

**EVIDENCE OF RESOURCE PARTITIONING AND NICHE SEPARATION  
BETWEEN HUMPBACK AND MINKE WHALES IN ANTARCTICA:  
IMPLICATIONS FOR INTERSPECIFIC COMPETITION**

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**ABSTRACT** Closely related sympatric species must differ in their ecological requirements or niches (*e.g.* diets) to avoid inter-specific competition. Body size and energetic models suggest smaller whales should target shallower, smaller, denser, prey aggregations than larger whales. The large sympatric pre-whaling Antarctic cetacean community suggests resource partitioning or non-limiting resources. We use Mantel's tests to elucidate physical and biological environmental variables affecting minke and humpback whale distribution patterns. We find distribution of both species most related to prey distribution, and species-specific differences in physical features which may aggregate prey or help determine ice free areas during winter. CART models including concurrent measurements of acoustically inferred prey aggregations show smaller minke whales consistently associating with significantly deeper krill aggregations across a range of spatial scales. Furthermore, we find evidence of minke whales targeting patches with larger individual krill and smaller aggregation area than humpback whales. These results indicate possible resource partitioning and niche separation mediated by food preferences and the biomechanics of body size, suggesting inter-specific competition is unlikely. Given accelerating rates of climate change around the Antarctic Peninsula, and the ecological importance of baleen whales still recovering from exploitation, our results can benefit organizations managing and conserving Antarctic cetaceans and ecosystems.

## INTRODUCTION

*'When animals with similar requirements, such as 2 or more closely related species, are found coexisting in the same area, careful analysis usually indicates that they are not actually competing with each other (Lack 1954, MacArthur 1958)'*

*-Connell 1961*

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). In a review of the potential for inter-specific competition amongst baleen whales, Clapham and Brownell (1996) discussed the criteria which must be met in order to demonstrate that such competition exists. The species in question must be shown to 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 in similar physical levels (*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 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 baleen whale species due in part to probable resource partitioning mediated by food preferences and the biomechanics of body size. While direct evidence has yet to be documented for baleen whales, there are indications from other marine systems and populations that provide a framework for understanding some of the qualifications or requirements for inter-specific competition.

Baleen whales have evolved unique life histories to take advantage of abundant, predictable, and seasonally persistent food resources: undergoing extensive seasonal migrations from tropical/temperate breeding/calving grounds in winter to higher latitude more productive foraging grounds in summer months (Brown and Lockyer 1984, De la Mare 1997). While on breeding grounds, whales typically do not eat, and only occasionally do during migration trips. Thus, their time on foraging grounds is single-mindedly spent in maximizing energy intake and storage. Because of the extraordinary energetic demands of such long migrations, coupled with the added burden of long gestation and lactation for females, these whales must consume an enormous amount of food and build up lipid stores to last more than half of the year.

The Southern Ocean around Antarctica is a biologically productive and rich area supporting persistent and large standing stocks of Antarctic krill (*Euphausia superba*), and large populations of top predators which depend on krill as a food resource (Laws 1977). Euphausiids form the primary link between primary producers and higher predators in the Antarctic marine ecosystem. With little exception, baleen whales in the Antarctic (blue, fin, sei, humpback, and minke) forage almost exclusively on Antarctic krill (Mackintosh 1965, Gaskin 1982, Kawamura 1994).

Prior to extensive commercial whaling harvest, large populations of several species of baleen whales coexisted around Antarctica. Clapham and Brownell (1996) noted that the existence of such a large, pre-exploitation sympatric whale community is strong evidence of either resource partitioning or a lack of resource limitation. It has been suggested, but unsubstantiated, that baleen whales in the Southern Ocean are not resource-limited, that their principle prey (Antarctic krill) was considered to exist in surplus numbers (Kawamura 1978). The lack of data on (1) the fine-scale distribution of whales, (2) the distribution of their prey, and (3) measures of food consumption have all compromised the ability to fully and reliably elucidate inter-specific relationships in the Antarctic whale community.

At the broad scale, Kasamatsu et al. (2000) found significant, positive spatial correlations between minke and blue whale densities, but no relationship between minke and humpback whales. These authors noted that whale distribution could depend on that of their prey, but did not include any measure of prey in their analyses. Furthermore, they suggest the possibility of interference competition between minke and humpback whales as a causal factor for the lack of a relationship between their distributions (Kasamatsu et al. (2000). Humpback (*Megaptera novaeangliae*) and minke (*Balaenoptera acutorostrata*) whales are the most abundant baleen whales inhabiting the near-shore waters of the Western Antarctic Peninsula (Thiele et al. 2004; Friedlaender et al. in press). Recently, Friedlaender et al. (in press) used concurrent measurements of both whale observations and an index of prey abundance to explore the meso-scale distribution of humpback and minke whales combined in the inner shelf waters of the Western Antarctic Peninsula. They found whale distributions most strongly linked to prey distribution and abundance as well as certain physical and bathymetric features (e.g. marginal ice edge, increased bathymetric slope) which may help to aggregate krill. Likewise, Thiele et al. (2004) found both minke and humpback whales to be associated with the sea ice boundary in the same geographic area.

Physiological constraints influence the diet of a species and ultimately shape most aspects of their ecology and behavior (Tershey 1992). Body size is one of the most

important features determining energetic requirements (Schmidt-Neilson 1984). Jarman (1974) found a general relationship between body size and feeding style of antelopes; smaller individuals selected higher quality food aggregations to satisfy their higher metabolic rates. If larger species have an advantage over smaller species in competing for food, it may be to the advantage of the smaller species to choose patches too scarce or small to be depended upon by the larger species (Jarman 1974).

One or more predators coexisting in an environment with fluctuating or patchy resources often forage on different densities of shared prey (Holling 1959, Abrams 1983). Considering food to be the most important resource regulating seabird populations, Piatt (1990) found that murres and puffins forage on fish schools of differing densities. If each species exhibits a different non-linear response to resource density, coexistence of two or more competitors limited by one resource is possible because of the minimal overlap in targeted prey levels. Furthermore, differing thresholds to prey density may be attributable to differences in body size (Piatt 1990).

Tershey (1992) found that baleen whales in the eastern North Pacific Ocean conform to ecological predictions of resource partitioning based on body size. Minke whales were less transient and fed on smaller patches of energetically high-quality fish, while larger blue and fin whales were more transient and fed on large patches of euphausiids. Additionally, Mori (2002) developed an optimal foraging diving model to demonstrate the effect of body size on diving behavior, and found that smaller diving animals would be more successful when prey patches were located in shallow water and the animals could choose dive depths to exploit them. Likewise, as optimal dive depth generally increased with body size, larger animals should be diving deeper to find prey.

Humpback and minke whales differ substantially in their body size and energetic requirements. Humpback whales average 15 meters in length when mature, and reach weights of 30-40 metric tons, while minke whales average 9-10 meters in length and around 10 tons (Leatherwood and Reeves 1993). This difference in body size leads to differences in both energetic demands and predicted diving ability. Air breathing mammals must balance the trade-offs of diving to depth for foraging and the need to breath air at the surface. The relationships described above suggest that larger bodied animals have a greater capacity to dive deeper and for more prolonged periods. Associated with this is an increased energetic demand for locomotion. If indeed prey are limiting (or have been) in the Antarctic, and there is a physiological constraint to diving and acquiring food, I would expect minke more so than humpback whales to be subject to such limitations. As these whale species evolved sympatric distributions and similar diets, it is not beyond reason to question how they coexist.

For other marine mammals, niche separation and geographic segregation have been suggested in several studies. Based on the known diets of several beaked whale species MacLeod et al. (2003) found those that were similar in their spatial distribution foraged on different sizes and types of prey, while species whose diets overlapped more considerably were found in different geographic areas. In the Gulf of Maine, both fin and humpback whales forage on sand lance and it has been suggested that fin whales may target patches of different size and depth than do humpbacks (Mayo et al. 1988). Ringed seals and harp seals in the Barents Sea feed on similar prey items and have nearly identical niches. However, harp seals prey on significantly larger cod which are

distributed in deeper water than small cod, and thus it appears that these seal species exploit different fractions of the same resource (Wathne et al. 2000).

Given the framework set forth by Clapham and Brownell (1996) and the known concurrence between humpback and minke whales, the goal of this paper is to better understand if sympatric humpback and minke whales partition resources in the inner shelf waters of the Western Antarctic Peninsula, and how they may minimize the potential for inter-specific competition. It has been suggested, but unsubstantiated, that prey in the Southern Ocean is non-limiting (Kawamura 1978). If this were the case, sympatric species may not show any signs of partitioning resources. Likewise, there have not been any data to suggest inter-specific competition between whale species. We will explicitly test how both minke and humpback whales are distributed in relation to physical features and the distribution of their prey throughout the water column to look for species-specific differences. More specifically, We will test the hypothesis that minke and humpback whales are distributed in such a way as to partition the available prey to minimize the potential for inter-specific competition. As both species target the same prey item, differences in the quality of a food source will be viewed in terms of patch density and extent and the size of constituent animals. We expect the more diminutive minke whales to be limited more in their dive times and depths, and therefore forage on patches higher in the water column. Likewise, their size relative to humpback whales would suggest energetic demands which would be met by foraging more efficiently on more profitable aggregations.

We thus expect smaller minke whales to be distributed in relation to smaller, denser, and shallower krill aggregations than larger humpback whales. Alternatively, if resources are non-limiting (or were not when these whales evolved means for partitioning resources), we would expect to find no partitioning, and only find differences in patch selection which would maximize the energetic demands of both species.

## MATERIALS AND METHODS

**Data collection.** Data were collected as part of the Southern Ocean GLOBEC program in and around the continental shelf waters of Marguerite Bay on the western side of the Antarctic Peninsula (Figure 1), between April- June 2001 and 2002. Environmental and whale sighting data were collected from the A.R.S.V *Laurence M. Gould* (LMG) and the R.V.I.B. *Nathaniel B. Palmer* (NBP). Multi-disciplinary oceanographic sampling from the NBP was conducted along pre-determined cross-shelf transect lines spaced 40km apart and oriented perpendicular to the coast to cover the extent of the study area.

**Cetacean surveys.** Whale sighting effort was conducted in fall of 2001 as part of the Southern Ocean GLOBal Ecosystem Dynamics (SO GLOBEC) research program in and around the continental shelf waters of Marguerite Bay on the western side of the Antarctic Peninsula. Line transect surveys were conducted from the A.R.S.V. *Laurence M. Gould* (LMG) and the R.V.I.B. *Nathaniel B. Palmer* (NBP) concurrent to multi-disciplinary oceanographic sampling. Whale sighting surveys were conducted on the NBP and LMG from 4 April – 1 June 2001 (Figure 1). As described in Friedlaender et al. (in press): trained observers worked from each vessel while underway along the survey grid, between process stations and other sites, or otherwise in transit. Each observer

searched in a 90° sweep from the bow of the ship to the perpendicular beam using naked eye or 7x50 Fujinon binoculars. In addition, 20x50 image-stabilized Zeiss binoculars were used to aid in species identification. Data were recorded on a laptop computer using a Windows-based sighting program (WinCruz Antarctic) that continuously logged the ship's position, course, and speed. Observers recorded environmental and sighting conditions (weather, visibility, glare, swell height, Beaufort sea state, and sea ice concentrations) and tracked changes as they occurred. Cetacean sightings were logged with a time and position stamp, distance and bearing from the ship, species identification, group size (high, low, and best estimate), presence of sea ice, behavior, sighting cue, and other comments. As noted in Thiele et al. (2004), most whales in the Antarctic are medium to large species, and thus can be detected in relatively high Beaufort sea states. Survey effort was abandoned when conditions were determined by the observer to have deteriorated enough (> sea state 5) to preclude the detection of most species: *e.g.* strong winds, fog or reduced visibility, large swell, etc.

**Environmental data.** Hydrographic data were collected from the NBP at predetermined sampling stations designed to cover the continental shelf and inshore regions surrounding Marguerite Bay. We use the same environmental variables as described in Friedlaender et al. (in press) (Table 1).

Hydrographic sampling stations were designed to provide coverage of the continental shelf to the north and south of Marguerite Bay (Klinck et al. 2004). In 2001, 81 stations were sampled, with each station 10 to 40 km apart (See Friedlaender et al. in press, Figure 1). Hydrographic measurements were made using a SeaBird 911+ Niskin/Rosette conductivity-temperature-depth (CTD) sensor system. Water samples were taken at a range of depths throughout the water column (See Klinck et al. 2004 for a detailed description). Surface water samples from all stations were used to determine chlorophyll-a concentrations ( $\text{g/m}^3$ ). Deep temperature maxima below 200 m were used to define and categorize water masses, specifically warmer waters relating to intrusions of circumpolar deep water (Chapman et al. 2004). Bottom depth for transects and sightings was calculated from the modified ETOPO8.2 15-second bathymetry grid (Bolmer et al. 2004).

We use ice edge information reported in Chapman et al. (2004) in this study. The marginal sea ice edge in and around Marguerite Bay was determined for each cruise as the transition zone where sea ice covered more than 15% of the ocean surface (Zwally et al. 1983). Observers recorded ice conditions initially and whenever they changed, allowing the ice edge to be reconstructed from visual effort. In the event that ice information was lacking from direct visual observation, weekly sea-ice concentration satellite imagery was used (National/Naval Ice Center, Washington DC, 2002: <http://www.natice.noaa.gov><http://www.natice.noaa.gov>).

All of the environmental variables were imported into ArcGIS 9.1 and point samples were interpolated using an inverse distance weighted function to create continuous surfaces (rasters) to sample from. 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, distance to the ice edge, and distance to the coast.

**Prey Data.** Estimates of the abundance of prey and measurements of krill aggregations were derived from acoustic survey data collected from the *NBP* concurrent to cetacean surveys, using the BIOMAPER-II towed body (BIO-Optical Multi-frequency Acoustical and Physical Environmental Recorder; Wiebe et al. 2002) . This instrument was towed behind the vessel between 20 and 300 m depth at a survey speed of 4-6 knots. Measurements of volume backscattering strength were recorded from pairs of up- and down-looking transducers at frequencies of 43, 120, 200, and 420 kHz, to maximum ranges of 300, 300, 150, and 100 m, respectively. The spatial resolution of the data was ca. 35 m along-track and 1.5 or 1 m vertically (for the 43/120 or 200/420 kHz systems, respectively). Full details concerning acoustic data collection are found in Lawson et al. (2004).

The abundance and distribution of prey was assessed in two ways. First, backscattering at 120 kHz was used as an index of overall zooplankton and micronekton biomass (following the approach of Lawson et al. 2004 and used in Friedlaender et al. in press). Average backscattering in 25-100 and 25-300 m depth intervals was calculated over 5 km along-track intervals centered at the location of each whale sighting.

Second, measurements were extracted from the overall acoustic record of the characteristics of individual krill aggregations in the vicinity of sighted whales. In order to discriminate backscattering arising from krill from that due to other zooplankton or micronekton, the acoustic data at 120 kHz were first subjected to a threshold backscattering level of -70 dB, derived on the basis of krill visual acuity. 'Patches' were defined as vertically or horizontally contiguous groups of super-threshold backscattering measurements. I use the word 'patch' simply to denote a non-random group of animals observed in the acoustic data, and do not intend it to imply anything about the degree of cohesion or organization of animals within the aggregation.

Aggregations attributable to krill were then identified on the basis of expected differences in mean backscattering between 43 and 120 kHz (Watkins and Brierley 2002, Demer 2004). Unfortunately, sensitivity and noise problems at 43 kHz during the 2001 survey led to numerous cases where this backscattering-difference method could not be applied. In such instances, krill aggregations were identified on the basis of the threshold backscattering criterion alone. Certain aggregations more likely composed of other animals, such as myctophid fishes, were also excluded on the basis of visual scrutiny. Comparisons to survey results from the following year (2002) when the 43 kHz system functioned properly suggest that this approach did not result in a substantially different description of krill aggregations, aside from there being more small and low-biomass aggregations extracted in 2001 that were the minimal detectable size set by the resolution of the system. In the absence of reliable 43 kHz data, it is difficult to assess whether such small aggregations are comprised of krill or some smaller and more weakly scattering zooplankton such as copepods. To account for the possibility of scatterers other than krill confounding our investigations of whale-krill relationships, We therefore performed all analyses on two datasets: the first with these small aggregations retained, and the second with them excised. Henceforth, these will be referred to as the 'unfiltered' and 'filtered' krill patch data, respectively.

Inversions of the multi-frequency acoustic data were performed to estimate the mean length and numerical density of krill in each acoustically-identified aggregation, in a manner similar to methods applied previously to euphausiid aggregations elsewhere

(e.g. Greenlaw 1979, Warren et al. 2003). By assuming that each aggregation was composed solely of krill of unimodal length distribution (Watkins et al. 1986, Miller and Hampton 1989), and that total backscattering in each patch was linearly related to the abundance of constituent animals (i.e., the echoes sum incoherently), theoretical predictions of backscattering expected at each of the four BIOMAPER-II frequencies were calculated using the target strength model of Lawson et al. (2006) and varying combinations of krill mean length and abundance. Observed mean backscattering in relation to frequency for each patch was then compared to these predictions, and krill length and density estimated on the basis of the best fit minimizing an error term defined as the sum of the squared differences between observed and predicted backscattering (each in log form) at each frequency. This inverse method was only applied to aggregations meeting both the threshold backscattering and backscattering-difference criteria, and was verified for certain instances where net and Video Plankton Recorder data provided confirmation that the acoustically-observed aggregations were indeed composed of krill, as well as independent estimates of animal length and abundance (Lawson, unpublished results).

Other measurements of patch features included the depth of the centroid of each aggregation, as well as total patch cross-sectional area (in depth and along-track distance). The mean volumetric density of biomass ( $\text{kg/m}^3$ ) was estimated on the basis of mean backscattering at 120 kHz and a target strength per kilogram of krill biomass derived from the target strength model of Lawson et al. (2006), the wet weight to length relationship of Wiebe et al. (2004), and the mean individual length estimated by the multi-frequency inversion. Due primarily to the range limitation of the 420 kHz system, krill length was estimated for only 496 of the 8371 aggregations observed. For aggregations where animal length was not estimated from the inverse method, the length used in biomass estimation was taken either as the length in the nearest neighboring patch (within 50 m vertically and 10 km horizontally) or as the median length for all aggregations observed during the survey. Each backscattering measurement in the patch was similarly converted to biomass, multiplied by the cross-sectional area (depth vs. along-track distance) represented by that measurement, and then summed to yield an estimate of total patch biomass. Total biomass is left here in units of kilograms per across-track meter, since the across-track extent of each patch is not measured by the acoustic system.

**Whale Species-Environment Relationships.** We first used Mantel's tests to explore which environmental features contribute 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. This test allows for a determination of which measured environmental variables best explain species distributions once their confounding mutual correlations and spatial structure are accounted for. Mantel's test essentially indicates whether samples that are similar in terms of the predictor (environmental) variable are also similar in terms of the dependent (whale presence) variable, and whether samples that are close together geographically have similar values for other variables (Schick and Urban 2000). For the purposes of this study, I was interested in determining whether there were differences in the distribution patterns of humpback and minke whales which could be explained by the



measured environmental variables. Friedlaender (Chapter 1) found a significant and persistent relationship between baleen whales and prey at various depths in the water column, but did not separate these relationships for individual species. We used the same suite of environmental variables as those used by Friedlaender et al. (in press) to test for species-specific differences in relation to physical and biological measures. Interpolated continuous surface grids of each variable were generated in ArcGIS 9.1, and samples of each environmental variable were taken at all locations where whale observations were made, and then randomly at an equal number of locations along our sighting transects where no whales were observed. Data were then analyzed using statistical methods contained in the 'ecodist' library in S-PLUS (SAS). Correlations were first run to look for general relationships between whales and environmental variables. Next, each individual variable was assessed for spatial autocorrelation: whether inherent spatial structure exists within the sample points, such that points that are close spatially are also close in their given variable's value. Partial Mantel's tests were then run to indicate which environmental variables have explanatory power with respect to the observed whale distribution patterns, once their spatial autocorrelation had been accounted for. Lastly, 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.

**Species-specific patch selection and resource partitioning.** In order to gain insight into how humpback and minke whales partition resources, we tested for differences in several characteristics of krill aggregations at or near locations where whales were sighted. We plotted all of the along-track krill aggregations detected by the aforementioned method, and overlaid whale sightings (Figure 1). We then sampled all of the krill aggregations found within 5000 m of each sighting as this distance relates to the greatest distance that whales were positively identified to the species level. Because of large variances in several of the krill patch metrics, we chose to use median values for cross-species comparisons.

Resources in the marine environment are dispersed with a vertical dimension. Given sympatric species with overlapping distributions, we presumed that whales might fundamentally partition resources through vertical separation of the water column. Therefore, we compared the median depth of krill aggregations found at sighting locations of humpback and minke whales, for all aggregations found within 5, 2.5, 1, and 0.5 km of each whale sighting.

In order to determine how other characteristics of krill aggregations influence species-specific distributions, we ran classification tree models in S-PLUS (SAS). We used tree-based classification models (Breiman et al. 1984) as an exploratory technique to elucidate the responses of predictor variables to our categorical whale species variables. Tree-based hierarchical models, such as CART (Classification and Regression Tree analysis), are based on binary recursive partitioning methods which aim to resolve relationships to response variables by recursively partitioning data into increasingly homogeneous sub-groups (Breiman et al. 1984). CART models can handle a broad range of response types, are invariant to monotonic transformations of the explanatory variables, are easy to construct and interpret, can interpret missing values in both

response and explanatory variables, and are able to capture interaction effects among predictor variables (De'Ath and Fabricius 2000). CART models are also an attractive analytical tool because, unlike linear models, they do not assume an *a priori* relationship between the response variable and predictor variables; rather the data are divided into several groups where each has a different predicted value of the response variable (Guisan and Zimmermann 2000, Redfern et al. 2006). Although CART has been used in marine ecological studies primarily for developing predictive models, as with most non-parametric statistical tools, CART is more suitable as an exploratory data analysis tool (Redfern et al. 2006).

We ran classification trees using whale species as the dependent variable, and medians for each whale sighting of the krill patch metrics mentioned above as response variables. We chose to have a minimum of 5 observations before splits, and had 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 (S-PLUS). We then ran cross-validation tests to determine whether the number of nodes generated by the model did indeed maximize 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. We ran two iterations of the CART models: 1) using the unfiltered krill patch dataset including all of the patch metrics and then using a subset without krill size and patch density; and 2) using the filtered data with the very small patches removed, including all of the patch metrics and then using a subset without krill size and patch density.

## RESULTS

**Species-specific Distribution Patterns: Mantel's Tests.** Significant spatial relationships were found between humpback and minke whales and several of the environmental variables considered. The Mantel's tests run on the distribution patterns of humpback (Table 2) and minke (Table 3) whales indicate simple correlations, autocorrelations, partial and pure partial relationships between each whale species and measured environmental variables. For humpback whales, there are significant simple, positive correlations with bathymetric slope and the index of the total amount of zooplankton in the water column between 25-300 m. There are also negative correlations with distance to the inner shelf water boundary and the distance to the coast. Nearly all of the environmental variables were found to be spatially autocorrelated, an expected result. When accounting for the spatial autocorrelation of each environmental variable, bathymetric slope ( $p < 0.025$ ) and zooplankton abundance between 25-300 m ( $p < 0.001$ ) remain significant contributors to the observed humpback whale distribution. After accounting for spatial autocorrelation, as well as the mutual confounding relationships to all other environmental variables, three features have a pure partial effect on the distribution of humpback whales: bathymetric slope ( $p < 0.038$ ) and distance to the coast ( $p < 0.017$ ) are similarly significant, while zooplankton abundance from 25-300 m ( $p < 0.001$ ) has an order of magnitude more explanatory power.

For minke whales, simple positive correlations exist with zooplankton in the upper 75 m of the water column, and negative correlations exist with the deep temperature maximum, bathymetric slope, distance to the marginal ice edge, and distance to the coast. The spatial autocorrelation of each environmental variable follows the same patterns as described above for humpback whales. Having accounted for spatial autocorrelation, the deep temperature maximum ( $p < 0.001$ ), distance to the marginal ice edge ( $p < 0.006$ ), and zooplankton abundance in the upper 75 m ( $p < 0.002$ ) remain significant positive predictor variables. And when accounting for both spatial autocorrelation and the mutual confounding relationships to all other environmental variables, both the deep temperature maximum ( $p < 0.001$ ) and zooplankton abundance in the upper 75 m ( $p < 0.001$ ) have positive pure partial effects on the distribution of minke whales. The results from the two species tables can be seen in the alternative representation path diagrams (Figures 2A and 2B).

**Inter-Specific Patch Selection.** A total of 949 (588 associated with humpback whales and 361 with minke whales) krill aggregations were sampled within 5000 m of whale sightings. A total of 32 groups of 61 humpback and 22 groups of 35 minke whales were sighted during visual survey effort. Median values and standard errors of krill patches associated with both minke and humpback whale sightings are shown in Table 4. Values are presented for both iterations of the filtering of acoustics data: with and without the smallest aggregations included.

**Depth of Krill Patches.** The median depth of krill aggregations was significantly greater for those associated with minke whales than for those associated with humpback whales ( $p = 0.001$ , Kruskal-Wallis rank sum test) at all spatial sampling ranges (500, 1000, 2500, and 5000 m; Figure 3). The absolute difference in median depth between the two species was 37 m (132 vs. 95 m) at the greatest spatial extent, and continued to increase with proximity to the whale sightings up to a difference of 99 m (163 vs. 65 m) at the 500 m sampling area (Table 5).

**Classification Trees.** Classification Trees were run to test for interspecific differences in patch characteristics between humpback and minke whales. The first tree generated using the unfiltered krill dataset contained 2 splits and 3 terminal nodes (Figure 4), confirmed by cross-validation tests as an appropriate number to minimize the overall deviance of the model. The residual mean deviance for the model was 0.047, and had a misclassification rate of 0.05 (1/20). Thus, in attempting to create homogeneous subgroups, one of the samples was incorrectly classified to a group containing only the other whale species. The primary split in the tree occurred at a median krill patch depth of 139 m. Only minke whales were found to associate with aggregations with a median depth  $> 139$  m. The second split occurred at a median krill length of 38.5 mm. Humpback whales were found to associate unambiguously with aggregations in  $< 139$  m depth and krill  $< 38.5$  mm. Minke whales (with one misclassified humpback whale) were found to associate with krill aggregations found  $> 139$  m and having krill  $> 38.5$  mm.

Since length estimates were only available for a subset of all sampled krill aggregations, we ran a second tree without these (as well as density which is a function of krill length estimates) to search for other potential contributing response variables. The

resulting tree had 3 splits and 4 terminal nodes (Figure 5). Cross-validation tests confirmed that deviance was minimized most with the selected model. The model selected depth of center of patch and patch area for inclusion in the final tree. The overall model had a residual mean deviance of 0.1323 (2.514/19), and a misclassification error rate of 0.17 (4/23). The primary split in the tree occurred at median patch depth of center 139.125 m. Only minke whales were found to associate with aggregations where median depth was >139 m, with no misclassifications. The second split in the tree came at a median patch area 61 m<sup>2</sup>. Below this area, minke whales were the predominant species. The third split came at patch depth of center 82.75 m. All of the whales which were associated with aggregations in median shallower than 82.75 m were humpbacks. Therefore, minke whales were classified with aggregations deeper than 139 m, or aggregations shallower than 139 m but less than 61 m<sup>2</sup> in area. Humpback whales were classified with aggregations less than 139 m deep (and more strongly with aggregations <82.75 m) and greater than 61 m<sup>2</sup> in area.

The second iteration of tree models using the filtered krill patch dataset indicates similar relationships as the previous trees in several ways. Using all the available patch metrics including krill length, the primary split is once again depth related: only minke whales are associated with patches of median depth >127 m (Figure 6). The second and only other split, however, occurs associated with patch density. Humpback whales were found to associate with more dense patches (median >7.6 g/m<sup>3</sup>) than minke whales. Overall, this tree had a misclassification rate of 0.11 (2/19), and a residual mean deviance of 0.42 (6.73/16). Removing estimates of krill lengths and patch density, the resulting tree maintains the primary split at a median depth of 127 m, with only minke whales found associating with patches greater than this depth (Figure 7). The only other split is related to median patch area at 646 m<sup>2</sup>. As most of the minke whales were associated with deeper patches, humpback whales dominate the association with patch area and the misclassification rate at this split is high. While the misclassification rate is similar to other trees (0.16), the residual mean deviance is greater (0.78), thus having less explanatory power.

## DISCUSSION

The distribution of baleen whales in the inner shelf waters of the Western Antarctic Peninsula in autumn is strongly associated with the distribution of their prey, and certain environmental features which may aid in prey retention (Friedlaender et al. in press). Similar to the approach of Kasamatsu et al. (2000), we use this knowledge of the concurrence in meso-scale distribution of both humpback and minke whales as motivation for examining how these species may partition resources and minimize the potential for inter-specific competition. At the species level, we find that humpback whale distribution is most related to an index of the total amount of zooplankton (including krill as well as other zooplankton and micronekton) in the upper 300 m of the water column, and secondarily to areas close to shore with highly variable bathymetric relief. Minke whales are found to be distributed in relation to the total amount of zooplankton in the upper 75 m of the water column and to a lesser degree by the deep water temperature maximum.

The former result is somewhat difficult to interpret, particularly in light of the findings from the classification trees where minke whales associate with krill aggregations deeper than humpback whales. It is important to note that this backscattering index confounds the presence of the whale's krill prey with that of other zooplankton and micronekton; this was the impetus behind separating the krill aggregations for more detailed analyses. Given that the depth range of backscattering associated with the humpbacks (25-300m) overlaps with that of the minkes (25-75m), it is also probably not appropriate to assign too much importance to this apparent difference in the depth intervals targeted by the two species. Perhaps the more important result is that regardless of these concerns, both whale species are highly correlated in a horizontal sense to areas of increased prey abundance.

The inter-specific differences in association with environmental variables may be explained by differences in residency patterns in the Antarctic. Humpback whales are seasonal residents using their time in Antarctic waters primarily to forage. Thus, they should distribute around prey and features which may aid in prey aggregation. Minke whales, conversely, are year-round residents and have differing environmental needs as sea ice begins to form in autumn and into winter. Access to open water and air is the most fundamental commodity which minke whales must have to survive through winter. The positive correlation between minke whales and the deep temperature maximum supports the idea of minke whales distributing in areas with a higher likelihood of remaining ice free during winter. Warmer waters in Marguerite Bay in autumn represent intrusions of circumpolar deep water from the Antarctic Circumpolar Current on to the continental shelf (Klinck et al. 2004). As the heat from this water may eventually be drawn towards the surface, its presence may coincide with polynyas, areas of open water which remain ice free throughout the winter. 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). And if polynyas also offer access to prey, minke whales can forage continuously, and are thus may be released from the pressure to store energy for a long fasting period of migration like humpback whales.

For resource-limited species with overlapping distributions and similar prey items, the most fundamental way to avoid competition is to partition resources (Schoener 1983). In the marine environment, this can be done in either a horizontal or vertical plane. When we look at discrete aggregations of krill, all of our various analyses suggest that humpback and minke whales partition resources vertically in the water column, giving us great confidence in this finding. At a range of spatial scales we find that the median krill patch depths are statistically different between locations of minke and humpback whales. At close range (500 m), the species target prey aggregations separated vertically by nearly 100 m. Separation was accentuated with increasing proximity to the whale but was also maintained to the full spatial extent of our analysis (5000 m), reaching a minimum difference in depth of around 30 m. This suggests that whales perceive their prey environment more accurately at closer ranges. This persistent relationship lends insight into the environment around which the whales distribute themselves and are able to perceive their prey. As mobile predators, baleen whales are able to place themselves in areas with high prey abundance, and move between energetically profitable areas. While these two species overlap in their horizontal distribution they may avoid inter-specific competition by targeting aggregations in different vertical portions of the water column.

Our prediction based on body size was that smaller minke whales will target shallower aggregations than humpback whales. Contrary to this prediction, we find that the smaller minke whales are often targeting krill aggregations at depths well below larger humpback whales. The primary node of our first classification tree analysis shows minke whales unambiguously associated with krill aggregations having a median depth >139 m (Figure 4). Using a comprehensive set of krill patch variables, we also find that minke whales associated with shallower aggregations are also associated with smaller (<62 m<sup>2</sup>) median krill patch area than humpback whales, supporting our predictions. Furthermore, humpback whales were then found to associate with krill aggregations at depths <82.75 m, increasing the vertical partitioning of resources between the two whale species.

When we added in estimates of individual krill size into our analyses, the primary node in the classification tree remained the vertical component of 139 m (Figure 5). However, the next and only other split in the tree was at krill length of 38.5 mm. There were no minke whales classified as being associated with aggregations containing krill <38.5 mm, only humpback whales were associated with krill of this length. In summary, some minke whales target deeper krill aggregations than humpback whales, and those minkes that do not, appear to target larger krill and smaller aggregations than humpbacks.

It is important to acknowledge certain limitations of the acoustic analysis of krill aggregations that may introduce some uncertainty into the patterns identified here. First, the acoustic methodologies are unable to distinguish among the various euphausiid species that may be present in the region. In particular, *Euphausia crystallorophias* was occasionally sampled with nets in this study area and time period (Kendra Daly *pers comm.*). Some of our acoustically-identified aggregations may thus be composed of this euphausiid species, confounding our understanding of the distribution of *Euphausia superba*, the main prey item for the whales under study here. Second, although the measurements of patch area and depth are quite robust to any error introduced via the acoustic analyses, the estimates of krill length involve more uncertainty. Despite any such uncertainty however, they should still provide relative information on the true length of animals in the aggregations, and it is such relative trends (e.g., certain aggregations having larger or smaller animals) that are capitalized upon by the CART analysis. Finally, 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. Such uncertainty particularly applies to the smallest aggregations extracted, where 43 kHz data were often unavailable. Filtering out these small aggregations resulted in a dataset where we can be more confident that all of the aggregations were indeed composed of krill. Although these small aggregations were numerically abundant, each was of very small biomass, and so the filtered dataset still comprises most of the total biomass present in the unfiltered data.

When we run similar models using this krill dataset where the aggregations that may not be composed of krill have been filtered out, the vertical separation between humpback and minke whales remains unambiguous. However, in shallower waters we find humpback whales associating with more dense krill aggregations than minke whales (Figure 6). When combined with other patch metrics krill length did not add to the tree model, but as krill length was exposed in the previous analysis as contributing to the

species-specific patch differences, we analyzed this single parameter and found significant differences between patches associated with minke (median length 40 mm, se. 0.82) and humpbacks (37 mm, se. 3.6). Given the inherent uncertainties surrounding estimates of krill length, these results do offer interesting insights.

These whales appear to be following the predictions of Tershey (1992; studying whales) and Jarman (1974; studying antelopes) based on body size in several ways. The smaller minke whales appear to be targeting smaller krill aggregations than humpbacks. While patch density did not fall out of our analysis of the unfiltered data as being a factor correlated with whale distribution, krill length did. Krill biomass increases with length. While biomass is not necessarily linearly related to total energy because of potential variability in lipid content, total lipid content in Antarctic krill sampled in this study region ranged from 15-30% of dry weight and does increase positively with age class and length (Ju and Harvey 2004). Additionally, as krill size increases, their surface area to volume ratio decreases, meaning that the relative amount of biomass made up of exoskeleton (i.e. un-digestible nutrients) should decrease with length. Because larger krill are more energetically valuable than smaller krill, minke whales are targeting higher quality aggregations than humpback whales. If smaller krill are found in denser aggregations than larger krill, I would expect this to have been indicated in our analysis. If krill patch density remains relatively constant regardless of average krill length, our results of aggregations with larger krill providing more energetic benefit than those with smaller krill has support. In fact, Table 3 indicates that patch density is higher for those near minke whales than humpback whales, making the energetic differences even greater.

We can also offer a competing hypothesis to address the finding of the second set of CART models that humpback whales might be targeting more dense krill patches in shallower waters, which appears to contradict the notion that the minke target higher quality aggregations. Whales preparing themselves for the coupled energetic demands of migration/fasting and reproduction should maximize their rate of energy storage just prior to leaving the feeding grounds. This would mean taking advantage of denser patches and the most available ones (i.e. closest to the surface to minimize locomotor 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 Western Antarctic Peninsula during this time will eventually migrate north. The same cannot be said for minke whales. There is a large, known population of minke whales which are resident and over-winter in the pack ice around Antarctica, and indeed minke were observed during cetacean surveys of the present study region later in the winter of 2001 (Thiele et al. 2004). If the minke whales which I am sighting are not preparing for a long fasting period/migration, they may not have the impetus to increase their energy stores quite as severely as humpback whales. Thus, minke whales would not necessarily be targeting the densest patches.

Vertical partitioning of resources in the water column with minke whales targeting aggregations at a greater depth than larger humpback whales requires physiological consideration. Using a phylogenetic analysis of diving in birds and mammals, Halsey et al. (2006) demonstrated that dive duration and dive depth scale with body size. Thus the optimal foraging model of Mori (2002) and comparative data from a phylogenetically broad group of diving endotherms suggest that smaller divers should be shallower divers. Similarly, our results counter the notion that larger body size affords a

greater ability to dive deeper and for longer durations since oxygen stores increase and mass-specific metabolic rates decrease with increasing body size (Kooyman 1989, Costa 1991). Yet, the spatial distribution of minke whales is correlated with prey aggregations that are 30-100 m deeper than those associated with the larger humpback whales. If minke whales are targeting these deeper prey aggregations, it represents a reversal of the body size predictions based upon both optimal foraging and physiological considerations.

It is possible that minke whales, as do other marine mammals, decrease the energetic costs of diving to such depths through a reduction in locomotor effort via gliding (Williams et al. 2000). Marine mammals that modify their locomotor patterns and take advantage of buoyancy changes at depth are able to reduce the energetic costs of diving by almost 60% (Williams et al. 2000). Schreer and Kovacs (1997) explain that baleen whales dive to shallower depths and for shorter durations than would be predicted from an allometric consideration of their body size as a consequence of prey being found in relatively shallow waters. However, comparisons of dive depth with the reported depth distribution of prey for blue and fin whales off California do not support this hypothesis (Croll et al. 2001). Rather, it is suggested that the high energetic demands of lunge feeding at depth likely deplete oxygen stores quickly and thus reduce dive duration (Croll et al. 2001, Acevedo-Guitierrez et al. 2002). Minke whales appear to be targeting smaller aggregations with larger krill than humpback whales and it is possible that these aggregations do not require multiple lunge feeding bouts during a single dive for the whale to make the dive profitable. Larger whales may be targeting aggregations with less energy content per unit area, and thus require more foraging bouts to acquire enough prey to outweigh the costs of lunge feeding. Furthermore, the smaller baleen whales typically have coarser baleen and fewer plates than larger whales (Gaskin 1982), suggesting that smaller whales are limited in the minimum size of prey they can handle. Thus, they may be adapted to forage only on prey large enough to meet their energetic demands. A careful study of the differences in baleen morphology would lend significant insights into this concept.

The apparent differences in prey patch selection between humpback and minke whales add to our understanding of baleen whale ecology in the Antarctic. Further investigation to explicitly understand the foraging behavior of these whales is integral to understanding the full breadth of the predator-prey/foraging relationships elucidated in this study. The vertical separation of the water column by minke and humpback whales is supported by multiple analytical tests and seems unambiguous. Other features of krill patches which are revealed in our analyses may be artifacts of the vertical partitioning between whales and the distribution of different life stages of krill in the water column in autumn. Recent technological advances have facilitated the construction of non-invasive, multi-sensor acoustic data logging tags (DTAG) which have been used to monitor the underwater activities of free-ranging whales (Matthews et al. 2001, Nowacek et al. 2001, Johnson and Tyack 2003). Combined with concurrent hydro-acoustic measurements of the distribution and characteristics of prey aggregations, such a study could add greatly to our understanding of how humpback and minke whales forage and interact with their prey.

The Western Antarctic Peninsula is warming at a faster rate than most areas on the planet, winter sea ice extent and duration in this area are shortening (Parkinson 2002), and krill density across large spatial and temporal scales is declining (Atkinson et al.



2004). Krill demography is tied directly to physical forcing, and their recruitment is profoundly influenced by climate variability (e.g. Loeb et al. 1997). Due to their dependence on a single prey item heavily influenced by climate forcing, krill predators (such as penguins, seabirds, seals and whales) are vulnerable to variability in prey and have been shown to alter their demography in response to changes in prey availability (Reid and Croxall 2001, Fraser and Hofmann 2003, Reid et al. 2005). However, virtually nothing is known about the dynamics of predator-prey interactions and the responses of baleen whales to the distribution of their prey in this ecosystem. Given this data gap, and the ecological importance of baleen whales as top predators in the Southern Ocean, focused research studies are of paramount importance.

The results of our study suggest possible resource partitioning and niche separation in autumn between humpback and minke whales in the nearshore waters off the Western Antarctic Peninsula. We have been able to determine inter-specific differences in the spatial distribution of minke and humpback whales in relation to individual prey size, as well as prey patch size, and depth. We concur with Clapham and Brownell (1996) in that resource partitioning exists and inter-specific competition between these sympatric whale species is unlikely. We suggest that there is evidence to support a theory of resource partitioning among humpback and minke whales in the Antarctic, which may have evolved before commercial exploitation, and still exists today. Given the long life spans and generation times of baleen whales, the mechanisms which gave rise to such ecological conditions would likely still be present today.

However, our results do not rule out the possibility that prey is limiting in the present environment. There may be physical limitations or density-dependent population demographics playing a role in the observed patterns as well. While the correlations we have found are indeed 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 alternative hypotheses and mechanistic possibilities aforementioned. We have presented 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 patch distribution can vary substantially between years in a given area (Lawson, unpublished data), 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, but are not robust enough for statistical comparisons. We do find median patch depth to be greater for minke (143 m) than humpback whales (106 m), and patch area greater for humpbacks (180 m<sup>2</sup>) than minkes (94 m<sup>2</sup>) (Table 4).

The results of this study and the indications of inter-specific resource partitioning and niche separation between minke and humpback whales off the Western Antarctic Peninsula will better enable scientists interested in the structure and function of marine ecosystems and predator-prey interactions. This information should also be considered by organizations and communities charged with managing and conserving depleted whale populations and understanding whale ecology (e.g. The International Whaling Commission, and The Commission for the Conservation of Antarctic Marine Living Resources). This work also represents a novel contribution to the paucity of data which exist relating whales and their prey in the Antarctic. A better understanding of species-specific prey preferences and associations is important for models being developed to

quantify the effects of climate change and variability across all trophic levels of the  
Antarctic marine ecosystem.

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

<b>Environmental Variable</b>	<b>Units</b>	<b>Sampling method</b>
Acoustic volume backscatter 25-100m (X25-75m)	decibels (relative to 1m <sup>2</sup> )	Continuous along track and interpolated fields
Acoustic volume backscatter 25-300m (X25-300m)	decibels (relative to 1m <sup>2</sup> )	Continuous along track and interpolated fields
Chlorophyll a (Chla)	g/m <sup>3</sup>	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.** Simple correlation and Mantel coefficients (p values) for multivariate analysis of the relationships between humpback whale sightings and environmental variables. The column Humpback shows simple correlations to environmental variables, significant relationships ( $p < 0.05$ ) are indicated. Column Space shows Mantel autocorrelation values for each environmental variable and associated p value in parentheses. Column Pyx/Space shows the Mantel partial values for the effect of each environmental variable on whale distribution, holding space constant. Column Pyx/\*\* shows the pure partial effects of each environmental variable on whale distribution accounting for space and the relationships to each other environmental variable.

	<b>Humpback (correlation)</b>	<b>Space (autocorrelation)</b>	<b>Pyx/space (partial)</b>	<b>Pyx/** (pure partial)</b>
humpback		0.042(0.124)		
Tmax	0	<b>0.329(0.001)</b>	-0.048(0.929)	-0.050(0.924)
Slope.bathy	0.270	<b>0.196(0.002)</b>	<b>0.114(0.025)</b>	<b>0.094(0.038)</b>
Chla	0	<b>0.217(0.001)</b>	-0.076(0.992)	-0.076(0.977)
Dist.inswb	-0.277	<b>0.214(0.001)</b>	-0.062(0.980)	-0.066(0.990)
Dist.slp	0	<b>0.213(0.001)</b>	0.009(0.303)	-0.020(0.762)
Bathy	0	<b>0.149(0.006)</b>	-0.035(0.732)	-0.077(0.980)
Dist.ice	0	<b>0.522(0.001)</b>	-0.026(0.759)	-0.012(0.610)
Dist.coast	-0.282	<b>0.392(0.001)</b>	0.017(0.293)	<b>0.059(0.017)</b>
X25-75m	0	-0.026(0.732)	-0.032(0.781)	-0.077(0.993)
X25-300m	0.291	<b>0.100(0.007)</b>	<b>0.274(0.001)</b>	<b>0.265(0.001)</b>

**Table 3.** Simple correlation and Mantel coefficients (p values) for multivariate analysis of the relationships between minke whale sightings and environmental variables. The column Minke shows simple correlations to environmental variables, significant relationships ( $p < 0.05$ ) are indicated. Column Space shows Mantel autocorrelation values for each environmental variable and associated p value in parentheses. Column Pyx/Space shows the Mantel partial values for the effect of each environmental variable on whale distribution, holding space constant. Column Pyx/\*\* shows the pure partial effects of each environmental variable on whale distribution accounting for space and the relationships to each other environmental variable.

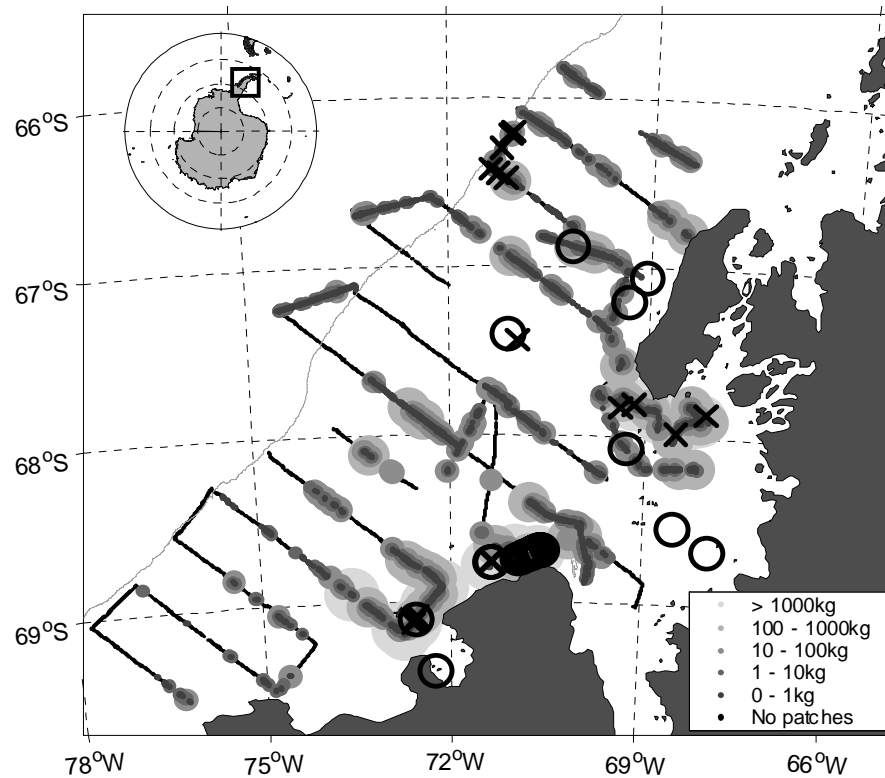
	<b>Minke (y)</b> <b>(correlation)</b>	<b>Space</b> <b>(autocorrelation)</b>	<b>Pyx/space</b> <b>(partial)</b>	<b>Pyx/**</b> <b>(pure partial)</b>
Minke		-0.075(0.983)		
Tmax	-0.02528	<b>0.329(0.001)</b>	<b>0.197(0.001)</b>	<b>0.187(0.001)</b>
Slope.bathy	-0.01744	<b>0.196(0.002)</b>	-0.095(0.987)	-0.085(0.949)
Chla	0	<b>0.217(0.001)</b>	0.0127(0.340)	-0.017(0.503)
Dist.inswb	0	<b>0.214(0.001)</b>	-0.055(0.907)	-0.084(0.994)
Dist.slp	0	<b>0.213(0.001)</b>	-0.003(0.499)	0.028(0.194)
Bathy	0	<b>0.149(0.014)</b>	-0.010(0.502)	-0.001(0.482)
Dist.ice	-0.206	<b>0.522(0.001)</b>	<b>0.124(0.006)</b>	0.055(0.117)
Dist.coast	-0.263	<b>0.392(0.001)</b>	0.004(0.400)	-0.026(0.789)
X25-75m	0.346	-0.026(0.747)	<b>0.187(0.002)</b>	<b>0.213(0.001)</b>
X25-300m	0	<b>0.100(0.007)</b>	-0.053(0.897)	-0.091(0.991)

**Table 4.** Median values and standard errors for krill patch variables associated with humpback and minke whales sampled at 5000 m, for both the ‘filtered’ and ‘unfiltered’ krill datasets in 2001 and unfiltered data in 2002.

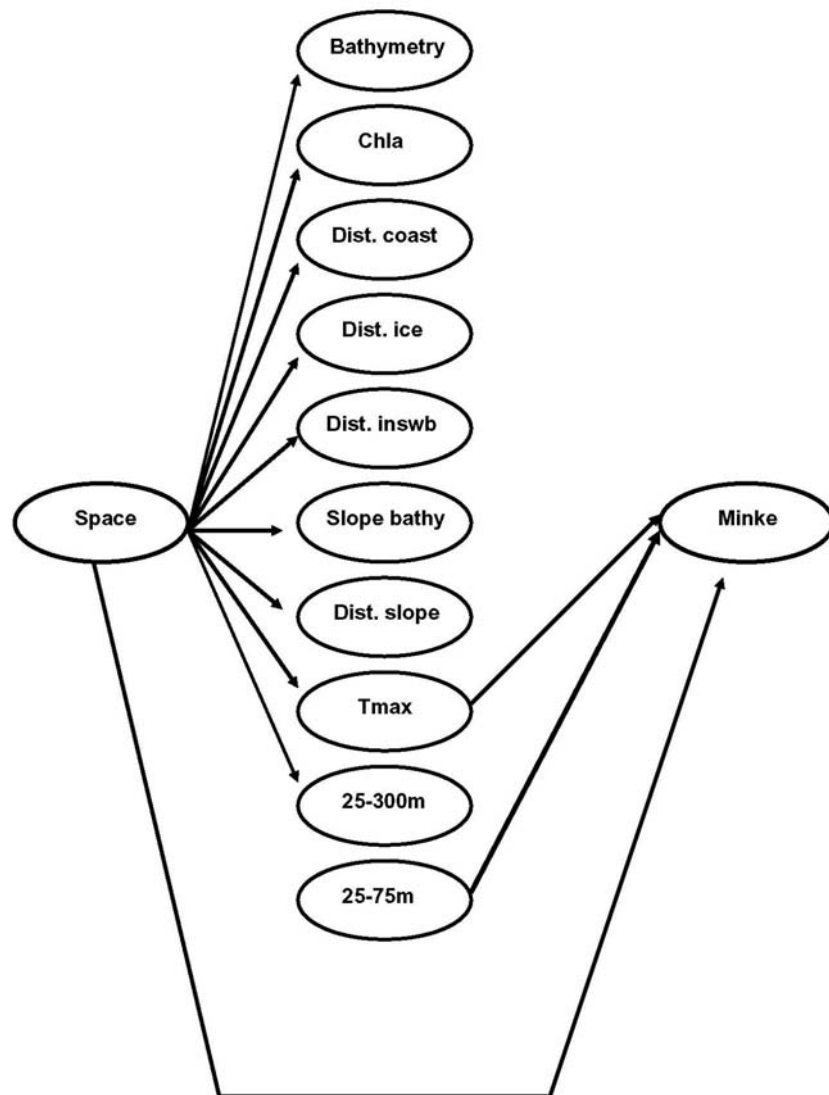
Species	Patch Depth (m)	Patch Area (m <sup>2</sup> )	Krill Length (mm)	Density (#/m <sup>3</sup> )	Biomass (g/m <sup>3</sup> )	Dataset
<b>Humpback</b>	94.8 (51.1)	101.3 (1884.2)	37.0 (10.5)	6.8 (140.5)	1.7 (3.4)	Unfiltered
<b>Minke</b>	137.8 (73.3)	61.2 (17.8)	39.5 (2.8)	8.4 (7.6)	2.2 (2.2)	Unfiltered
<b>Humpback</b>	80.6 (13)	594.5 (53.2)	37 (3.6)	10.5 (96.5)	4.9 (1.6)	Filtered
<b>Minke</b>	164 (18.7)	2813 (66148)	40 (0.82)	39.9 (14.27)	8843 (6181)	Filtered
<b>Humpback</b>	105.7 (17.2)	180 (610)	N/A	6.4 (57.1)	N/A	Unfiltered
<b>Minke</b>	142.8 (57.4)	94.5 (7.22)	N/A	6.1 (0.7)	N/A	Unfiltered

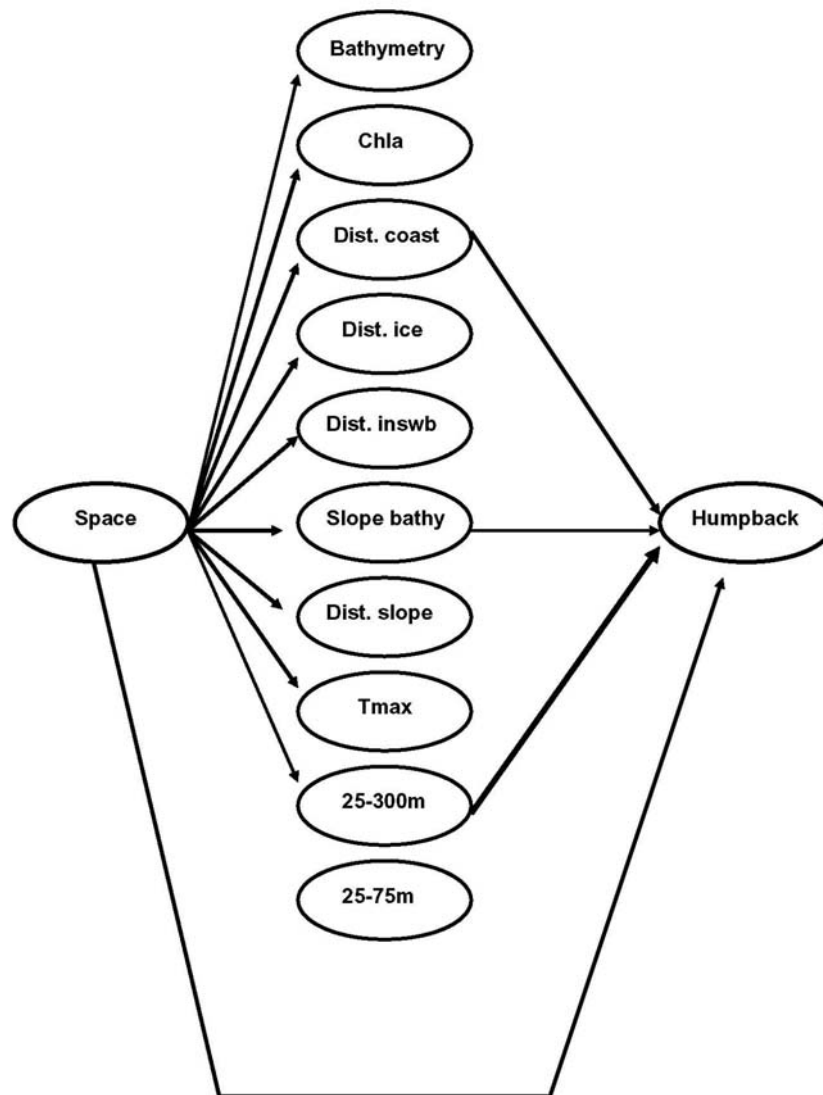
**Table 5.** Median depth of the center of krill aggregations associated with humpback and minke whales at varying spatial ranges between 500-5000m.

<b>Buffer Distance (m)</b>	<b>Species</b>	<b>Depth of Patch Center (m)</b>	<b>Std. Dev.</b>
500	M.n.	64.97	94.39
500	B.a.	163.96	35.85
1000	M.n.	84.74	15.36
1000	B.a.	147.59	11.75
2500	M.n.	76.88	52.57
2500	B.a.	135	10.4
5000	M.n.	94.8	51.1
5000	B.a.	137.8	73.3



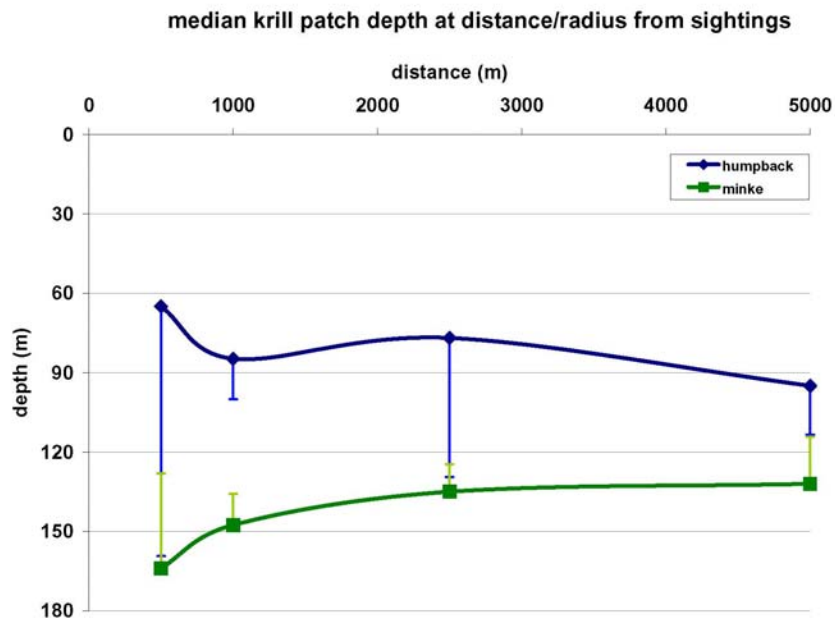
**Figure 1.** Study area of Marguerite Bay, Western Antarctic Peninsula. Krill aggregations detected from BIOMAPER-II hydro-acoustic surveys are indicated as expanding grey circles, with larger and lighter circles indicating aggregations of larger biomass. The smallest dot size (shown in black) indicates locations where surveying was conducted but no patches were detected. Aggregation biomass is in units of kilograms per across-track meter. Humpback whale sightings are shown as black x's and minke whale sightings as black circles.



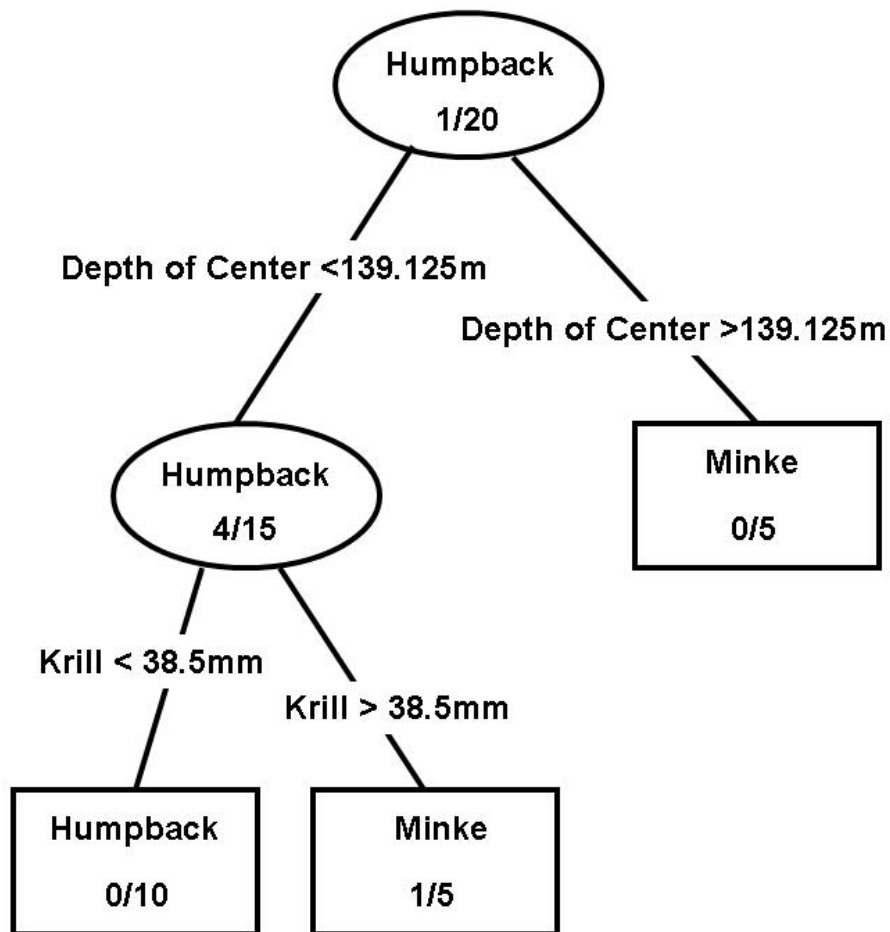


**Figure 2A&B.** Path diagrams of the Mantel's tests indicating relationships between humpback (A) and minke (B) whales and environmental variables. Bold arrows indicate significant relationships, and line thickness relates to the relative strength of the relationship. Lines from Space to each environmental variable indicate spatial autocorrelation, while lines from environmental variables to whale species indicate a pure partial effect of that variable on the observed distribution of each whale species. The line from space to each whale species indicates residual spatial variation in each species distribution not accounted for by the measured environmental variables.

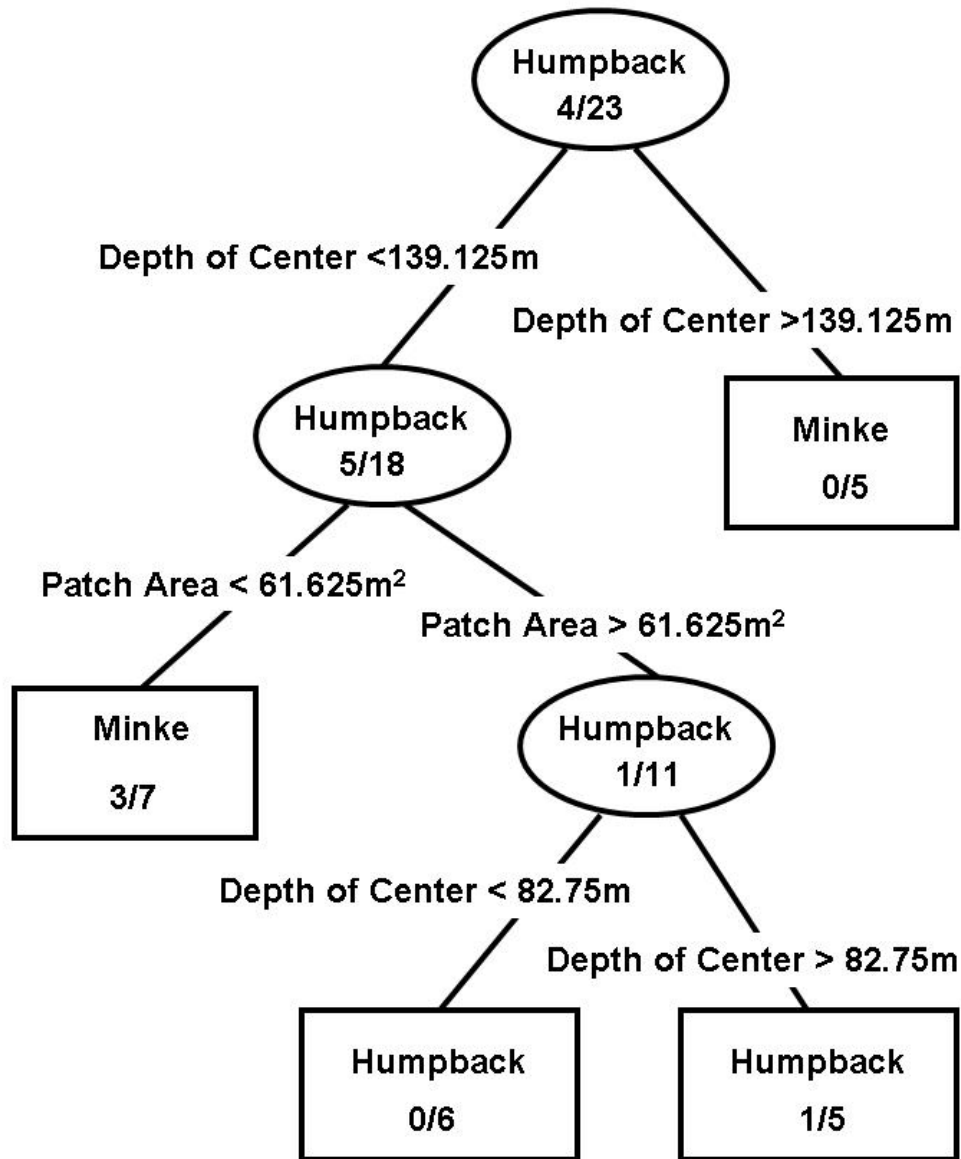




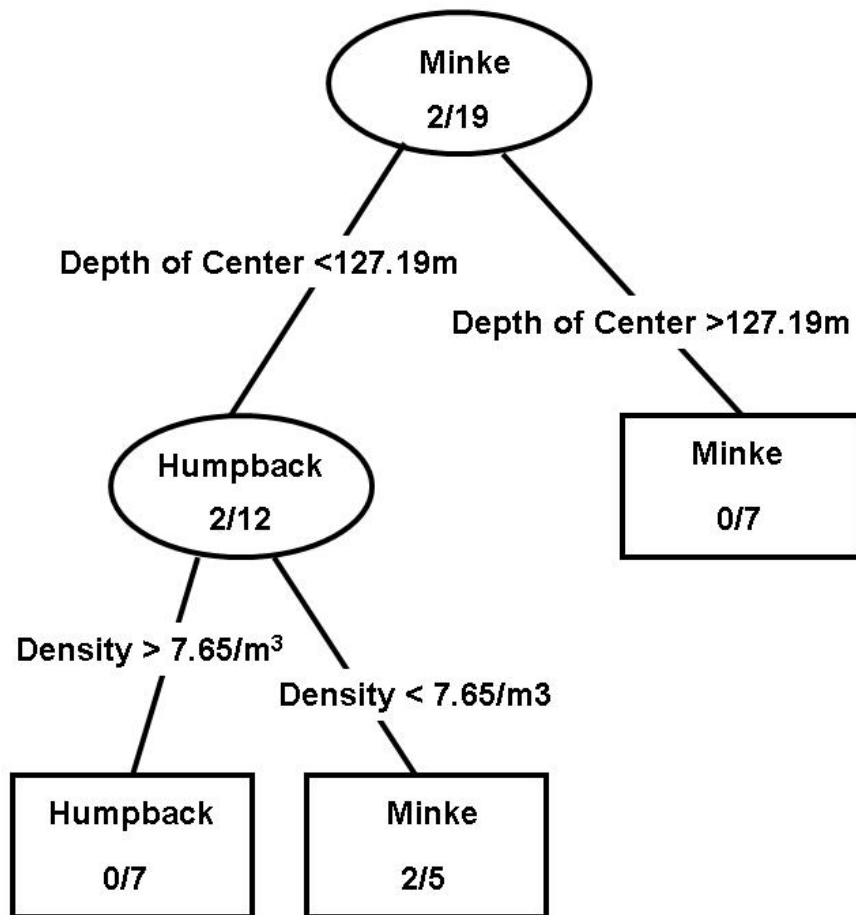
**Figure 3.** Graph of the relationship between median depth for all krill aggregations found within a range of distances (500, 1000, 2500, and 5000 m) from humpback and minke whale sightings. Smoothed lines have been fit for each species, and standard error bars are indicated.



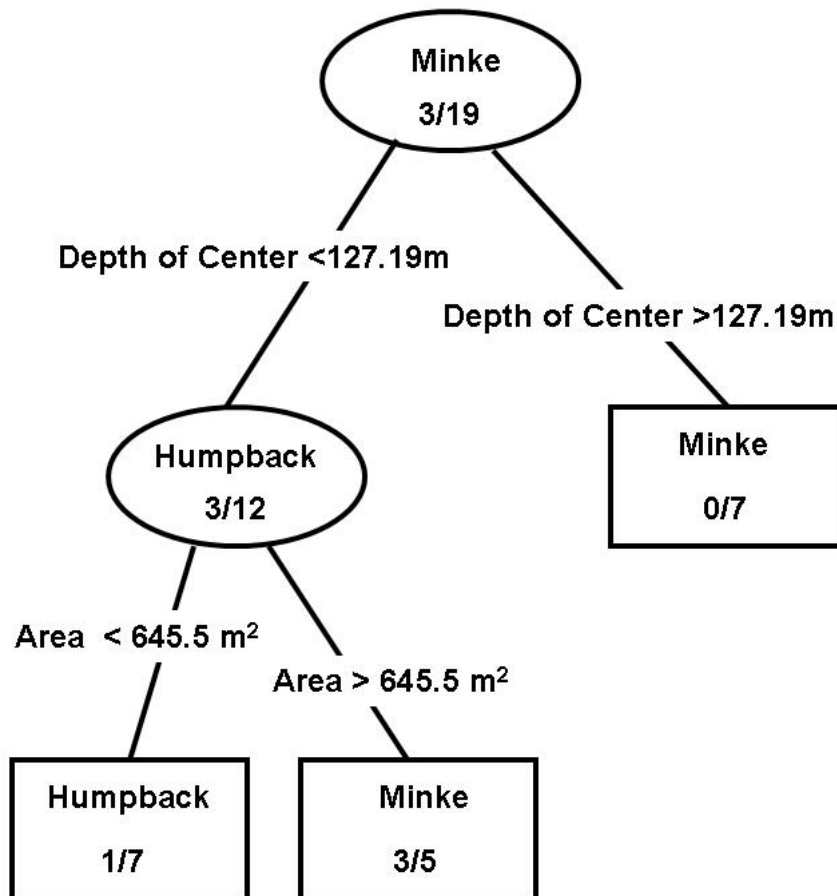
**Figure 4.** Classification tree of the relationship between krill patch characteristics including estimates of krill lengths within a given patch and humpback and minke whale sightings. The krill dataset here is the unfiltered version, where all aggregations are considered in analysis, including the smallest ones. The primary split in the tree is made at a median krill patch depth of 139.125 m. The second split occurs at an estimated krill length of 38.5 mm. The numbers at each of the terminal nodes indicate the number of misclassified response variables (whale species)/the total number of observations at the terminal node.



**Figure 5.** Classification tree of the relationship between krill patch characteristics (unfiltered dataset) and humpback and minke whales. The primary split in the tree is made at a median krill patch depth of 139.125 m. The second split occurs at median patch area of 61.625 m<sup>2</sup>, and the third split occurs at the median patch depth of 82.75 m. The numbers at each of the terminal nodes indicate the number of misclassified response variables (whale species)/the total number of observations at the terminal node.



**Figure 6.** Classification tree of the relationship between krill patch characteristics and humpback and minke whales using the dataset where the smallest aggregations of less certain composition were filtered out. The primary split in the tree is made at a median krill patch depth of 127 m. The second split occurs at median patch density of  $7.65 \text{ \#/m}^3$ . The numbers at each of the terminal nodes indicate the number of misclassified response variables (whale species)/the total number of observations at the terminal node.



**Figure 7.** Classification tree of the relationship between krill patch characteristics and humpback and minke whales using filtered dataset. The primary split in the tree is made at a median krill patch depth of 127 m. The second split occurs at median patch area of 645.5 m<sup>2</sup>. The numbers at each of the terminal nodes indicate the number of misclassified response variables (whale species)/the total number of observations at the terminal node.