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

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

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

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50 **INTRODUCTION**

51 Many species of baleen whale migrate seasonally to high-latitude feeding
52 grounds. Historically, much of our knowledge regarding their distribution and feeding
53 habits was linked to commercial catch records (e.g. Mackintosh and Wheeler 1929,
54 Matthews 1937, Tynan 1998). Recently, more rigorous and interdisciplinary studies have
55 begun describing species-specific distribution patterns in relation to physical
56 environmental features (Zerbini *et al.* 2006) and prey availability (Friedlaender *et al.*
57 2006). However, little quantifiable information exists examining how sympatric species
58 of baleen whales distribute and how, if at all, they partition resources and avoid
59 competition on their feeding grounds.

60 The Southern Ocean around the Antarctic Peninsula supports large standing
61 stocks of Antarctic krill (*Euphausia superba*), and large populations of top predators
62 (Laws 1977, Ross *et al.* 1996), including many species of baleen whales, which
63 preferentially forage on Antarctic krill (Mackintosh 1965, Gaskin 1982, Ichii and Kato
64 1991). Clapham and Brownell (1996) noted the existence of such a large sympatric
65 whale community prior to extensive commercial harvesting as strong evidence of either
66 resource partitioning or a lack of resource limitation. For closely related sympatric
67 species to coexist, they must differ to some degree in their ecological requirements or
68 niches (*e.g.*, diets) to avoid inter-specific competition (Pianka 1974, Schoener 1983).
69 Clapham and Brownell (1996) discussed criteria necessary to demonstrate if, in fact,
70 competition in this community might exist. The species in question must be resource
71 limited (Milne 1961), have substantial spatio-temporal overlap in their distribution, and
72 must occupy similar ecological niches. The former is predicated on having similar prey

73 types (*e.g.*, age class of common prey item), as well as foraging on prey patches of
74 similar characteristics (*e.g.*, patch depth, size, etc.) Although the potential for some direct
75 competition may exist, the influence of any such interaction on depleted and recovering
76 whale populations in the Antarctic is difficult to assess, given the paucity of appropriate
77 data for analysis (Clapham and Brownell 1996).

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

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

93 Humpback and minke whales are the most abundant baleen whales inhabiting the
94 near-shore waters of the Western Antarctic Peninsula (WAP) (Thiele *et al.* 2004;
95 Friedlaender *et al.* 2006). Recently, Friedlaender *et al.* (2006) used concurrent

96 measurements of both whale observations and an index of prey abundance to explore the
97 meso-scale distribution of sympatric humpback and minke whales combined in the inner
98 shelf waters of the WAP. These authors found whale distributions most strongly linked
99 to prey distribution and abundance, and to certain physical and bathymetric features (e.g.
100 ice edge, increased bathymetric slope) which may help to aggregate krill (*e.g.*, Brierley *et*
101 *al.* 2002). Likewise, Thiele *et al.* (2004) in a study of the same region found both minke
102 and humpback whales in summer months to be associated with the sea ice boundary.
103 While humpback whales apparently utilize the open water areas and ice edge zone,
104 Ainley *et al.* (2007) indicated that the marginal ice zone around the WAP may reflect a
105 habitat edge for pagophilic minke whales more frequently inhabiting deeper pack ice
106 habitats.

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

114

115 **MATERIALS AND METHODS**

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

119 2006). All environmental variables and their sampling methodologies are found in Table
120 1. Hydrographic data were collected continuously and at predetermined sampling
121 stations covering the continental shelf and inshore regions (Klinck *et al.* 2004).
122 Bathymetric data were extracted from Bolmer *et al.* (2004)'s 15 second spatial resolution
123 grid. We use ice edge information from Chapman *et al.* (2004) as determined via the
124 method of Zwally *et al.* (1983).

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

131 The abundance and distribution of the whale's krill prey was assessed from
132 acoustic survey data collected from the *RVIB Nathaniel B Palmer* concurrent to cetacean
133 surveys. The analytical methods developed and tested in Lawson *et al.* (2008A,B) were
134 used to identify krill and estimate krill biomass density (g/m^3) from multi-frequency (43,
135 120, 200, 420 kHz) volume backscattering data at a resolution of ca. 35 m along the
136 survey transects and 1.5 m in depth, to a maximum depth that varied between 320 and
137 600 m (see Lawson *et al.* (2004, 2008A) for full details on acoustic data collection). For
138 comparison to the distribution of whales, biomass density estimates were vertically
139 integrated over a depth range of 1-300 m (although the surface bubble layer mostly
140 precluded biomass estimates shallower than 25 m) and then averaged over 5 km along-

141 track intervals, centered at the location of each whale sighting, to yield mean krill
142 biomass per unit of surface area (g/m^2) in the vicinity of each whale.

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

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

161 We used Mantel's tests to explore which environmental features contributed to
162 the observed distribution patterns of humpback and minke whales. Mantel's tests
163 combine multiple linear regressions applied to distance (dissimilarity) matrices generated

164 from spatially referenced sample locations. These tests allowed us to determine which
165 variables best explained species distributions once their confounding mutual correlations
166 and spatial structure were accounted for (Mantel 1967; Schick and Urban 2000). Data
167 were analyzed in the ‘ecodist’ library in S-PLUS (SAS). Pure partial Mantel’s tests were
168 run to determine which variables significantly contribute to the observed whale
169 distribution patterns. The pure partial test accounts for spatial autocorrelation of each
170 variable as well as its inherent relationship or correlation to all other measured
171 environmental variables.

172 To determine how characteristics of krill aggregations influenced species-specific
173 distributions, we ran classification tree models using the R-part functions of the statistical
174 package R. Tree-based hierarchical models, such as CART (Classification and
175 Regression Tree analysis), employ binary recursive partitioning methods to resolve
176 relationships to response variables by partitioning data into increasingly homogeneous
177 sub-groups (Breiman *et al.* 1984). CART models are an attractive analytical tool
178 because, unlike linear models, they do not assume *a priori* relationships between
179 response and predictor variables; rather the data are divided into several groups where
180 each has a different predicted value of the response variable (Guisan and Zimmerman
181 2000, Redfern *et al.* 2006).

182 We ran classification trees using whale species as the predictor variable, and
183 medians of the krill aggregation metrics (depth, area, mean krill length, mean numerical
184 density, mean biomass density) for all aggregations within 5 km of each whale sighting
185 as response variables. We chose a minimum of 5 observations before splits, and a
186 minimum node size of 10 observations. We then used an optimal recursive shrinking

187 method to prune the tree model. This method shrinks lower nodes to their parent nodes
188 based upon the magnitude of the difference between the fitted values of the lower nodes
189 and the fitted values of their parent nodes (R). Cross-validation tests then determined
190 whether the number of nodes generated by the model maximized the amount of deviance
191 explained, and did not over-fit the data. This technique optimally shrinks the
192 classification tree to include the maximum number of terminal nodes as a function of the
193 greatest reduction in residual mean deviance.

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

199

200 **RESULTS**

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

209 pure partial effects on the occurrence of minke whales, with minke whales associated
210 with colder deep water temperatures and regions close to shore.

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

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

224 The median depth of krill aggregations associated with minke whales was
225 significantly greater than those associated with humpbacks ($p= 0.001$, Kruskal-Wallis
226 rank sum test) across a range of spatial scales (500, 1000, 2500, and 5000 meters; Figure
227 3). The absolute difference in median depth between the two species was 28 meters (118
228 vs. 90 meters) at the greatest spatial extent measured. This difference increased with
229 proximity to the sightings up to 81 meters (135 vs. 54 meters) at a 500 meters sampling
230 radius. We also found no significant difference ($p=0.72$) between the median aggregation

231 depths associated with minke whales when humpback whales were also present versus
232 when they were sighted alone (127 meters, stdev = 45 versus 124 meters, stdev = 86).

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

245

246 **DISCUSSION**

247 We provide evidence which supports resource partitioning between humpback
248 and minke whales during autumn in the near-shore waters of the Western Antarctic
249 Peninsula. In a horizontal sense, the distribution of humpback and minke whales was
250 similar: both species associated with regions close to shore, with humpback whales
251 additionally associated with regions of increased krill biomass and minke whales with
252 colder deep water temperatures. In a vertical sense, humpback whales were associated
253 with krill aggregations in the upper portion (<~133 meters) of the water column, while

254 minke whales associated unambiguously with deeper krill aggregations. The presence of
255 humpback whales made no difference in the depth of krill aggregations associated with
256 minke whales, supporting the conclusion that minke whales may indeed feed deeper
257 regardless of the presence of other whales, and thus that there is no competitive influence
258 on the vertical nature of their aggregation selection.

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

273 The primary (and only subsequent) split in the CART analysis, depth of krill
274 aggregations, may also be due at least in part to an association between minke whales and
275 large, dense krill aggregations. While there is tremendous variability in the krill
276 aggregation metrics, Table 3 indicates a greater range of aggregation areas and higher

277 median krill biomass density associated with minke whales than for humpback whales.
278 Indeed, many of the largest and most dense krill aggregations found around Marguerite
279 Bay were in deep water (Ashjian *et al.* 2004, Lawson *et al.* 2004, Lawson *et al.* 2008B),
280 and the apparent split between the whale species on the basis of aggregation depth
281 detected by the CART analysis may relate to these correlations between aggregation
282 depth and size or density.

283 It is important to acknowledge certain limitations of our acoustic analysis that
284 introduce some uncertainty into the patterns identified here (and see Lawson *et al.*
285 2008A,B for a comprehensive discussion of sources of uncertainty). First, the acoustic
286 methodologies were unable to distinguish between the two species of aggregating
287 euphausiid known to inhabit this region, *Euphausia superba* and *E. crystallorophias*
288 (Ross *et al.*, 1996). Some of our acoustically-identified aggregations may thus be
289 composed of this latter euphausiid species, confounding our understanding of the
290 distribution of *Euphausia superba*, the main prey item for the whales under study here. In
291 addition, all of the acoustic analyses of krill aggregations are affected to some extent by
292 uncertainty in whether the acoustically-identified aggregations were indeed composed of
293 euphausiids rather than some other zooplankton or micronekton. It should also be noted
294 that the observations of whale distribution and krill aggregation features examined here
295 were made during the day only, and that at least some of the krill in this region are known
296 to migrate vertically on a diel basis, occupying deeper waters in aggregations of higher
297 density during the day than night (Zhou and Dorland 2004; Lawson 2006, unpublished
298 results). With the present data, it is not possible to assess whether the observed daytime
299 partitioning of the krill resource on the basis of depth by the two whale species is

300 modified during the night when the krill migrate to shallower waters; it is possible that
301 partitioning continues but is shifted to shallower depths. Further investigation into this
302 question is warranted.

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

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

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

339 Our results do not rule out the possibility that prey is not limiting in the present
340 environment. There may be physical limitations or density-dependent population
341 demographics playing a role in the observed patterns as well. However, the current
342 number of baleen whales (with the possible exception of minke whales) in this ecosystem
343 is well below pre-whaling numbers (Baker and Clapham 2004), requiring a substantial
344 decrease in overall prey availability to make them limiting. While the correlations we

345 have found are consistent with resource partitioning, the scope of this research limits our
346 ability to determine the causal mechanisms or links. Dedicated behavioral research
347 efforts could explore some of the mechanistic possibilities aforementioned. We have
348 analyzed data from one year of a two year field project because of limited overlap in
349 hydro-acoustic and whale sighting data in the second year. There is evidence that krill
350 aggregation distribution can vary substantially between years in a given area (Lawson *et*
351 *al.* in press B), and it is possible that the relationships we have found are not stable over
352 time. However, with the limited data we have for comparison from our second year, we
353 find similar species-specific relationships which support our findings: median
354 aggregation depth was greater for minke (143 meters) than humpback whales (106
355 meters).

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

548

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

553

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

556

557 **Figure 3.** Median depth for all krill aggregations found within a range of distances (500,
558 1000, 2500, and 5000 m) from humpback and minke whale sightings. Smoothed lines
559 have been fit for each species, and standard error bars are indicated.

560

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

563

564 **Table 1.** The unit of measure, and sampling method for environmental variable collected
 565 during SO GLOBEC and used in Mantel's tests of species-specific distribution patterns.
 566

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 <i>et al.</i> 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.

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570 **Table 2.** Mantel coefficients (p values) for multivariate analysis relating humpback and
571 minke whale sightings to environmental variables. The columns show the Mantel pure
572 partial effects of each variable on whale distribution accounting for space and the
573 relationships to each other environmental variable. Significant relationships (and their
574 direction) are shown in bold.
575
576

	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)

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

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Species	Aggregation Depth (m)	Aggregation Area (m²)	Krill Length (mm)	Numeric Density (#/m³)	Biomass Density (g/m³)
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)

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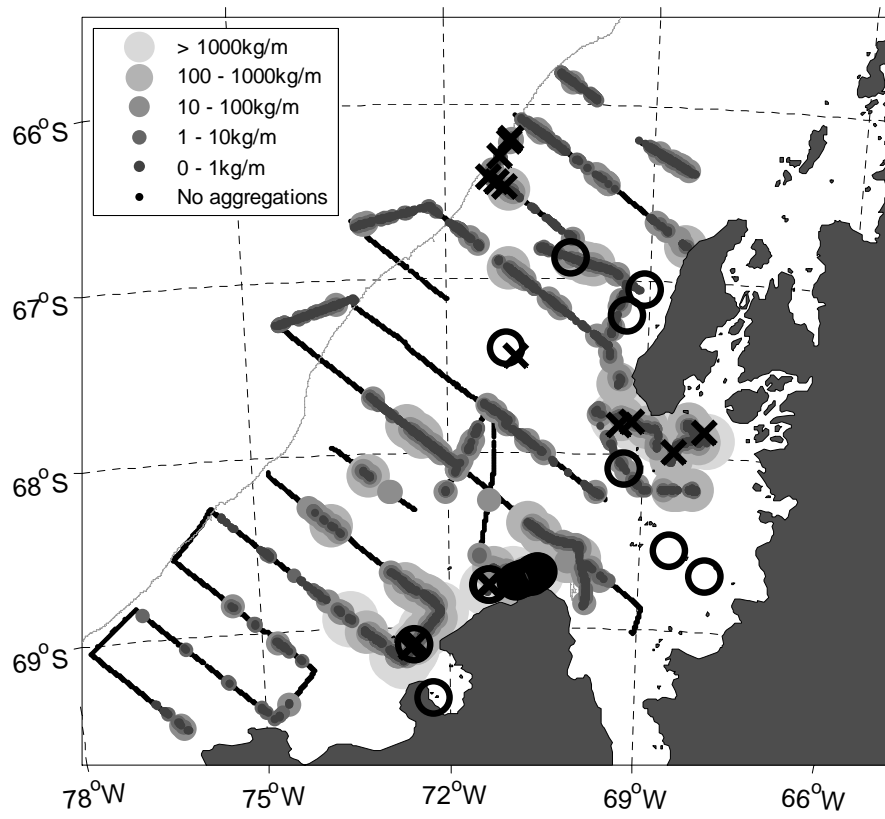


Figure 1.

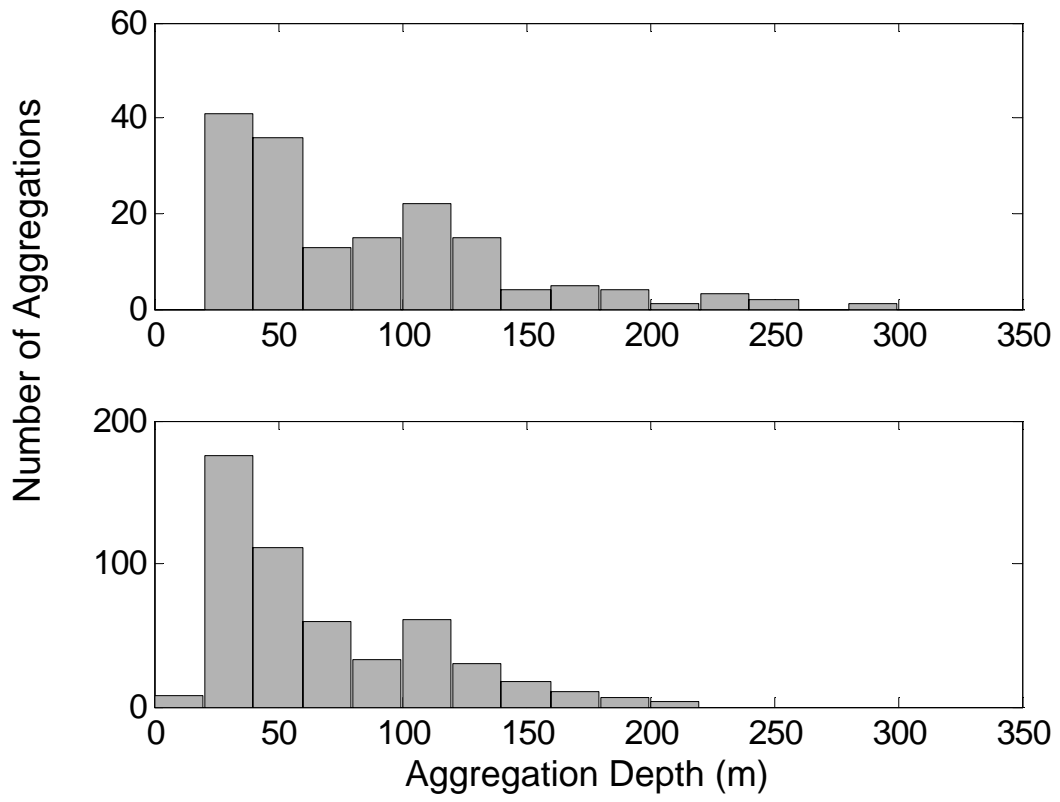


Figure 2.

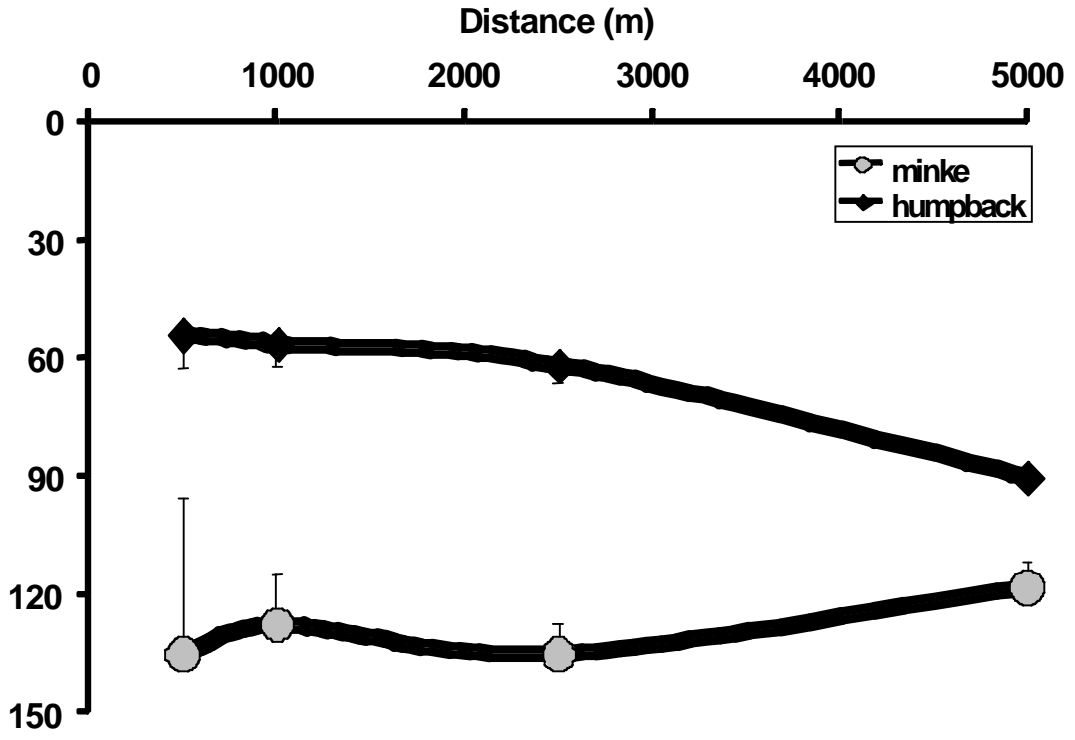


Figure 3.

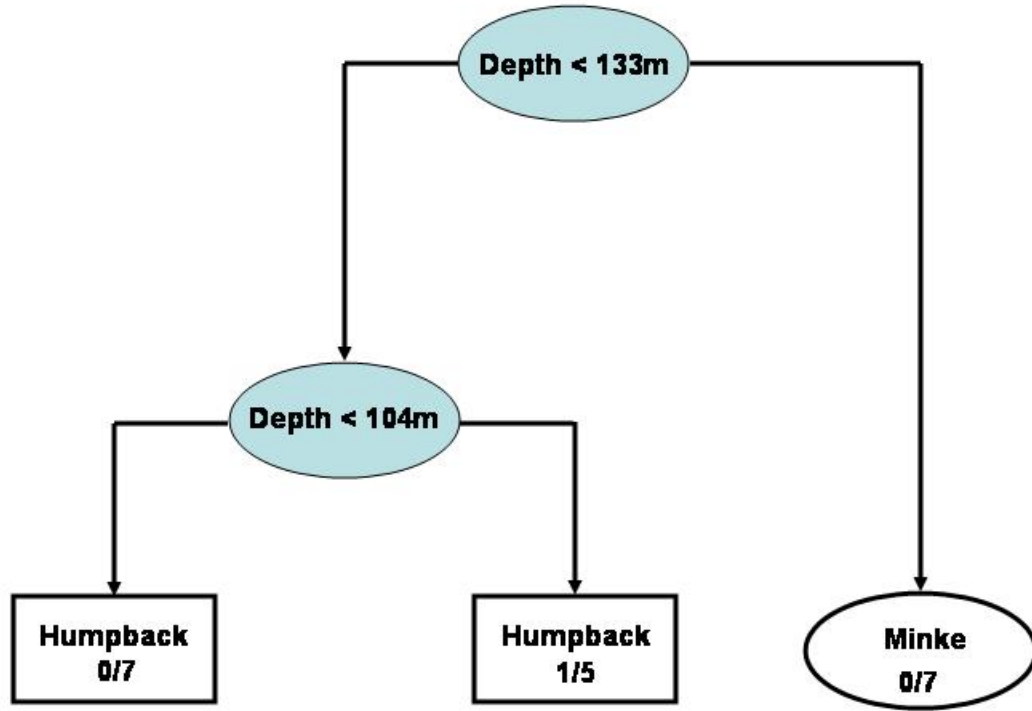


Figure 4.