EVIDENCE OF RESOURCE PARTITIONING BETWEEN HUMPBACK AND MINKE WHALES AROUND THE WESTERN ANTARCTIC PENINSULA

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ABSTRACT: For closely related sympatric species to coexist, they must differ to some degree in their ecological requirements or niches (*e.g.*, diets) to avoid inter-specific competition. Baleen whales in the Antarctic feed primarily on krill, and the large sympatric pre-whaling community suggests resource partitioning among these species or a non-limiting prey resource. In order to examine ecological differences between sympatric humpback and minke whales around the Western Antarctic Peninsula, we made measurements of the physical environment, observations of whale distribution, and concurrent acoustic measurements of krill aggregations. Mantel's tests and Classification and regression tree models indicate both similarities and differences in the spatial associations between humpback and minke whales, environmental features, and prey. The data suggest (1) similarities (proximity to shore) and differences (prey abundance versus deep water temperatures) in horizontal spatial distribution patterns, (2) unambiguous vertical resource partitioning with minke whales associating with deeper krill aggregations across a range of spatial scales, and (3) that interference competition between these two species is unlikely. These results add to the paucity of ecological knowledge relating baleen whales and their prey in the Antarctic and should be considered in conservation and management efforts for Southern Ocean cetaceans and ecosystems.

Keywords: diving and foraging behavior, krill, spatial analysis, whales, Antarctica

INTRODUCTION

Many species of baleen whale migrate seasonally to high-latitude feeding grounds. Historically, much of our knowledge regarding their distribution and feeding habits was linked to commercial catch records (e.g. Mackintosh and Wheeler 1929, Matthews 1937, Tynan 1998). Recently, more rigorous and interdisciplinary studies have begun describing species-specific distribution patterns in relation to physical environmental features (Zerbini *et al.* 2006) and prey availability (Friedlaender *et al.* 2006). However, little quantifiable information exists examining how sympatric species of baleen whales distribute and how, if at all, they partition resources and avoid competition on their feeding grounds.

The Southern Ocean around the Antarctic Peninsula supports large standing stocks of Antarctic krill (*Euphausia superba*), and large populations of top predators (Laws 1977, Ross *et al.* 1996), including many species of baleen whales, which preferentially forage on Antarctic krill (Mackintosh 1965, Gaskin 1982, Ichii and Kato 1991). Clapham and Brownell (1996) noted the existence of such a large sympatric whale community prior to extensive commercial harvesting as strong evidence of either resource partitioning or a lack of resource limitation. For closely related sympatric species to coexist, they must differ to some degree in their ecological requirements or niches (*e.g.,* diets) to avoid inter-specific competition (Pianka 1974, Schoener 1983). Clapham and Brownell (1996) discussed criteria necessary to demonstrate if, in fact, competition in this community might exist. The species in question must be resource limited (Milne 1961), have substantial spatio-temporal overlap in their distribution, and must occupy similar ecological niches. The former is predicated on having similar prey types (*e.g.,* age class of common prey item), as well as foraging on prey patches of similar characteristics (*e.g.,* patch depth, size, etc.) Although the potential for some direct competition may exist, the influence of any such interaction on depleted and recovering whale populations in the Antarctic is difficult to assess, given the paucity of appropriate data for analysis (Clapham and Brownell 1996).

Nonetheless, Clapham and Brownell (1996) postulate that competition is unlikely between Antarctic baleen whale species due in part to probable resource partitioning mediated by food preferences and potentially the biomechanics of body size. It has been suggested, but not substantiated, that baleen whales in the Southern Ocean are not resource-limited, because their prey exists in densities exceeding their requirements (Kawamura 1978). The lack of information on the fine-scale distribution of whales, their prey, and estimates of food consumption has prevented a full examination of inter-specific relationships in the Antarctic whale community.

At a broad scale, Kasamatsu *et al.* (2000) found significant, positive spatial correlations between minke (*Balaenoptera acutorostrata*) and blue whale (*Balaenoptera musculus*) densities, but no relationship between minke and humpback whales (*Megaptera novaeangliae*). These authors suggested the possibility of interference competition between minke and humpback whales as a causal factor for the lack of a relationship between their distributions, but did not include measurements of prey in their analyses to determine how each species is affected by its distribution and availability.

Humpback and minke whales are the most abundant baleen whales inhabiting the near-shore waters of the Western Antarctic Peninsula (WAP) (Thiele *et al.* 2004; Friedlaender *et al.* 2006). Recently, Friedlaender *et al.* (2006) used concurrent measurements of both whale observations and an index of prey abundance to explore the meso-scale distribution of sympatric humpback and minke whales combined in the inner shelf waters of the WAP. These authors found whale distributions most strongly linked to prey distribution and abundance, and to certain physical and bathymetric features (e.g. ice edge, increased bathymetric slope) which may help to aggregate krill (*e.g.*, Brierley *et al.* 2002). Likewise, Thiele *et al.* (2004) in a study of the same region found both minke and humpback whales in summer months to be associated with the sea ice boundary. While humpback whales apparently utilize the open water areas and ice edge zone, Ainley *et al.* (2007) indicated that the marginal ice zone around the WAP may reflect a habitat edge for pagophilic minke whales more frequently inhabiting deeper pack ice habitats.

The goal of the present study was to examine ecological differences between sympatric humpback and minke whales in the inner shelf waters of the WAP. We used spatially explicit techniques to characterize and compare the distribution of each whale species to environmental variables, and the distribution, abundance, and behavior of their common prey, Antarctic krill. Overall, our results provided strong support for niche separation, and are thus consistent with a consequent lack of inter-specific competition between humpback and minke whales around the Western Antarctic Peninsula.

MATERIALS AND METHODS

We use cetacean sighting information and environmental data collected as part of the Southern Ocean GLOBal ECosystem dynamics program (GLOBEC) between April-June 2001 around the continental shelf waters of Marguerite Bay (see Friedlaender *et al.*

2006). All environmental variables and their sampling methodologies are found in Table 1. Hydrographic data were collected continuously and at predetermined sampling stations covering the continental shelf and inshore regions (Klinck *et al.* 2004). Bathymetric data were extracted from Bolmer *et al.* (2004)'s 15 second spatial resolution grid. We use ice edge information from Chapman *et al.* (2004) as determined via the method of Zwally *et al.* (1983).

All environmental variable data were imported into ArcGIS 9.1 and interpolated using an inverse distance-weighted function to create continuous surfaces (rasters) from which to sample. Similarly, Euclidean distance surfaces were generated for a set of environmental features including distance to the inner shelf water boundary, distance to areas of increased bathymetric slope (>15% of change in depth from shallowest to deepest point within a grid cell), distance to the ice edge, and distance to the coast.

The abundance and distribution of the whale's krill prey was assessed from acoustic survey data collected from the *RVIB Nathaniel B Palmer* concurrent to cetacean surveys. The analytical methods developed and tested in Lawson *et al.* (2008A,B) were used to identify krill and estimate krill biomass density (g/m^3) from multi-frequency (43, 120, 200, 420 kHz) volume backscattering data at a resolution of ca. 35 m along the survey transects and 1.5 m in depth, to a maximum depth that varied between 320 and 600 m (see Lawson *et al.* (2004, 2008A) for full details on acoustic data collection). For comparison to the distribution of whales, biomass density estimates were vertically integrated over a depth range of 1-300 m (although the surface bubble layer mostly precluded biomass estimates shallower than 25 m) and then averaged over 5 km along-track intervals, centered at the location of each whale sighting, to yield mean krill biomass per unit of surface area (g/m^2) in the vicinity of each whale.

Measurements were also made of the characteristics of each observed krill aggregation, including aggregation depth and total cross-sectional area (in depth and along-track distance), as well as the mean density of krill present by number and biomass (Lawson *et al.* 2008B). The multi-frequency inverse method of Lawson *et al.* (2008A) was used to estimate the mean length of krill in each aggregation, although due primarily to the range limitation of the 420 kHz system, krill length could not be estimated for every aggregation observed. An index of total aggregation biomass was calculated by multiplying each estimate of biomass density (g/m^3) by the depth and along-track distance represented by that estimate, and then summing over all measurements within each aggregation. This index is left in units of kilograms per across-track meter, since the across-track extent of each aggregation is not measured by the acoustic system.

Sensitivity and noise problems associated with the 43 kHz system resulted in some ambiguity in whether those acoustically-detected aggregations that were the minimum size that could be resolved by the system were comprised of krill or more weakly scattering zooplankton such as copepods. We therefore excluded such aggregations from the analysis. Although these small aggregations were numerous, each was of very small biomass and filtering them from the dataset still retained most of the total biomass present (see Lawson *et al.* 2008A,B for further details).

We used Mantel's tests to explore which environmental features contributed to the observed distribution patterns of humpback and minke whales. Mantel's tests combine multiple linear regressions applied to distance (dissimilarity) matrices generated from spatially referenced sample locations. These tests allowed us to determine which variables best explained species distributions once their confounding mutual correlations and spatial structure were accounted for (Mantel 1967; Schick and Urban 2000). Data were analyzed in the 'ecodist' library in S-PLUS (SAS). Pure partial Mantel's tests were run to determine which variables significantly contribute to the observed whale distribution patterns. The pure partial test accounts for spatial autocorrelation of each variable as well as its inherent relationship or correlation to all other measured environmental variables.

To determine how characteristics of krill aggregations influenced species-specific distributions, we ran classification tree models using the R-part functions of the statistical package R. Tree-based hierarchical models, such as CART (Classification and Regression Tree analysis), employ binary recursive portioning methods to resolve relationships to response variables by partitioning data into increasingly homogeneous sub-groups (Breiman *et al.* 1984). CART models are an attractive analytical tool because, unlike linear models, they do not assume *a priori* relationships between response and predictor variables; rather the data are divided into several groups where each has a different predicted value of the response variable (Guisan and Zimmerman 2000, Redfern *et al.* 2006).

We ran classification trees using whale species as the predictor variable, and medians of the krill aggregation metrics (depth, area, mean krill length, mean numerical density, mean biomass density) for all aggregations within 5 km of each whale sighting as response variables. We chose a minimum of 5 observations before splits, and a minimum node size of 10 observations. We then used an optimal recursive shrinking method to prune the tree model. This method shrinks lower nodes to their parent nodes based upon the magnitude of the difference between the fitted values of the lower nodes and the fitted values of their parent nodes (R). Cross-validation tests then determined whether the number of nodes generated by the model maximized the amount of deviance explained, and did not over-fit the data. This technique optimally shrinks the classification tree to include the maximum number of terminal nodes as a function of the greatest reduction in residual mean deviance.

In an effort to understand whether whales were responding to differences in the vertical distribution of krill aggregations, or whether the krill were responding to whale predation, we also compared the frequency distribution of the depth of krill aggregations in the presence and absence of whales. We then ran a Kruskal-Wallace non-parametric analysis to test whether the frequency distribution differed between the two groups.

RESULTS

We found significant spatial relationships between humpback and minke whales and several environmental variables (Table 2). Mantel's tests revealed that all environmental variables were spatially auto-correlated for both whale species, and two had a pure partial effect on the distribution of humpback whales: distance to the coast ($p<0.01$), and krill biomass from 25-300 meters ($p<0.001$). The latter variable had an order of magnitude more explanatory power than the former based on p-values. Humpback whales thus associate with areas of increased prey abundance and close to shore. The deep temperature maximum ($p<0.0001$) and distance to shore ($p<0.0001$) had pure partial effects on the occurrence of minke whales, with minke whales associated with colder deep water temperatures and regions close to shore.

A total of 411 (282 associated with humpback whales and 129 with minke whales) krill aggregations were sampled within 5000 meters of whale sightings (Figure 1). Thirty-two groups of humpbacks (comprised of 61 individuals) and 22 groups of minke whales (comprised of 35 individuals) were sighted. Relevant metrics of krill aggregations associated with these sightings are shown in Table 3.

Krill aggregations of highest biomass were associated with regions close to land where bathymetry was highly variable and waters at depth were cooler than what was available over the continental shelf as a whole (Figure 1; Lawson *et al.* 2008B). In a vertical sense, the distribution of krill aggregations was bimodal, with one mode at depths shallower than ca. 75 meters and one at greater depths. This bimodality was evident both when whales (minke and humpback whales combined) were present and absent (Figure 2) , although the distributions differed significantly in the presence versus absence of whales (p=0.0007, Kruskal-Wallace rank sum test).

The median depth of krill aggregations associated with minke whales was significantly greater than those associated with humpbacks (p= 0.001, Kruskal-Wallace rank sum test) across a range of spatial scales (500, 1000, 2500, and 5000 meters; Figure 3). The absolute difference in median depth between the two species was 28 meters (118 vs. 90 meters) at the greatest spatial extent measured. This difference increased with proximity to the sightings up to 81 meters (135 vs. 54 meters) at a 500 meters sampling radius. We also found no significant difference (p=0.72) between the median aggregation depths associated with minke whales when humpback whales were also present versus when they were sighted alone (127 meters, stdev = 45 versus 124 meters, stdev = 86).

Tree models indicated a fundamental difference in the depth of krill aggregations associated with humpback and minke whales. Using all the available aggregation metrics, the primary node showed only minke whales associated with aggregations of median depth greater than 133 meters (Figure 4a). All of the humpback whales, and one of the minke whales, were associated with aggregations of median depth shallower than this. The second and only other split was again associated with depth, splitting the humpbacks into two sub-groups, the deeper of which also included the one minke whale not associated with the > 133 meters group resulting from the primary split. Only humpback whales were found to associate with aggregations shallower than 104 meters. Overall, this tree's misclassification rate was 0.05, with a residual mean deviance of 0.31: in attempting to create homogeneous subgroups, one of the minke whale samples was incorrectly classified to a group containing otherwise only humpback whales.

DISCUSSION

We provide evidence which supports resource partitioning between humpback and minke whales during autumn in the near-shore waters of the Western Antarctic Peninsula. In a horizontal sense, the distribution of humpback and minke whales was similar: both species associated with regions close to shore, with humpback whales additionally associated with regions of increased krill biomass and minke whales with colder deep water temperatures. In a vertical sense, humpback whales were associated with krill aggregations in the upper portion (<~133 meters) of the water column, while minke whales associated unambiguously with deeper krill aggregations. The presence of humpback whales made no difference in the depth of krill aggregations associated with minke whales, supporting the conclusion that minke whales may indeed feed deeper regardless of the presence of other whales, and thus that there is no competitive influence on the vertical nature of their aggregation selection.

A bi-modal depth distribution of krill aggregations in the water column, with modes around 50 meters and between 100-150 meters (Figure 2), was apparent both when whales are present and absent. Although these depth distributions were significantly different in the presence and absence of whales (p=0.0007), the general shape of the distribution remained constant. While we cannot unequivocally show that the whales are responding to the krill's distribution and not the krill responding to one whale species differently than the other, this similarity in depth distribution supports our position that it is the former: humpback and minke whales partition resources vertically in the water column. At close ranges (within 500 meters of a sighting), the two species associate with prey aggregations separated vertically by nearly 100 meters. Separation was accentuated with increasing proximity to the whale but was maintained at the greatest spatial extent of our analysis (5000 meters). Thus, while these two species may overlap in their horizontal distribution, they associate with prey aggregations in distinct levels of the water column.

The primary (and only subsequent) split in the CART analysis, depth of krill aggregations, may also be due at least in part to an association between minke whales and large, dense krill aggregations. While there is tremendous variability in the krill aggregation metrics, Table 3 indicates a greater range of aggregation areas and higher median krill biomass density associated with minke whales than for humpback whales. Indeed, many of the largest and most dense krill aggregations found around Marguerite Bay were in deep water (Ashjian *et al.* 2004, Lawson *et al.* 2004, Lawson *et al.* 2008B), and the apparent split between the whale species on the basis of aggregation depth detected by the CART analysis may relate to these correlations between aggregation depth and size or density.

It is important to acknowledge certain limitations of our acoustic analysis that introduce some uncertainty into the patterns identified here (and see Lawson *et al.* 2008A,B for a comprehensive discussion of sources of uncertainty). First, the acoustic methodologies were unable to distinguish between the two species of aggregating euphausiid known to inhabit this region, *Euphausia superba* and *E. crystallorophias* (Ross *et al.*, 1996). Some of our acoustically-identified aggregations may thus be composed of this latter euphausiid species, confounding our understanding of the distribution of *Euphausia superba*, the main prey item for the whales under study here. In addition, all of the acoustic analyses of krill aggregations are affected to some extent by uncertainty in whether the acoustically-identified aggregations were indeed composed of euphausiids rather than some other zooplankton or micronekton. It should also be noted that the observations of whale distribution and krill aggregation features examined here were made during the day only, and that at least some of the krill in this region are known to migrate vertically on a diel basis, occupying deeper waters in aggregations of higher density during the day than night (Zhou and Dorland 2004; Lawson 2006, unpublished results). With the present data, it is not possible to assess whether the observed daytime partitioning of the krill resource on the basis of depth by the two whale species is modified during the night when the krill migrate to shallower waters; it is possible that partitioning continues but is shifted to shallower depths. Further investigation into this question is warranted.

Differences in the residency and migratory patterns of minke and humpback whales may lend insights into the observed differences in the prey characteristics with which each species associates. Whales preparing themselves for the coupled energetic demands of migration/fasting and reproduction should maximize their rate of energy storage just prior to leaving feeding grounds. This could mean taking advantage of the most accessible prey aggregations (i.e. closest to the surface to minimize energetic costs of diving). This study was conducted during autumn, just prior to the initial advance of annual sea ice. The vast majority, if not all, of humpback whales found around the WAP during this time will eventually migrate north. The same cannot be said for minke whales. An unknown number of minke whales remain and over-winter in the pack ice around Antarctica. In fact, minkes were observed during cetacean surveys in the study region later in the winter of 2001 and 2002 (Thiele *et al.* 2004). If the minke whales which were sighted in fall are not preparing for an extensive migration, they may not be increasing their energy stores as much as humpback whales, and thus not associating with the most easily accessible and shallowest prey. Alternatively, at this point in the season many migrating whales may have already left the area, lowering overall cetacean density. It is plausible that the resource partitioning found in our research is a function of the cetacean community structure at this time of year. Whether this is the case throughout the rest of the feeding season has yet to be determined.

Access to open water for breathing is the most fundamental commodity which minke whales must have to survive winter in the Antarctic. The correlation between minke whales and proximity to shore supports Ainley *et al.* (2007)'s finding of increased minke whale sighting rates in proximity to coastal ice-free polynyas in fall. Such coastal polynyas are known to occur around the Antarctic in winter (*e.g.*, Anderson 1993), and several reports indicate concentrations of air-breathing krill predators associated with areas of both warm water upwelling (Plotz *et al.* 1991) and polynyas (Burns 2002). If polynyas also offer access to prey, minke whales would be able to forage continuously, and thus may be released from the pressure to store energy for a long fasting period of migration. The minke whales might thus be associated with these coastal regions during our fall survey period in preparation for the arrival of winter ice cover.

Our findings suggest that resource partitioning exists amongst baleen whales in the Antarctic marine ecosystem. This resource partitioning among humpback and minke whales may have evolved before commercial exploitation diminished many whale populations, and still exists today. Given the long life spans and generation times of baleen whales, the mechanisms and forces which gave rise to such ecological conditions would likely still be present today.

Our results do not rule out the possibility that prey is not limiting in the present environment. There may be physical limitations or density-dependent population demographics playing a role in the observed patterns as well. However, the current number of baleen whales (with the possible exception of minke whales) in this ecosystem is well below pre-whaling numbers (Baker and Clapham 2004), requiring a substantial decrease in overall prey availability to make them limiting. While the correlations we have found are consistent with resource partitioning, the scope of this research limits our ability to determine the causal mechanisms or links. Dedicated behavioral research efforts could explore some of the mechanistic possibilities aforementioned. We have analyzed data from one year of a two year field project because of limited overlap in hydro-acoustic and whale sighting data in the second year. There is evidence that krill aggregation distribution can vary substantially between years in a given area (Lawson *et al.* in press B), and it is possible that the relationships we have found are not stable over time. However, with the limited data we have for comparison from our second year, we find similar species-specific relationships which support our findings: median aggregation depth was greater for minke (143 meters) than humpback whales (106 meters).

The present findings also have implications for cetacean management and conservation practices in the Southern Ocean. Our results do not support recent speculation regarding inter-specific competition in the Antarctic, notably that Antarctic minke whales have been negatively impacted through interference competition with increasing populations of humpback whales (*e.g.,* Fujise *et al.* 2006, Konishi *et al.* 2006, IWC 2007). We provide evidence to support resource partitioning between humpback and minke whales in the near-shore waters off the Western Antarctic Peninsula. Minke whales associated unambiguously with deeper krill aggregations than humpback whales. These findings add to the paucity of data describing the ecology of baleen whales and predator-prey relationships in the Southern Ocean and may provide useful in light of changing environmental and prey conditions throughout the Antarctic marine ecosystem.

ACKNOWLEDGMENTS

We thank the officers and crew of the *Nathaniel B Palmer* and *Lawrence M Gould* for their cooperation in conducting field work. We also thank the whale observers and members of the BIOMAPER team without whom these data could not have been collected. We are grateful to Drs. E. Hofmann, R. Barber, P. Wiebe, D. Thiele and A. Read and anonymous reviewers for their thoughtful and constructive comments. This research was supported by the International Whaling Commission, the Duke University Marine Laboratory, NSF US Antarctic Program Grant OPP-9910307 as part of the Southern Ocean GLOBEC project, and a Fulbright Scholarship and Office of Naval Research Grant N00014-03-1-0212 (to G. Lawson).

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FIGURE LEGENDS

Figure 1. Study area of Marguerite Bay, Western Antarctic Peninsula. Krill aggregations detected from BIOMAPER-II hydro-acoustic surveys are indicated as expanding grey circles indicating an index of total aggregation biomass (kg/m). Humpback whale sightings are shown as black x's and minke whale sightings as black circles.

Figure 2. Daytime depth distribution of krill aggregations in the presence (top plot) and absence (bottom plot) of whales from 0-250 meters

Figure 3. Median depth for all krill aggregations found within a range of distances (500, 1000, 2500, and 5000 m) from humpback and minke whale sightings. Smoothed lines have been fit for each species, and standard error bars are indicated.

Figure 4. Classification tree showing the relationships between all krill aggregation characteristics and humpback and minke whale sightings.

Table 1. The unit of measure, and sampling method for environmental variable collected during SO GLOBEC and used in Mantel's tests of species-specific distribution patterns.

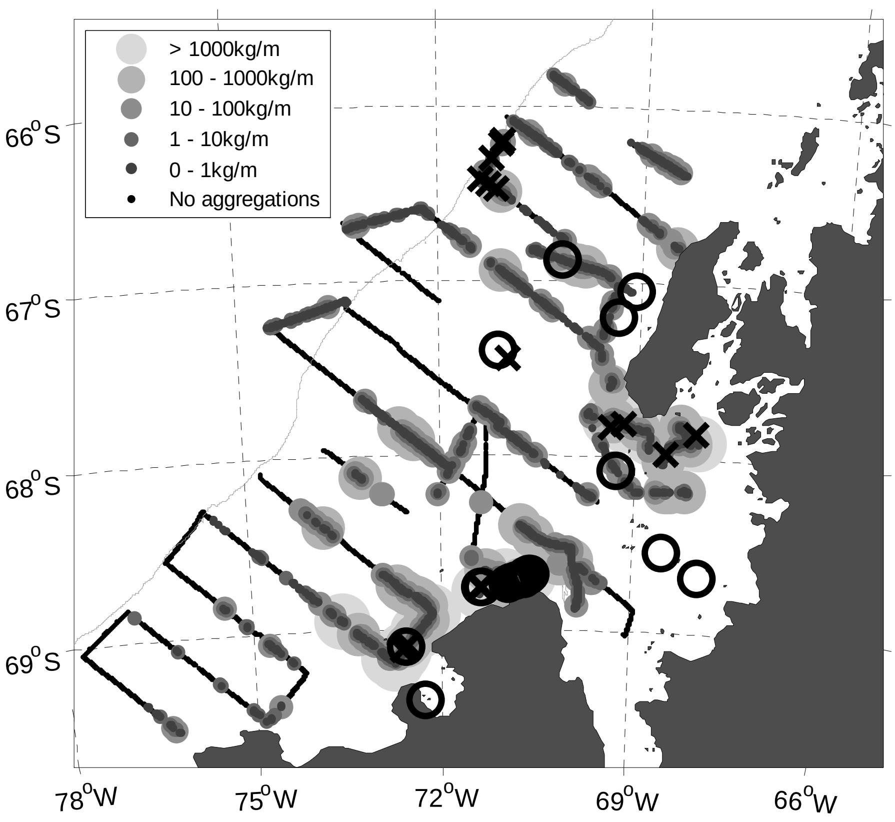
Environmental Variable	Units	Sampling method
Krill biomass 1-300m (X1-300m)	g/m^2	Continuous along track and interpolated fields
Chlorophyll a (Chla)	g/m^3	Interpolated grids from sampling stations
Bathymetry (bathy)	Meters	ETOPO modified bathymetry grid (Bolmer *et al.* 2004)
Slope of bathymetry (Slope.bathy)	Degree change/grid cell	Grid cells calculated from bathymetry grid
Water temperature maximum below 200m (Tmax)	°C	Interpolated grids from sampling stations
Distance from coast (Dist.coast)	Meters	Straight line distance grids
Distance from ice edge (Dist.ice)	Meters	Straight line distance grids
Distance from high slope (Dist.slp)	Meters	Straight line distance grids
Distance from inner shelf water boundary (Dist.inswb)	Meters	Straight line distance grids from reclassified deep temperature max.

Table 2. Mantel coefficients (p values) for multivariate analysis relating humpback and minke whale sightings to environmental variables. The columns show the Mantel pure partial effects of each variable on whale distribution accounting for space and the relationships to each other environmental variable. Significant relationships (and their direction) are shown in bold.

	Humpback	**Minke**
Tmax	0.022(0.09)	**0.280(0.0001) (-)**
Slope.bathy	-0.019(0.95)	-0.041(0.992)
Chla	-0.003(0.56)	-0.019(0.887)
Dist.inswb	-0.028(0.98)	-0.111(0.999)
Dist.slp	-0.03(0.98)	0.060(0.999)
Bathy	0.007(0.23)	-0.221(0.998)
Dist.ice	-0.130(0.99)	-0.096(0.998)
Dist.coast	**0.120(0.01)(-)**	**0.447(0.0001) (-)**
X1-300m	**0.064(0.001) (+)**	0.016(0.133)

Table 3. Median values and standard errors for krill aggregation variables associated with humpback and minke whales sampled at 5000 m, and all krill aggregations measured in the absence of whales.

Species	Aggregation Depth (m)	Aggregation Area (m^2)	Krill Length (mm)	Numeric Density (#/m^3)	Biomass Density (g/m^3)
Humpback	90.0 (2.7)	210 (2069)	36.5 (1.1)	11.6 (23.8)	11.5 (0.02)
Minke	118.5 (6.1)	202 (8960)	39 (0.5)	8.0 (3.8)	16.3 (0.03)
No Whales	53.3 (0.8)	193 (521)	35.3 (0.3)	6.2 (1.3)	4.7 (0.01)



> 1000kg/m
100 - 1000kg/m
10 - 100kg/m
1 - 10kg/m
0 - 1kg/m
No aggregations
66°S
67°S
68°S
69°S
78°W
75°W
72°W
69°W
66°W

Figure 1.

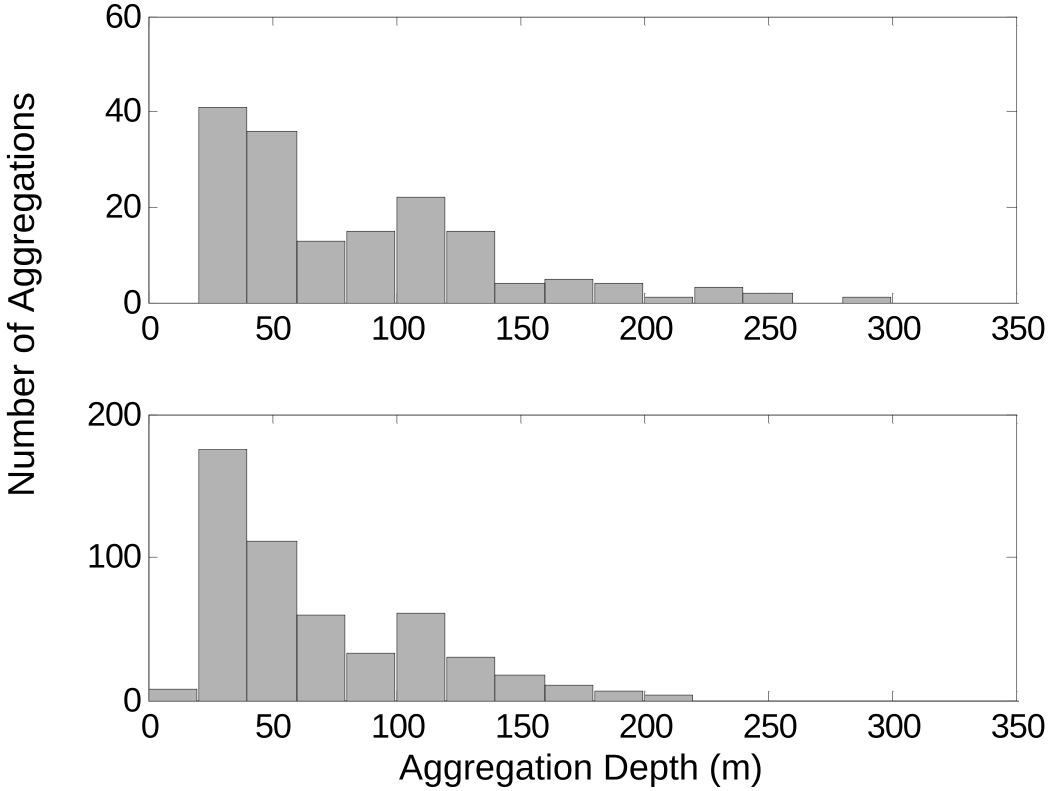

60
40
20
0
0
50
100
150
200
250
300
350
200
100
0
0
50
100
150
200
250
300
350
Number of Aggregations
Aggregation Depth (m)

Figure 2.

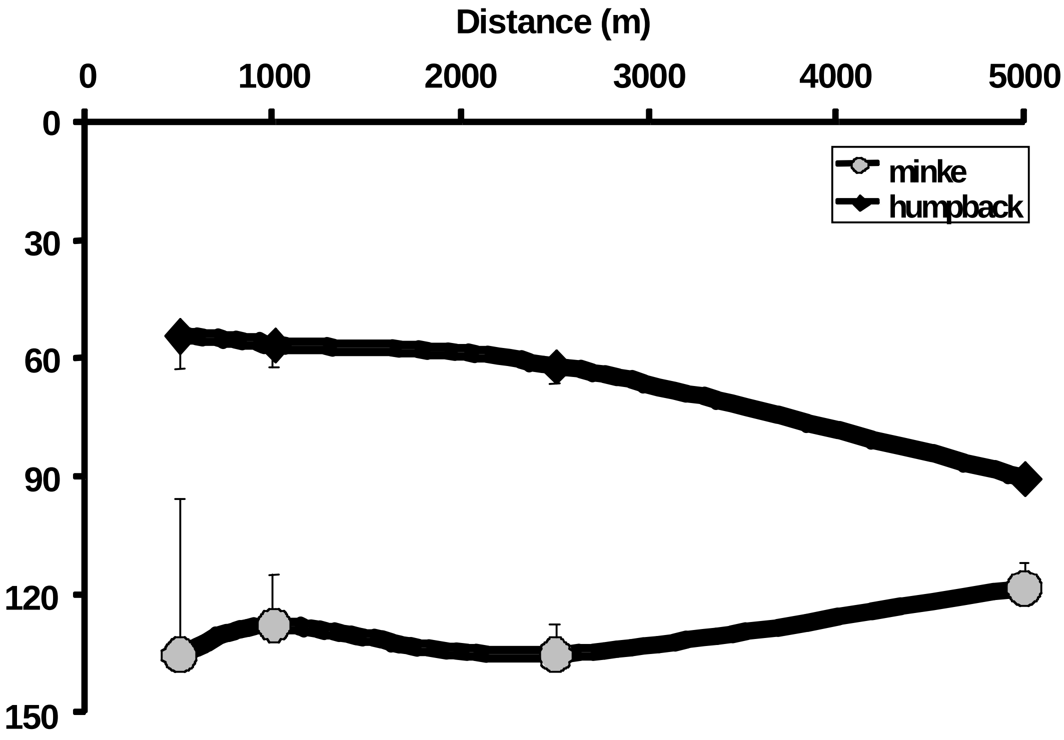

Distance (m)
0
1000
2000
3000
4000
5000
0
30
60
90
120
150
minke
humpback

Figure 3.

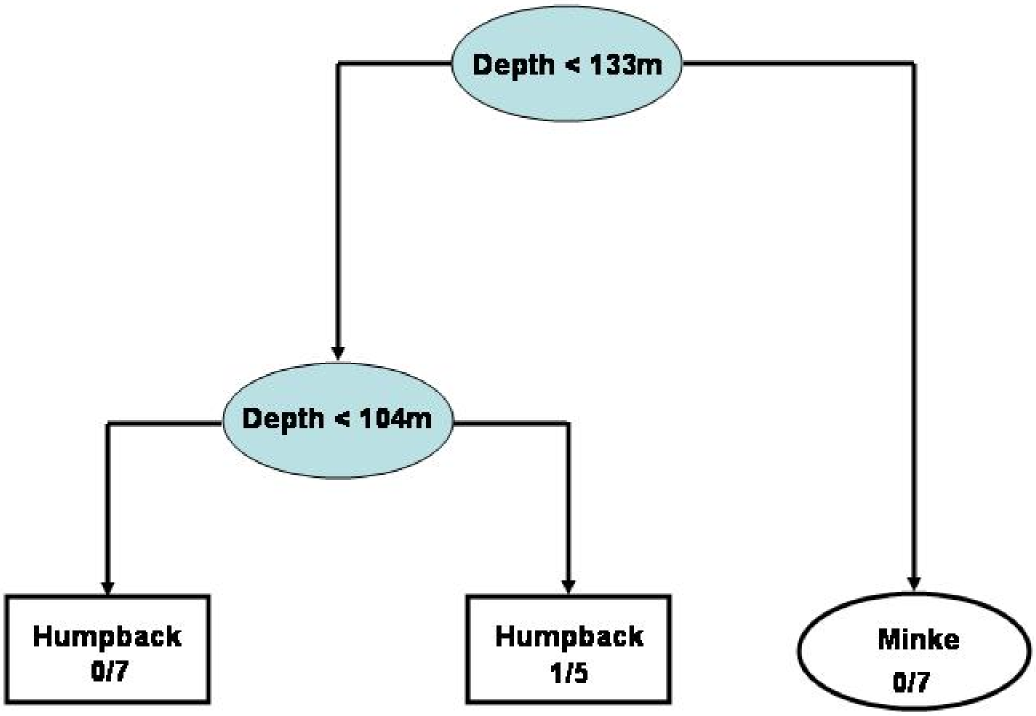


Figure 4.