analyses were performed using the software R version 3.1.0 (R Core Team 2014) and the packages geepack version 1.2-0 (Højsgaard et al. 2006) and MESS version 0.3-2 (Ekstrom 2014).

Results

This study included a total of 354 separate killer whale tracking sessions coming from 44 different whales (26 males and 18 females) of 16 matrilines and 10 pods, which were collected over 6 years. Only a small number of the tracks (12) were from juvenile whales (<14 years; as defined by Ford and Ellis 2006). The final model retained water depth, killer whale activity state, sex and their two- and three-way interactions as predictors of killer whale occurrence (ΔQIC=−28). The Wald chi-squared test found no significant effect of activity, or interaction between depth and activity, but confirmed that the three-way interaction between water depth, activity state and sex ($\chi^2=28.9$, $df=2$, $p=<0.001$; Table 2). Wald-*Z* tests for the three-way interaction (W_resting=13.8, W_travelling=28.9; $p=<0.001$; Table 3) show that females found in deeper water are more likely to be resting or travelling than foraging. Thus, whilst there is no interaction between depth and activity for males, there is for females, and in contrast to their male counterparts, female whales tend to forage in shallower water (i.e. generally but not always closer to shore) (Fig. 2). Although, overall, the activity-sex interaction was not significant, some explanation for the lack of distinction between the locations of sexes overall may be found in the fact that the best model found a more greater chance of observing females resting or travelling than for males. The factor year did not improve the QIC (Table 4). It was therefore not retained in the model and suggests that inter-annual variability does not affect the probability of killer whale occurrence. In addition, the probability of killer whale occurrence was not determined by pod affiliation.

Discussion

Sex-based differences in feeding location

The primary objective of the study was to provide a quantitative assessment of temporary, sex-based dispersal amongst northern resident fish-eating killer whales in Johnstone Strait. Based on their social organisation of matrilineal family groups and incidental observations during other researches, our findings confirm partly our expectations; killer whales used all habitats equally when travelling and resting together, but adult males and females tended to forage in waters of different depths. Females fed over shallow waters, generally close to shore. However, males were not found to forage over areas with greater depths (i.e. generally, mid-strait) as expected; rather, they appeared to have no clear preference where they rested, travelled or foraged. This suggests that the driver

Table 2 Output Wald chi-squared test to determine the significance of covariates in the generalized estimating equation model explaining killer whale occurrence in relation to depth, activity and sex using an autoregressive correlation structure and logit link

Covariates	*df*	χ^2	*P* (>|chi|)
Depth	1	216.4	<0.001*
Activity	2	1.1	0.57
Sex	1	0.0	1.00
Depth:activity	2	3.5	0.17
Depth:sex	1	0.4	0.54
Activity:sex	2	1.1	0.57
Depth:activity:sex	2	28.9	<0.001*

Terms added sequentially. Variables with $p<0.05$ are indicated by an asterisk

Table 3 Summary results of the generalized estimating equation model explaining killer whale occurrence in relation to depth, activity and sex using an autoregressive correlation structure and logit link

Model term	Coefficient estimate	SE	Wald-*Z*	Pr (>|*W*|)
Intercept	2.58e—09	8.50e−02	0.00	1.00
Activity (reference level: foraging)				
Resting	9.47e—11	2.52e−10	0.14	0.71
Travelling	4.56e—11	1.36e−10	0.11	0.74
Sex (reference level: male)				
Female	−1.73e−09	1.82e−01	0.00	1.00
Activity:sex				
Resting:female	1.61e−09	4.83e−10	11.10	<0.001*
Travelling:female	1.69e−09	3.52e−10	23.10	<0.001*
Depth	8.92e−12	7.51e−13	141.31	<0.001*
Depth:activity				
Depth:resting	2.25e−13	7.97e−13	0.08	0.78
Depth:travelling	1.23e−13	4.50e−13	0.07	0.78
Depth:sex				
Depth:female	−5.76e−12	1.12e−12	26.19	<0.001*
Depth:activity:sex				
Depth:resting:female	5.89e−12	1.59e−12	13.8	<0.001*
Depth:travelling:female	5.95e−12	1.11e−12	28.9	<0.001*

Variables with $p<0.05$ are indicated by an asterisk. Activity state and killer whale sex were specified as factors, and the respective reference levels were foraging and male. The intercept represents males foraging at 0 water depth, and the coefficients represent differences from the reference values

for this partitioning is not kin selection; i.e., males are not avoiding shallow waters to leave more food available to females with dependent calves. In contrast, the simplest explanation is that physiological constraints are driving the sites where individuals are searching for prey. Our interpretation is that males are capable of conducting shallow and deep dives and consequently hunt in both shallow and deep waters; females, many of which have dependent calves, have more modest breath-holding capabilities and preferentially forage in shallower waters closer to shore. Alternative hypotheses do exist. This population is known to engage in prey sharing amongst females and juveniles (Ford and Ellis 2006) but not amongst adult males. It could be that the limited diving capability of calves and juveniles, not adult females, is limiting foraging habitat of adult females. Few tracks of juveniles or calves were recorded, owing to the difficulty in identifying them reliably at long distances (Williams et al. 2002a). Our novel findings open up exciting opportunities to test competing hypotheses on other killer whale ecotypes around the world. If the physiological constraint (rather than the kin

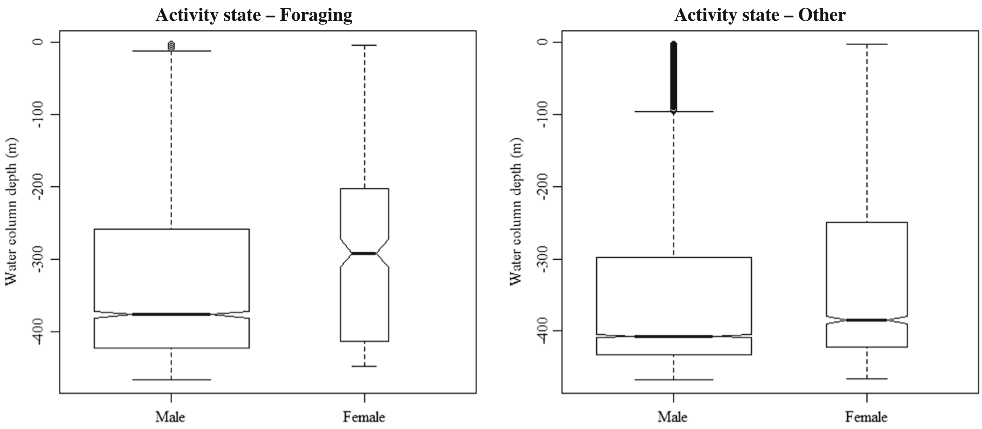

Fig. 2 Box plot representation of the occurrence of male and female killer whales over different water column depths when **a** foraging or **b** performing other activities (resting and travelling). The *middle line* of the box represents the median and the *upper* and *lower lines* the quartiles. The whiskers represent the most extreme values within 1.5 times the interquartile range, and the outliers are plotted as individual points. Box widths are proportional to the square roots of the number of observations in the groups. The notch defines the 95 % confidence interval around the median

Table 4 Quasi-Akaike information criterion (QIC) and quasi-likelihood under the independent model information criterion (QICu) for generalized estimating equation model analysis relating killer whale occurrence to demographic and genealogical variables (sex, age and pod), temporal variables (month and year) and activity state (resting, travelling or foraging)

Covariates	QIC	QICu	ΔQIC	ΔQICu
Depth × activity × sex + age + year + pod	42,699	42,721	0	0
Depth × activity × sex + age + year	42,681	42,703	−18	−18
Depth × activity × sex + age	42,671	42,693	−28	−28
Depth × activity × sex	42,671	42,691	−28	−30

All models have an autoregressive correlation structure

selection) hypothesis is correct, it should hold true for other ecotypes, such as Bigg's (transient) mammal-eating killer whales. In populations with strong cooperative foraging, such as the Norwegian herring-eating ecotype (Similä and Ugarte 1993), we may see that the entire group stays within the depths that can be accessed by the shallowest diving members of the group. The Strait of Gibraltar population of killer whales that chases and exhausts tuna at high speed (Guinet et al. 2007) may offer an unusual opportunity to test the physiological constraint hypothesis. There is a wide range of body size and sexual dimorphism in populations of this species around the world (Williams et al. 2011). If the physiological constraint hypotheses were true, we would expect to see the least segregation in foraging habitats between sexes in the populations that show the least sexual dimorphism. We encourage spatial analysis of prey capture events in other killer ecotypes to expand our knowledge from new information about one population to a new understanding of the species as a whole. Killer whales are known to have high caloric requirements that increase with size and during lactation (Lusseau et al. 2004; Williams et al. 2011). In size dimorphic species, differences in morphology, energy requirements and/or physiological capabilities may require the sexes to use different foraging strategies or different habitats (Beck et al. 2007; Ruckstuhl 2007; Staniland and Robinson 2008). On an intra-specific level, this may serve to maximise fitness by reducing intersexual competition for food (Kie and Bowyer 1999; Breed et al. 2006). The finding that killer whales disperse during foraging activities (i.e. as evidenced by the significant two-way interaction term) suggests that it may reduce competition when meeting individual metabolic requirements, whilst they synchronise their behaviour and movements with those of the rest of the group. With their dramatically larger body size, males are capable of deeper and longer dives than females (Schreer and Kovacs 1997; Baird et al. 2005; Miller et al. 2010). The fact that males do not entirely abandon the nearshore, shallow waters used by females for hunting would suggest that reducing intra-matriline competition is a secondary benefit, rather than the primary driver for the pattern we observed. Amongst southern resident killer whales, males were found to dive deeper, more frequently than females, and this finding was interpreted as a strategy to reduce intra-matriline prey competition (Baird et al. 2005). The two explanations—an evolutionary solution to reduce competition or differences in physiological limits—may not be mutually exclusive. Female mate preference and sexual selection for large males, as a proxy for greater dive capacity, would result in sexual dimorphism, a tendency towards niche partitioning, and reduced intra-matriline competition. The segregation in foraging habitats that we have documented may reflect differences in diet. Dietary specialisation within a population may also reduce intra-specific food competition (Kie and Bowyer 1999). These killer whales show strong preference for the largest salmonid species, namely, Chinook salmon, which in turn shows a drastic increase in weight with age (Candy and Quinn 1999; Ford and Ellis 2006). Chinook salmon that are able to dive deep (>200 m) are larger (fork length, 87.2 cm) than the ones that remain nearer the surface (fork length, 77.3 cm; Candy and Quinn 1999). Ford and Ellis (2006) did not find a significant difference in the mean age of Chinook salmon taken by adult male and female killer whales. In the present study, no data were available on the diving behaviour of individual killer whales, the kind of prey taken and the relative prey availability over different depths. Although activity state and bottom depth seemed to affect the probability of occurrence, we cannot detect a preference for particular depths and cannot conclude that foraging over different depths also results in a difference in diets or prey preference.

Annual effect

The way in which sexual differences in foraging behaviour are manifested may be dependent on the local environment and spatial and temporal heterogeneities in prey resources (Staniland and Robinson 2008). Ford et al. (2010) hypothesised that the decline of the northern killer whale population was caused by a sudden decline in their primary salmonid prey, which could not be compensated for by preying on alternative prey resources that remained in abundance. Because this may have caused greater competition within groups, we predicted that years of low prey abundance may have forced male killer whales to segregate from the social unit and forage over deeper waters more often when compared with years of high prey abundance. However, in our study, the probability of occurrence did not differ between years and males did not prefer specific areas to forage. Importantly, our 8-year study happened to sample years of relatively low abundance of Chinook salmon relative to average values observed during the 25-year study by Ford et al. (2010). It is important to repeat this study in years of high Chinook salmon abundance, to see if the spatial segregation in foraging habitat we observed disappears when prey density is high and to see whether males follow matriarchs into shallow water to feed in years when prey are scarce (Brent et al. 2015).

Conclusions

This study provides quantitative results showing differences in feeding location between adult males and females amongst the northern resident killer whale population. Although it is very difficult to deduce the evolutionary drivers for the ecological segregation we found, our results are consistent with the hypothesis that sexual segregation reduces competition within the matriline, although this may be an unintended side effect of physiological constraints. Adult males appear to feed individually and do not appear to benefit from sharing prey (Ford and Ellis 2006). We do not intend to take observations from a single location and a single population to draw general inference about the biology of the species as a whole. On the contrary, it is our hope that this study's predictions can be tested with additional, focused studies on other populations and ecotypes of the species to assess the generality of our findings and to test the interpretations we propose. The fact that adult males do not participate in prey sharing in this population (Ford and Ellis 2006), in addition to large physiological differences between males and females in this highly dimorphic species, supports the theory that the group as a whole benefits from allowing females and juveniles preferential access to places where fish are easiest to catch and relegating adult males to feeding habitats that would be marginal from the perspective of a female constrained by shorter and shallower diving capabilities than that of a male. This in turn is consistent with sexual selection for larger males, because the larger the male, the bigger the swimming and diving capabilities, the greater the niche partitioning that that male can facilitate and the less intra-family competition we would expect as a result. Overall, our findings are consistent with the prediction from Bain (1989), who suggested that the philopatric males in resident killer whale populations might 'disperse' ecologically rather than geographically. In sperm whales (*Physeter macrocephalus*), the typical mammalian dispersal pattern of female philopatry and male dispersal plays out on a global scale; males feed in high latitudes, whereas females are constrained mainly to low latitudes (Lyrholm et al. 1999). We found that northern resident killer whales in our study area showed an analogous niche partitioning on a microscale, with females and calves constrained to nearshore, shallow waters and males having access to the entire area. Despite vast differences in spatial scale, the end result is the same; females can share prey with juveniles and calves, but adult males reduce competition for food resources with other members of their maternal groups. We suspect that a similar process may be taking place in the cosmopolitan killer whale, but more studies on a wide range of killer whale ecotypes are needed before any conclusions about evolutionary drivers can be reached. Our findings build on an extensive knowledge base of foraging ecology in this species and our understanding of the evolution of sociality in killer whales (Baird 2000; Ford et al. 2000, 2010; Ford and Ellis 2006), but it also has immediate and practical implications for the effective management of the particular population under study. The northern resident killer whale population has a vulnerable status, caused by its small population size, the reliance on populations of Chinook salmon and their sensitivity to human activities. The parapatric southern resident killer whales in the transboundary waters of BC and Washington State are listed as 'endangered' in both Canada and the USA. The recovery strategies call for management measures to reduce human impacts on this population, which may include a marine protected area that is closed to whale-watching traffic (NMFS 2008; DFO 2011). Our findings have implications for spatial planning efforts to promote endangered species recovery. Because resident killer whales are most vulnerable to disturbance during feeding activities, a no-boat protected area would be of greatest benefit to the population if it protects feeding hot spots (Ashe et al. 2010). Our new findings suggest that any protected area would have to go sufficiently far offshore to include the deep-water feeding habitats of males as well as females; otherwise, one runs the risk of simply displacing impacts farther offshore. This would reduce anthropogenic disturbance on females but increase the stressors on males.

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