Spatial association between hotspots of baleen whales and demographic patterns of Antarctic krill *Euphausia superba* suggests size-dependent predation

Jarrod A. Santora[1,2,*], Christian S. Reiss[2], Valerie J. Loeb[3], Richard R. Veit[4]

[1]**Farallon Institute for Advanced Ecosystem Research, PO Box 750756, Petaluma, California 94952, USA**

[2]**Antarctic Ecosystem Research Division, Southwest Fisheries Science Center, 3333 Torrey Pines Ct., La Jolla, California 92037, USA**

[3]**Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, California 95039, USA**

[4]**Biology Department, College of Staten Island, City University of New York, 2800 Victory Boulevard, Staten Island, New York 10314, USA**

ABSTRACT: We examined the spatial association between baleen whales and their principal prey, Antarctic krill *Euphausia superba* near the South Shetland Islands (Antarctic Peninsula) using data collected by the US Antarctic Marine Living Resources (AMLR) program during January surveys from 2003 through 2007. Whale distributions were determined using ship-based visual surveys, while data on krill distribution, abundance, and demographic characteristics were derived from net hauls. Approximately 25 000 km of transects and 500 net hauls were sampled over 5 yr. We defined hotspots based on statistical criteria to describe persistent areas of occurrence of both whales and krill. Hotspots were identified, and whales and krill length-maturity classes exhibited distinct spatial segregation in their distribution patterns. We found that baleen whales aggregated to krill hotspots that differed in size structure. Humpback whales *Megaptera novaeangliae* were associated with small (<35 mm) juvenile krill in Bransfield Strait, whereas fin whales *Balaenoptera physalus* were associated with large (>45 mm) mature krill located offshore. Overlapping these size-dependent krill distributions, Antarctic minke whales *B. bonaerensis* were associated with intermediate sized krill (35–44 mm). The correlation among different whale species and krill swarms of differing size composition presents an intriguing pattern that deserves further study.

KEY WORDS: Antarctica · *Euphausia superba* · Krill · Fin whale · Humpback whale · Minke whale · Spatial association · Hotspot

INTRODUCTION

Many species of baleen whales migrate from their winter breeding grounds in the tropics to summer feeding grounds south of the Antarctic Convergence, where they feed primarily on Antarctic krill *Euphausia superba* (Mackintosh 1965, Laws 1977, Tynan 1997, 1998, Kasamatsu et al. 1998, Zerbini et al. 2006). Despite their ecological importance, past exploitation, and dominant role in the ecosystem, rather little is

known about the foraging habitats of each species of baleen whale near the South Shetland Islands, Antarctica (Fig. 1), a region known for its elevated krill biomass (Laws 1977, Siegel 1988, Loeb et al. 1997, Reilly et al. 2004, Reiss et al. 2008), active krill fishery (Marin & Delgado 2001, Hewitt et al. 2004, Jones & Ramm 2004), and historical whaling (Mackintosh 1965, Laws 1977). Whales are often associated with krill (Reid et al. 2000, Murase et al. 2002, Friedlaender et al. 2006), and there is evidence that whales exhibit preferences for
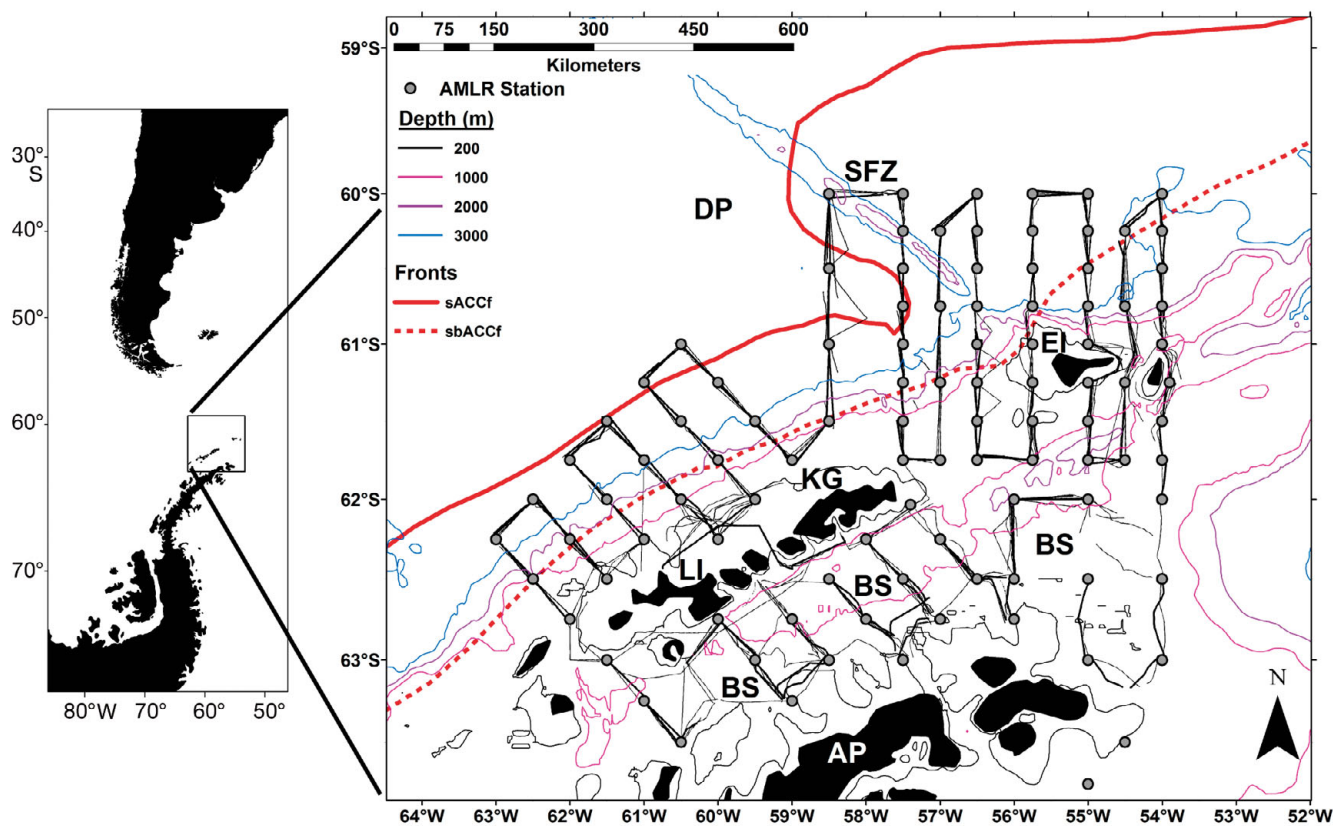
Fig. 1. Survey effort and cruise track during 2003–2007 US Antarctic Marine Living Resources (AMLR) surveys near the South Shetland Islands. A total of 1027 h and approximately 25 000 km of cruise track were sampled. Dots indicate location of net sampling stations; ~100 stations were sampled annually. Position of fronts are from Orsi et al. (1995) and are used in reference to average. sACCf: southern Antarctic Circumpolar Current front, sbACCf: southern boundary of the Antarctic Circumpolar Current front, AP: Antarctic Peninsula, BS: Bransfield Strait, EI: Elephant Island, DP: Drake Passage, KG: King George Island, LI: Livingston Island, SFZ: Shackleton Fracture Zone

particular sizes of krill (Fiedler et al. 1998, Croll et al. 2005, Friedlaender et al. 2008, 2009).

Antarctic krill exhibit a circumpolar distribution in the Southern Ocean, with the largest concentrations located in the Southwest Atlantic (Atkinson et al. 2004), an oceanographically complex region characterized by the eastward flowing Antarctic Circumpolar Current (ACC) and bathymetrically controlled flow associated with the Shackleton Fracture Zone and, more regionally, continental and island shelves (Thompson et al. 2009). Krill biomass in the Southwest Atlantic varies temporally due to interannual variability of reproductive effort and recruitment success (Loeb et al. 1997) and also presumably from between-year differences in advective transport (Fach et al. 2002, Murphy et al. 2004). Recent data suggest that the density of krill in the Scotia Sea has declined by more than 80% since the 1970s associated with declines in sea-ice extent and duration (Atkinson et al. 2004). Additionally, the West Antarctic Peninsula is among the most rapidly changing environments on the planet,

and both surface and mid-water temperatures have increased since the 1950s (Gille 2002, Meredith & King 2005). Given the recent and rapid changes in the environment, the apparent decline in their principal prey, and the potential interactions with the krill fishery, a better understanding of the foraging patterns and spatial distribution of whale populations in the Southern Ocean is necessary, as historically predictable feeding areas may be altered by climate change (de la Mare 1997, Tynan 1998, Kaschner et al. 2006, Redfern et al. 2006), potentially impacting recovery of some populations.

Near the South Shetland Islands during summer, length-maturity classes of Antarctic krill exhibit different spatial distribution patterns (Siegel 1988, 2005, Hewitt & Demer 1993, Siegel & Loeb 1995). Smaller krill are generally found in coastal/shelf waters, extending across the Bransfield Strait and south of the South Shetland Islands. In contrast, larger krill are found offshore near the shelf break and slope areas (Siegel 1988, 2005, Siegel & Loeb 1995). This apparent

spatial segregation of krill classes permits investigating their relationships to foraging whales and to quantify the key aspect of feeding areas used by whale species. At least 3 species of baleen whales regularly forage in this area (Reilly et al. 2004, Thiele et al. 2004, Williams et al. 2006). Krill size is important to the feeding ecology of krill-dependent predators, because small (5 to 10 mm) differences in the mean length of krill or the maturity stage of female krill have large energetic consequences (Ichii et al. 2007, Chapman et al. 2009, Färber-Lorda et al. 2009). Energy density (joules g^{-1} dry weight) of krill increases exponentially with length, and even more so for gravid females (Färber-Lorda et al. 2009). For whales, whose principal goal is to feed before returning to winter breeding grounds, exploiting areas of high krill density may create overlapping distributions and competition among species. Moreover, insight into prey quality and selection by marine mammals will improve estimation of consumption rates of prey and parameterization of food web models (Trites et al. 1997, Pauly et al. 1998, Reilly et al. 2004, Kaschner et al. 2006).

We examined the spatial associations of humpback *Megaptera novaeangliae*, fin *Balaenoptera physalus*, and Antarctic minke *B. bonaerensis* whales in relation to size distributions within krill swarms over a 5 yr period. We examined the spatial distribution and abundance of krill length-maturity classes and whales to map predictable locations containing high and persistent concentrations (i.e. hotspot analysis; Hyrenbach et al. 2000, Piatt et al. 2006, Yen et al. 2006). By using randomization techniques and spatial regression modeling that addresses spatial autocorrelation, we determined whether patterns of overlap among whales and krill are simply correlative or whether patterns reflect stronger relationships indicative of spatial partitioning. Specifically, we analyzed spatial clustering of krill length-maturity classes and baleen whale species to determine (1) whether there are predictable locations where whale species and krill length-maturity classes occur annually, and (2) whether hotspots of baleen whales and krill overlap within and between areas. This information has important implications for conservation of baleen whales and management of the krill fishery in the Southern Ocean.

MATERIALS AND METHODS

Field methods. The US Antarctic Marine Living Resources (AMLR) program has collected data on the distribution, abundance, and demographic characteristics of krill in the South Shetland Island (SSI) region since 1990. Beginning in 2003, seabirds and mammals were censused along transects to map the distribution and relative abundance of seabirds and marine mammals within the AMLR survey area (Fig. 1). Data reported here are from January surveys from 2003 through 2007. Standardized surveys are conducted along inshore and offshore (usually north-south) transects with stations spaced at ca. 55 km intervals across a 108 700 km^2 area in Drake Passage and Bransfield Strait waters surrounding the SSI (Elephant, King George, and Livingston Islands; Fig. 1). The US AMLR program has defined areas based on historical sampling (the Elephant Island Area) and the location of predator field camps (the West Shelf, on the north side of Livingston Island and within Bransfield Strait). Transects and station locations were fixed, and about 100 plankton stations were sampled each survey (~23 d).

Krill sampling. Krill were sampled at the fixed survey grid stations with a 1.8 m Isaacs-Kidd Midwater Trawl fitted with 505 µm mesh plankton net and a calibrated flow meter (General Oceanics, model 2030). The nets were fished obliquely from 170 m or ca. 10 m above bottom to the surface in shallow waters and filtered ca. 2500 to 4000 m^3 of water. Abundance of krill from net tows is standardized to no. m^{-2} of sea surface by integrating over the tow depth. Net samples were processed aboard ship, and all postlarval krill in samples with <100 individuals were measured (total length to the nearest mm), sexed, and staged for reproductive maturity (Siegel & Loeb 1995). For larger samples, at least 100 krill were randomly sampled and analyzed. We pooled krill into 3 length-maturity classes that comprised small (13–34 mm) 1 yr old juveniles, intermediate (35–44 mm) 2 yr old immature males and mature females, and large (45–65 mm) 3 yr old and older mature individuals (Siegel & Loeb 1995).

Cetacean survey. Baleen whale distribution and abundance data were collected during transits between oceanographic/net stations along fixed transects, distributed around the SSI (Fig. 1). Ship speed during transits was 10 knots (~18.6 km h^{-1}). Visual surveys were conducted each year by trained observers using standard line transect theory (Heinemann 1981, Buckland et al. 1993). Observers used hand-held binoculars (10 × 50) and were located at a height of 13 m above sea level. Weather conditions permitting, all cetacean sightings recorded were observed in a 180° arc forward of and up to 3 km away from the vessel (Reid et al. 2000, Santora et al. 2009). Sighting data were entered into a computer using real-time mapping software, and positions were logged every 15 s while underway. For each whale sighting, a best-estimate spatial position, bearing, and a perpendicular distance estimate to the ship′s trackline were logged (Heinemann 1981, Buckland et al. 1993). Sea surface state (Beaufort scale) and visibility (e.g. fog, glare) were monitored continuously by the observer. Survey effort

during unfavorable conditions (e.g. Beaufort >6, heavy fog) was excluded from the data set. The pooled data analyzed here represent a total of 1019 h (203 ± 20 [SD] h annually) of observations made over approximately 25 000 km of survey tracklines (Fig. 1).

We calculated the relative abundance of whales using sighting data (Reid et al. 2000, Thiele et al. 2004, Ainley et al. 2007). Data were standardized to estimate relative abundance of whales by calculating indices of sightings per unit effort (SPUE) and individuals per unit effort (IPUE) to examine interannual changes in whale abundance (Zerbini et al. 2004, Redfern et al. 2006). A unit of effort is reported as the number of hours surveyed d^{-1}. A total of 82 d (16 to 18 d yr^{-1}) were sampled during 2003 to 2007 for an average of 12.5 ± 2.9 (SD) h d^{-1}. We used nonparametric statistics (Kruskal-Wallis tests) to determine if SPUE or IPUE varied inter-annually (Zar 1999).

Analytical methods. *Data binning:* The primary objective of the data binning was to generate a composite suite of maps to quantify spatial variability in the overlap between whales and their krill prey. Therefore, we combined all 5 yr of survey data (i.e. net hauls, cetacean sightings) into a geographic information system (GIS) in ArcView (ESRI 2007) where data reduction and analysis was conducted. We binned the survey data into 42 cells, each 0.5° latitude × 1° longitude or approximately 2860 km^2 in size. This cell size was chosen because it covered 2 to 3 net sampling stations $cell^{-1}$ and yet was fine enough to track changes in krill demography across the SSI region (i.e. shelf–shelf break–oceanic environs; Siegel 2005). Only cells that were sampled during at least 4 of the 5 yr were used in subsequent analyses. For each survey, we estimated the total number of whales sighted and mean abundance of the 3 krill length-maturity classes in each cell annually and then weighted this by the survey effort (i.e. transect distance, net samples) conducted in each year.

Hotspot mapping and clustering analysis: To detect the locations (cells) of persistent clustering of whales and krill, we used the Getis-Ord *G* statistic (Getis & Ord 1992, Ord & Getis 1995, Swenson & Howard 2005). The Getis-Ord *G* statistic (a *Z*-score) identifies clusters of points with values higher in magnitude than would be expected due to random chance. We defined hotspots as areas where there is a statistically significant level of clustering (>1 SD; Swenson & Howard 2005). The *Z*-score for each cell was estimated based on a randomization test, for the combined 5 yr dataset. We then mapped hotspots based on the location of significant *Z*-scores by representing distinct clusters of krill and whales (mean ± SD per cell) as an index of spatial clustering over 5 yr. We categorized hotspots as non-significant (<1 SD), medium (1 to 1.9 SD), and

high (>2 SD). Furthermore, we conducted a bootstrap analysis and Monte Carlo randomization test (5000 runs) to estimate correlation coefficients and confidence intervals for comparing associations of whales with krill length-maturity classes (Legendre & Legendre 1998, Zar 1999).

Spatial relationships between whales and krill: We used 2 complementary techniques to examine the spatial association between whales and their krill prey. We used 2 different spatially-explicit regression models to account for the effects of spatial autocorrelation and spatial error in whale and krill distributions (Anselin et al. 2006, Santora et al. 2009), and we calculated 2-dimensional correlograms to examine the correlation between krill and whales. The objective of the spatial regression modeling is to test whether baleen whale species are spatially associated with particular krill length-maturity classes. Spatial regression models are similar to generalized linear models, except they have spatially explicit parameters to account for both autocorrelation and spatial dependency (Ferguson & Bester 2002, Anselin et al. 2006). We employed 2 spatially explicit regression models in a GIS platform (Anselin et al. 2006; GeoDaS Software) using Maximum Likelihood Estimation and Akaike Information Criteria (AIC) to examine differences between models (Burnham & Anderson 2002). The 2 models were:

$$Y = \rho W_y + X_i \beta + \varepsilon \qquad (1)$$
$$Y = Xi\beta + \varepsilon, \text{ where } \varepsilon = \lambda W_\varepsilon + \xi \qquad (2)$$

where Y is whale abundance (ind. $cell^{-1}$), X_i is krill abundance (i = length-maturity class no. m^{-2} $cell^{-1}$), β is a regression coefficient, and ε is a random error term that is identically and independently distributed. The first model (Eq. 1) has spatial lag components: ρ, a spatial autoregressive coefficient, and W_y, a spatially varying lag term. The spatial lag model takes into account whether the dependent variable Y in place i is affected by the independent variables in both place i and j. That is, events in 1 place may predict an increased likelihood of similar events in neighboring places. In the spatial error model (Eq. 2), spatial autocorrelation is not an additional variable in the model as in the spatial lag model (Eq. 1) but rather affects the covariance structure of the spatial error terms, where λ is an autoregressive coefficient, W_ε is a spatially varying error term, and ξ is a vector of identically and independently distributed error terms. The spatial error model takes into account the probability that the error terms (i.e. spatial autocorrelation of residuals) across different spatial units are correlated as a function of geographic distance. We concluded that a whale species was significantly associated with krill if a particular krill length class was a significant predictor of whale abundance.

Propagation of spatial error (i.e. uncertainty) in testing the spatial association of whales and krill is likely to vary according to distance, sampling resolution, and measurement technique (Legendre & Legendre 1998, Ferguson & Bester 2002). We determined whether each model accounted for the spatial dependency of whales in relation to krill using a likelihood ratio test (LRT; Anselin et al. 2006). Here the objective was to determine whether the inclusion of spatial autocorrelation influenced the outcome of the model results. For the LRT test, a critical value greater than $\alpha = 0.05$ (i.e. not significant) indicates that the spatial regression model (lag or error) likely accounts for spatial dependency between whales and krill.

In addition to testing for spatial association at lag 0, we determined the range (i.e. scale) of spatial association between whales and krill by calculating 2-dimensional isotropic cross-correlograms to quantify the association of whales and krill over increasing lags equal to our initial cell size (~2860 km^2; Legendre & Legendre 1998, Tobin & Bjørnstad 2003). The range of spatial correlation was characterized by the number of consecutive positive lags before falling below 0 (Reid et al. 2004, Santora et al. 2009).

RESULTS

Whale sightings and relative abundance

Humpback, fin, and Antarctic minke whales were frequently sighted around the SSI over the 5 yr study period (Table 1). Humpback whales were most often sighted, followed by fin and minke whales. There was no difference among years in the sighting rate of humpback (Kruskal-Wallis: $H = 4.22$, p = 0.37), fin ($H = 5.33$, p = 0.25), or minke whales ($H = 6.74$, p = 0.15). The SPUE and IPUE for whales observed during 2003 to 2007 show that whale sightings and individuals counted were consistent over time (Fig. 2). In addition, the ratio between the number of sightings and individuals counted was nearly constant among years (Fig. 2).

Table 1. Total whales (individual sightings and groups) for 5 US Antarctic Marine Living Resources (AMLR) surveys (January, 2003 to 2007)

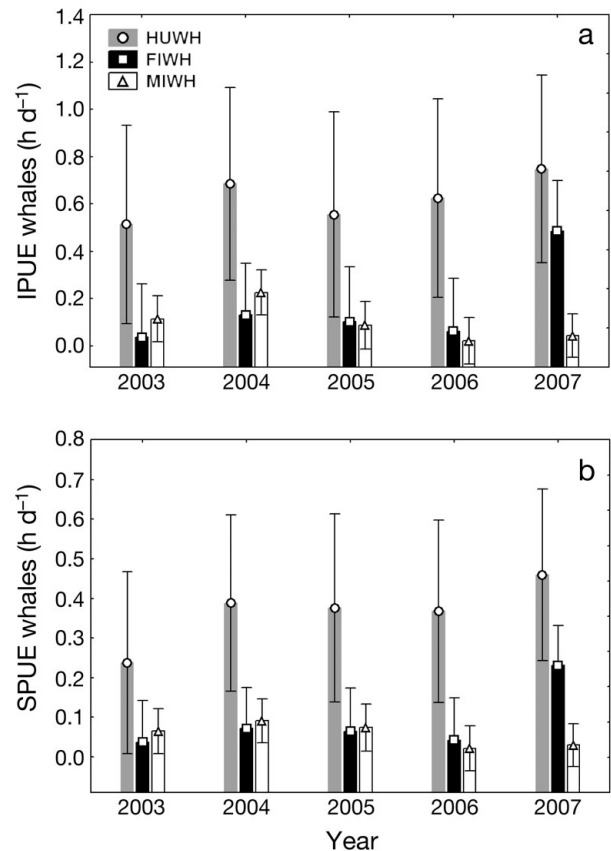| Species	No. of groups	No. of animals
Humpback whale	397	664
Fin whale	97	184
Minke whale	51	96
Total	545	944

Fig. 2. Standardized survey effort for whales (no. h^{-1} d^{-1}): (a) IPUE: individuals per unit effort, and (b) SPUE: sightings per unit effort (± 95% CI). HUWH: humpback whale; FIWH: fin whale; MIWH: Antarctic minke whale. During 2003–2007, days = 82, hours = 1027, and average h d^{-1} = 12.5

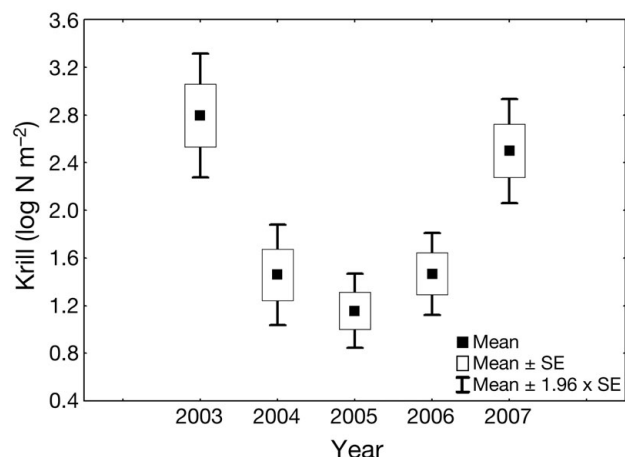

Fig. 3. *Euphausia superba*. Net-based mean abundance (log N m^{-2}) of Antarctic krill collected around the South Shetland Islands between 2003 and 2007

Krill abundance and length frequency

The abundance of krill varied among years (Kruskal-Wallis $H = 34.65$, p < 0.01, Fig. 3). This variability in abundance was due to strong recruitment events in 2003 and 2007 (Reiss et al. 2008) and reflects an order of magnitude increase in abundance over these years (Fig. 3). In some years (e.g. 2004), a single modal length was observed, while in others (e.g. 2003 and 2007) bi-modal length frequencies were found reflecting new recruitment (1 yr olds) combined with remaining older animals in the study area (Fig. 4). In general, krill lengths were larger in the Elephant Island region and smaller in Bransfield Strait (Fig. 4). Krill length classes exhibited strikingly different spatial distributions that reflect concentrations of large (44–65 mm) mature adults in oceanic ACC waters and small (13–34 mm) juvenile classes concentrated in coastal Bransfield Strait waters (Fig. 5, Table 2).

Hotspots of krill length-maturity classes

Spatial composite mapping of krill by length-maturity classes revealed hotspots that reflected segregation by size, and aggregation within areas (Table 2, Fig. 5). Nine hotspots of small krill were found, and the abundance of krill in these ranged from ~22 to 73 m^{-2} (Table 2, Fig. 5a). These hotspots were found in Bransfield Strait. Moreover, the 4 highest hotspots were not randomly distributed within Bransfield Strait but instead were concentrated over the deep basins, areas of known recirculation. Intermediate-length krill hotspots were not as spatially restricted as those of the small krill. Their high hotspots were found north of Elephant Island and also within eastern Bransfield

Strait (Table 2, Fig. 5b). The 13 medium hotspots (Z-scores between 1 and 1.96 SD of the mean) were found along the north side of Bransfield Strait and north of Elephant Island, indicating a broader spatial distribution than hotspots associated with small krill (Fig. 5a). Due to their affinity for the shelf break region and offshore waters, hotspots of large krill were distributed along the shelf break north of the SSI. The 21 hotspots exhibited densities between 6 and 16 m^{-2}. The highest hotspots (Z-scores > 2 SD) for the large-krill length class were focused mostly north of Elephant Island across 4 contiguous cells (Table 2, Fig. 5c). Although large krill were less abundant than intermediate or small krill length classes, their hotspots exhibited a much broader and contiguous spatial distribution. This result is likely attributable to temporal differences in maturation and the propensity of sexually mature krill to aggregate near the shelf break where spawning occurs.

Hotspots of foraging whales

When the spatial distribution of whales is mapped onto the $0.5 \times 1°$ cells (n = 42), clear differences in habitat use among species are visible (Fig. 5d–f). Humpback, fin, and minke whale hotspots are spatially separated from each other, and the hotspots of each species were neither randomly distributed throughout the survey area nor randomly distributed within sub-areas. For example, humpback whale hotspots were present in Bransfield Strait, whereas fin whale hotspots were present offshore. Minke whale hotspots were distributed over the shelf and along the shelf edge. The mean number of humpback whales in the 13 medium and 4 high hot spots were between 22 and 49 whales
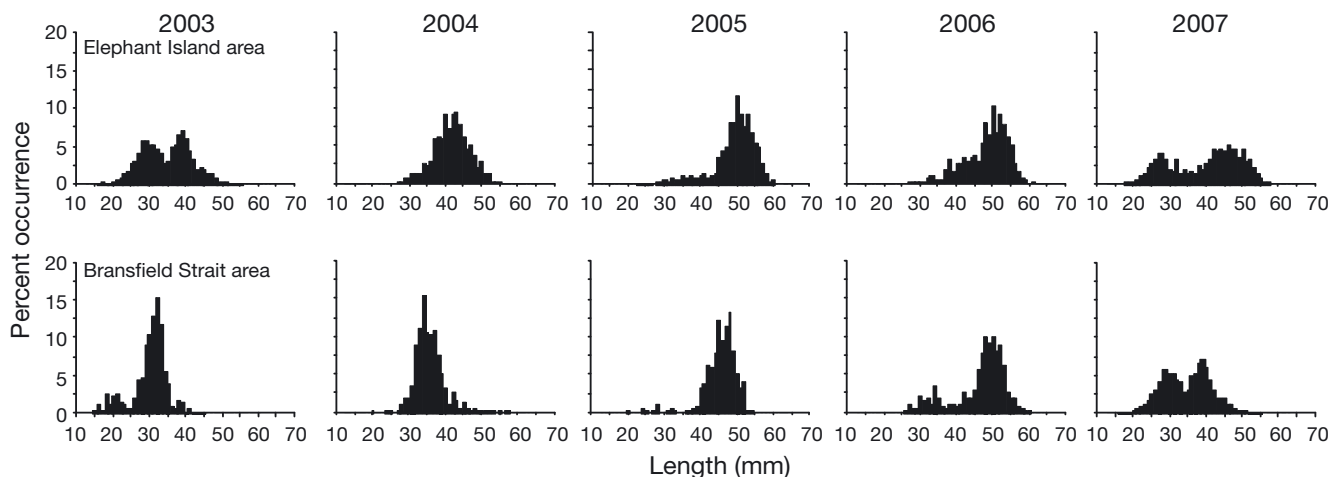

Fig. 4. *Euphausia superba*. Length frequency distributions of krill (1 mm increments) collected within the Elephant Island and the Bransfield Strait regions of the US Antarctic Marine Living Resources (AMLR) survey area from 2003 through 2007. See Fig. 1 for locations
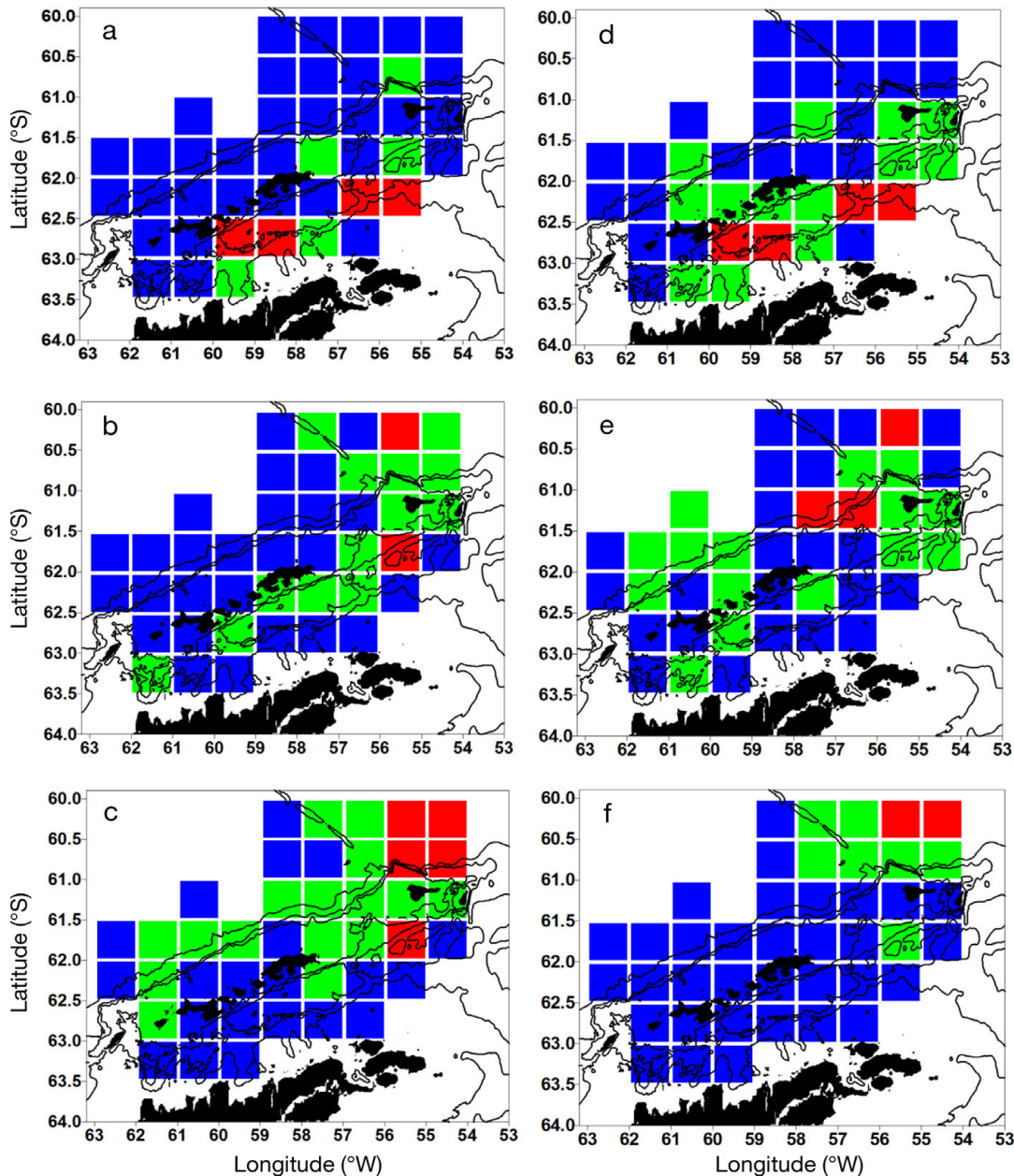
Fig. 5. Composite hotspot maps (42 cells) of krill length classes (a) 13–34 mm, (b) 35–44 mm, (c) 45–65 mm and baleen whales, (d) humpback, (e) minke, and (f) fin from 2003 through 2007. Color indicates high (red, *Z*-score > 2 SD), medium (green, *Z*-score = 1–1.96 SD), and non-significant (blue) hotspots; refer to Table 2 for mean ± SD. Cell size is ~2860 km^2

cell^{-1} (Table 2). The 4 high humpback whale hot spots were not randomly distributed within Bransfield Strait, and were found associated with the deep basins and in the same cells as the hotspots for small krill length classes (Fig. 5a,d). The mean number of fin whales in medium and high hotspots ranged from 11 to 29 (Table 2). Both intermediate and high fin whale hotspots were located north of Elephant Island in the northeast corner of the study area, east of the Shackleton Fracture Zone (Fig. 1), in waters characterized by

the ACC (Fig. 5f). These 2 hotspots are associated with 2 of the 5 cells containing high hotspots for large krill (Fig. 5c). Although Antarctic minke whales were far less numerous in our surveys than were humpback or fin whales (Table 2), we did identify regions where they were repeatedly encountered (Fig. 5e). In contrast to the rather distinct and contiguous fin and humpback whale hotspots, the minke whale distribution was patchy and irregular. Nevertheless, 3 hotspots for minke whales were found: 2 were located near the

Table 2. Hotspots are categorized as 'non-significant' (NS, <1 SD), 'medium' (1 to 1.9 SD), and 'high' (>2 SD) for krill length classes (mean ± SD for N m^{-2} cell^{-1}) and whale abundance (mean ± SD for no. whales cell^{-1}). Values in parentheses represent the number of cells used to calculate the mean for each hotspot. See Fig. 5 for locations

	High	Medium	NS
Krill			
13–34 mm	(4) 72.88 ± 11.66	(5) 21.98 ± 2.73	(33) 2.32 ± 2.85
35–44 mm	(2) 30.33 ± 12.88	(13) 7.31 ± 2.07	(27) 0.97 ± 0.98
45–65 mm	(5) 16.51 ± 5.46	(16) 6.32 ± 2.05	(21) 1.72 ± 1.21
Baleen whales			
Humpback	(4) 48.75 ± 12.45	(13) 22.00 ± 5.70	(25) 2.68 ± 3.19
Minke	(3) 11.00 ± 1.73	(15) 3.13 ± 1.30	(24) 0.17 ± 0.38
Fin	(2) 29.00 ± 1.41	(7) 11.71 ± 4.42	(33) 0.93 ± 1.32

Table 3. Relationship between whales and krill length-maturity classes (n = 42 cells); correlation and 95% CI estimated from a bootstrap and Monte Carlo analysis (5000 randomizations). Significant values are shown in **bold**

Krill	r	Lower 95%	Upper 95%	p
Humpback whale				
13–34 mm	0.484	0.212	0.687	**0.0006**
35–44 mm	0.136	−0.175	0.423	0.3754
45–65 mm	−0.078	0.231	−0.373	0.6216
Fin whale				
13–34 mm	0.061	−0.247	0.358	0.703
35–44 mm	0.418	0.132	0.641	**0.05**
45–65 mm	0.59	0.348	0.758	**0.0002**
Minke whale				
13–34 mm	0.007	0.226	−0.377	0.603
35–44 mm	0.323	0.021	0.571	**0.033**
45–65 mm	0.251	−0.057	−0.515	0.112

shelf break west of Elephant Island, and 1 was offshore. A number of medium hot spots were present over the west shelf, a region where no humpback or fin whale hotspots were found (Fig. 5e).

Correlations between hotspots of whales and krill length-maturity classes

The randomization test indicated that hotspots of krill size classes and whale species exhibited significant correlations (Table 3). For example, small krill were correlated with humpback whales (r = 0.48, p = 0.0006) but large krill were not (r = −0.07, p = 0.62, Table 3). In contrast to humpback whales, fin whales were associated with large krill (r = 0.59, p = 0.0002) but not small krill (p = 0.703). Fin whales were also weakly correlated with intermediate-sized krill (r = 0.42, p = 0.05, Table 3). Intermediate-sized krill were correlated with minke whales (r = 0.32, p = 0.033) more

than small (r = 0.007, p = 0.603) or large krill classes (r = 0.25, p = 0.112).

Spatial association of whales and krill length-maturity classes

Both spatial regression models indicated that the distribution of humpback whales was associated with small-krill length classes (Fig. 5, Table 4), and the models were able to account for the spatial dependency of humpback whales on krill (LRT = 3.33, p = 0.068 and LRT = 0.59, p = 0.439, respectively; Table 4). On the other hand, fin whales were spatially associated with large-krill length classes, but there was no spatial dependency of fin whales on krill (LRT = 10.05, p = 0.001 and LRT = 6.86, p < 0.01, respectively; Table 4). In contrast to humpback and fin whales, spatial regression models applied to Antarctic minke whales showed that they are spatially associated with intermediate sized krill (Table 4). The LRT indicates that these models were able to account for the spatial dependency of Antarctic minke whales on krill (LRT = 1.96, p = 0.16 and LRT = 1.765, p = 0.184, respectively; Table 4).

Lastly, to address the scale of these spatial associations and size of whale-krill hotspots, we quantified the association between whales and krill length-maturity classes over a range of spatial lags to examine the degree of correlation over increasing lags (i.e. cells). Spatial cross-correlation between humpback whales and krill length-maturity classes showed a positive lagged correlation with small krill up to 3 cells and had a persistently negative association with larger krill (Fig. 6a). In contrast, fin whales were positively correlated over ~3 cells with large krill and a negative association with small krill (Fig. 6b), indicating that the scale of whale–krill hotspots is similar for humpback and fin whales. We found no evidence of lagged spatial correlation between Antarctic minke whales and krill length classes (Fig. 6c).

DISCUSSION

Our study showed that baleen whales and krill occur in persistent locations. The hotspots of whale abundance were clearly correlated with areas of persistent

Table 4. Results of spatial regression analyses for spatial lag and spatial error models of association between humpback, fin, and minke whales and 3 krill length classes (13–34, 35–44, and 45–65 mm), using Akaike Information Criteria (AIC). W_y is a spatial lag variable within the regression framework to examine the spatial autocorrelation in structuring the patterns between krill and whales. W_ε is the spatial error term in the regression model to determine whether the error structure is correlated. Significant values are shown in **bold**

Variable	Coefficient	SE	Z-value	p
Humpback whale				
Spatial lag model: $r^2 = 0.344$, AIC = 139.17				
Constant	0.990	0.430	2.298	**0.021**
13–34 mm	0.448	0.152	2.955	**0.003**
35–44 mm	−0.021	0.249	−0.087	0.930
45–65 mm	−0.127	0.253	−0.500	0.616
W_y	0.249	0.119	2.089	**0.036**
Spatial error model: $r^2 = 0.282$, AIC = 139.903				
Constant	1.460	0.431	3.389	**0.006**
13–34 mm	0.449	0.156	2.874	**0.004**
35–44 mm	0.012	0.255	0.049	0.960
45–65mm	−0.155	0.271	−0.573	0.566
W_ε	0.152	0.131	1.163	0.244
Fin whale				
Spatial lag model: $r^2 = 0.545$, AIC = 106.675				
Constant	−0.227	0.255	−0.890	0.373
13–34 mm	−0.081	0.099	−0.815	0.415
35–44 mm	0.149	0.164	0.908	0.363
45–65 mm	0.488	0.171	2.858	**0.004**
W_y	0.382	0.104	3.645	**0.0005**
Spatial error model: $r^2 = 0.508$, AIC = 107.866				
Constant	0.125	0.317	0.395	0.692
13–34 mm	−0.064	0.101	−0.639	0.522
35–44 mm	0.144	0.161	0.893	0.371
45–65 mm	0.487	0.181	2.684	**0.007**
W_ε	0.376	0.115	3.256	**0.001**
Minke whale				
Spatial lag model: $r^2 = 0.22$, AIC = 101.758				
Constant	0.341	0.256	1.328	0.184
13–34 mm	−0.178	0.097	−1.827	0.067
35–44 mm	0.326	0.160	2.037	**0.042**
45–65 mm	0.042	0.164	0.255	0.798
W_y	0.192	0.125	1.537	0.124
Spatial error model: $r^2 = 0.216$, AIC = 99.951				
Constant	0.462	0.271	1.703	0.088
13–34 mm	−0.172	0.096	−1.783	0.074
35–44 mm	0.296	0.156	1.889	0.058
45–65 mm	0.078	0.168	0.463	0.643
W_ε	0.191	0.129	1.482	0.138

krill abundance. There were differences between whale species in the size class of krill over which they aggregated. Humpback whales tended to aggregate over small krill (13–34 mm), whereas fin whales aggregated over large krill (45–65 mm) and minke whales overlapped intermediate size krill. We do not know whether the whales actually selected swarms having these size classes, or whether whales and krill coincidentally chose these particular habitats. Nevertheless, the spatial association is an intriguing one and should be considered by agencies responsible for krill fishing decisions.

Spatial segregation of krill by maturity classes near the SSI during summer is well documented (Siegel 1988, 2005, Siegel & Loeb 1995). The smallest krill, 1 yr old juveniles (≤34 mm), are concentrated over deep basins in Bransfield Strait, while the large mature stages (3 yr and older, >44 mm) are primarily found along the shelf-break and in proximity to the ACC. Intermediate-sized immature and small mature stages (35–44 mm) are between and/or overlapping these 2 groupings (Siegel 1988, Siegel & Loeb 1995). This pattern has been attributed to differences in maturation and the propensity of sexually mature krill to aggregate near the shelf break.

The seemingly small differences in mean krill length (~5 to 10 mm) between areas represent large differences in energy density g^{-1} dry weight of krill (Ichii et al. 2007, Chapman et al. 2009, Färber-Lorda et al. 2009). For example, mean energy density for a 40 mm
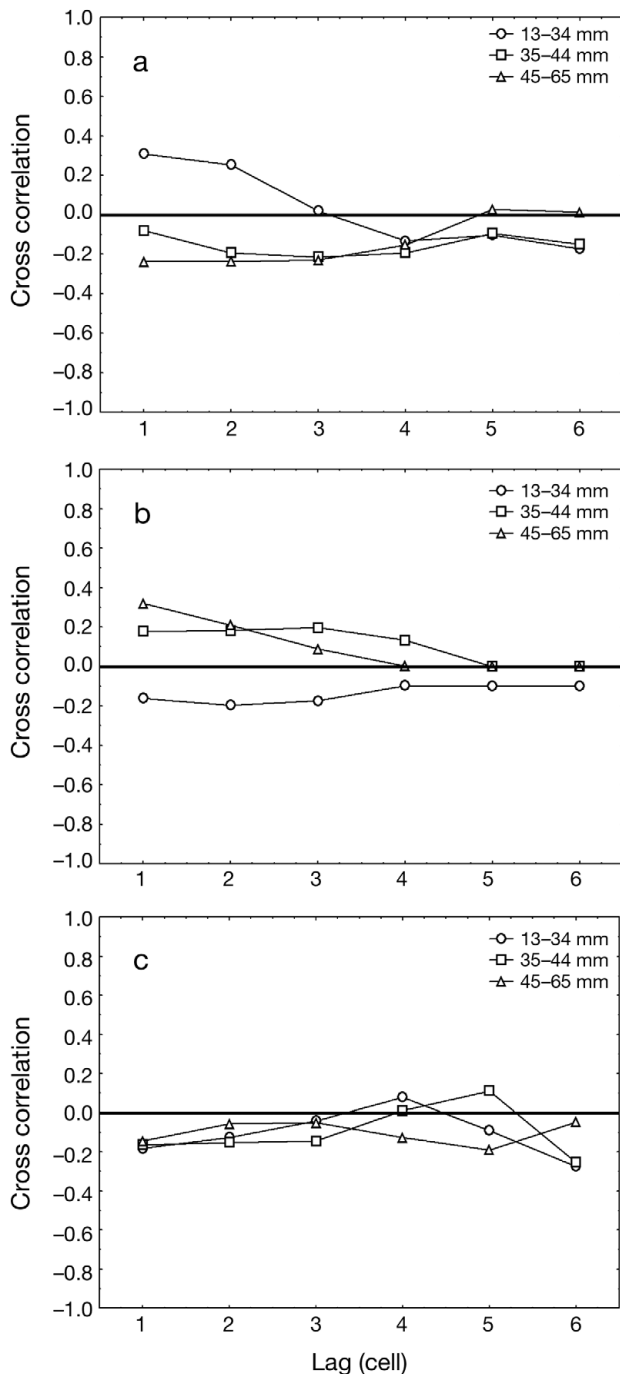
Fig. 6. Spatial cross-correlation between whales and krill length classes: (a) humpback, (b) fin, and (c) minke. Lag equals cell size ~2860 km^2

maturity classes that differ energetically. This has implications for understanding prey quality and selection by marine mammals (Pauly et al. 1998), fishery interactions (Trites et al. 1997, Kaschner et al. 2006), parameterization of Antarctic food web models, and improved estimation of consumption rates by baleen whales (Reilly et al. 2004, Hill et al. 2007).

A number of recent studies have examined the influence of environmental and biological factors affecting whale distribution in the Western Antarctic Peninsula (Thiele et al. 2004, Friedlaender et al. 2006, 2008, 2009) and Scotia Sea (Reid et al. 2000). In most of these studies, the authors clearly showed that at mesoscales (~100s of km), baleen whales exhibit a strong affinity with their principal prey. For example, using data collected from 2 field seasons, Friedlaender et al. (2006) showed that the relative abundance of baleen whales (combined minke and humpback) off the West Antarctic Peninsula, while correlated with a suite of biological and non-biological variables, were ultimately correlated with krill. Our results establish that foraging grounds of humpback whales coincide with aggregations of small krill in Bransfield Strait, while those of fin whales occur in oceanic waters near Elephant Island where large sexually mature krill are most abundant. Overlapping these distinct distributions, Antarctic minke whales are associated with intermediate-sized krill. This indicates that these species may partition foraging habitat to avoid direct competition on the basis of a shared prey item (Piatt & Methven 1992, Friedlaender et al. 2009).

The morphology of baleen whales (i.e. body size, fluke, flippers, baleen plates) is associated with hydrodynamic performance, and is linked to feeding behavior, prey type, and habitat preference (Laws 1977, Gaskin 1982, Panigada et al. 1999, Woodward et al. 2006). Fin, humpback, and Antarctic minke whales differ in size and feeding strategy (Watkins & Schevill 1979, Gaskin 1982, Whitehead & Carlson 1988, Piatt & Methven 1992, Woodward et al. 2006). Moreover, baleen plates differ among species in terms of size, shape, and coarseness of fringes (Gaskin 1982), which may influence their selection of prey. Humpback whales, which display a variety of feeding mechanisms (Whitehead & Carlson 1988, Woodward et al. 2006) occasionally feed by 'bubble-netting' (i.e. swimming below a prey aggregation, releasing bubbles to concentrate the prey and then engulfing them; Johnston & Wollman 1984), while fin whales perform 'lunge side-feeding' at the surface (Gaskin 1982) and at depth (Goldbogen et al. 2006).

Feeding strategies of baleen whales may rely on differing behaviors of krill (e.g. vertical distribution, swarm structure) that could also explain their habitat selection and spatial segregation. Our study shows that

krill (male or female) is approximately 1.75 kJ g^{-1} dry weight, while mean energy density of a krill (male or non-gravid female) of 50 mm is approximately 3.75 kJ g^{-1} dry weight. In contrast, a gravid 50 mm krill has more than 6 kJ g^{-1} dry weight (Ichii et al. 2007, Färber-Lorda et al. 2009). Our study shows that species of baleen whales are likely utilizing different krill length-

fin whales are likely cueing on aggregations of large (>44 mm) mature krill associated with hydrographic features such as the shelf-slope front and/or resulting from krill reproductive behavior (Siegel & Loeb 1995). In contrast, humpback whales may rely on the dense schooling of juvenile (<34 mm) krill over the deep basins of Bransfield Strait (Tarling et al. 2009). However, we did not examine feeding behavior of whales in relation to krill patch structure or behavior, and more study is needed to understand how foraging whales select krill patches at finer scales (<1 km) and how they influence krill distribution and swarm structure. Furthermore, it is important to note that this study focused on horizontally-based spatial associations between whales and krill and did not examine the role that vertical distribution of krill plays on whale spatial distribution. This is an important component that has consequences for the energetic demands of each whale species and likely affects the diving abilities and depths at which whales feed (i.e. different species could be targeting krill at different depths).

We documented fewer sightings of Antarctic minke whales than either humpback or fin whales, which might indicate that they potentially avoid the habitat we surveyed. However, Antarctic minke whales may be under-sampled during our surveys due to their small size and low detectability (Ainley et al. 2007) or because they occur in areas we do not sample well (e.g. nearshore coastal waters; there is also no pack ice near the SSI during January). Future research could investigate these concerns by use of small boat surveys in coastal waters (Warren et al. 2009) to better understand habitat selection of Antarctic minke whales near the SSI.

The geographic persistence of hotspots exhibited by whales and krill length classes reported in this study suggests that physical features of the environment may be important in affecting their distributions (Hyrenbach et al. 2000). Among these are persistent oceanographic features like fronts, eddies, and the bathymetrically controlled circulation (Tynan 1997, 1998, Cotté & Simard 2005, Ingram et al. 2007, Michaud & Taggart 2007). For example, Ingram et al. (2007) showed that fin and common minke whales partition foraging habitat primarily due to bathymetry and hydrography in the Bay of Fundy, North Atlantic. Also in that area, Michaud & Taggart (2007) showed that North Atlantic right whales *Eubalaena glacialis* exploit a localized and recurrent feature within the Bay of Fundy that traps the copepod *Calanus finmarchicus*, a major prey item, in a narrow band accessible to them. Such habitat specificity has also been argued for some toothed whale species (Praca et al. 2009).

Bathymetrically derived retention areas are likely features that can accumulate krill within portions of the Bransfield Strait and north of Elephant Island (Wilson et al. 1999, Thompson et al. 2009). Drifter trajectories in this region show a considerable coincidence between areas where drifters are retained and the location of krill and whale hotspots. In Bransfield Strait, recirculation occurs over the deep basins (Wilson et al. 1999). Drifters (and presumably less motile animals) can be aggregated within these retention zones for a significant period of time (days to weeks; Thompson et al. 2009). North of Elephant Island, the bathymetric feature known as the Shackleton Fracture Zone deflects the flow of the ACC to the north and south, resulting in the development of a persistent eddy northeast of Elephant Island (Fig. 1). Additionally, northward flowing water exiting the Weddell Sea impinges the northeast Elephant Island shelf and is deflected to the southwest, creating very complicated hydrographic conditions including fronts and eddies (Thompson et al. 2009). Thus the influence of bathymetric features on prevailing current flow may form recurring localized retention zones that concentrate krill, providing predictable foraging grounds for whales to exploit (Croll et al. 2005).

Data limitation and recommendations

Estimation of the prey field is an important source of variability and uncertainty in modeling the spatial association of whales and krill. To date, there are 2 ways of assessing prey distribution potentially used by whales: direct sampling of prey using nets and indirect sampling using hydroacoustics. The benefit of net sampling is in measuring prey quantity, quality, and size; the drawback is coarse spatial sampling, which may miss and inadequately assess prey patch distribution. Hydroacoustic sampling has the advantage of mapping multi-scale features of horizontal and vertical prey distribution; but yields no information on prey demography. Previous studies have relied heavily on hydroacoustics to relate krill distribution and foraging whales (Piatt & Methven 1992, Reid et al. 2000, Friedlaender et al. 2006, 2009). Our study is unique in having direct assessment of krill demography coincidental with ongoing marine mammal observations over so many years. An investigation of foraging whales relative to acoustically-based estimates of krill distribution (horizontal and vertical) is required to examine the role of krill patch structure for predicting spatial interactions with whales near the SSI. Furthermore, given the dominance of biomass of *Euphausia superba* in the ecosystem, it is assumed that baleen whales here are primarily feeding on that species. We did not directly sample whale diet (e.g. stomach samples, scats), so they may consume other co-occurring euphausiids like

Thysannoessa macrura, which is found throughout the SSI region (Nordhausen 1992). Likewise, in some other areas, these 3 species of whale may feed on schooling fish that can be forced into very tightly packed aggregations by the whales. There are no such schooling species in the Antarctic Peninsula area. However, myctophids can occur in dense aggregations at depth (>100 m), but less is known about deep foraging in these species.

Our study focused on high summer and thus did not track changes in whale and krill distribution across the complete season of peak krill biomass in the region (late December to early March; Siegel 1988). Our study was restricted to 1 mo in each year, and this could bias our results because both whales and krill likely exhibit intra-seasonal movements. Given that the SSI are nearly devoid of krill prior to the spring and after the fall transition periods (Siegel 1988, Hewitt et al. 2004), there are likely shifts in whale foraging areas associated with seasonal movements of krill. Seasonal changes in krill distribution could impact the length of whale feeding seasons, potentially influencing their energy reserves available for breeding, especially if such changes are associated with size and nutritional quality of krill within feeding hotspots. Dalla Rosa et al. (2008) investigated the movement of humpback whales using satellite tags and found considerable site fidelity and repeated migratory routes throughout the Antarctic Peninsula region. The tracks of whales tagged in their study (n = 11) showed considerable overlap with the Bransfield Strait hotspots we identified in this study. Future investigations could profitably focus on how seasonal changes in krill distribution affect fine-scale movements of whales to fully understand the dynamic nature of whale–krill interactions.

There is some evidence from the literature that the humpback whales we observed over the 5 yr period were the same animals (Stevick et al. 2004). This has important implications beyond simply predicting their foraging areas. Based on photographs and natural tag return rates, Stevick et al. (2004) showed that most humpback whales in the West Antarctic Peninsula region during summer were derived from the west coast of South America. Our results indicate that the sighting rate, numbers, and location of humpback whales did not vary significantly over the 5 yr period. If these are the same individuals each year, then knowledge of their summer foraging grounds may provide an opportunity to better understand the reproductive dynamics of humpback whales. Given the likely decline in krill biomass associated with diminished sea-ice and climate warming (Loeb et al. 1997, Atkinson et al. 2004), the reproductive success of humpbacks may be affected (Croxall et al. 1999, Leaper et al. 2006). This has been demonstrated for calving success of

southern right whales *Eubalaena australis*, which is related to sea surface temperature anomalies (a proxy for krill availability) around South Georgia (Leaper et al. 2006). Such a hypothesis could be tested by monitoring humpback breeding success on their South American breeding grounds in relation to changes in krill populations on summer feeding grounds near the SSI.

Implications for conservation and management of whales and krill

The spatial structure of whale foraging grounds near the SSI has significant implications for management of the Antarctic krill fishery (Marin & Delgado 2001, Jones & Ramm 2004) and conservation of baleen whales (Mori & Butterworth 2004, Kaschner et al. 2006). The krill fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Historically, the largest harvest occurs in the southwest Atlantic in the vicinity of the SSI and South Orkney Islands (Jones & Ramm 2004). Specifically, historical krill catches have been associated with the area northeast of Elephant Island, coincident with the feeding areas of fin whales. More recently, the fishery has expanded into Bransfield Strait, where humpback whales feed. The cause for this shift in fishing effort has not been established but may result from changes in krill distribution (Kawaguchi et al. 2006). Nevertheless, increased fishing activity may lead to an increase in spatial overlap between fishing vessels and whales near the SSI.

CCAMLR has proposed partitioning the southwest Atlantic into 15 small-scale management units (SSMU) as a mechanism to relocate krill harvesting activities away from land-based predator reproductive sites (Hewitt et al. 2004). Within the SSI area, 8 SSMUs have been designated within Bransfield Strait and around Elephant Island. A specific consequence of this management scheme is to force the krill fishery into offshore oceanic waters during the reproductive period for land-based predators. This could lead to increased interactions between fin whales and krill trawlers. Despite the proposed SSMU concept, recent movements of the krill fishery into Bransfield Strait may also increase interactions between humpback whales and fishing vessels. Some CCAMLR members (SC-CCAMLR 2008) have argued that the proposed SSMU management of the krill fishery is still immature, placing in jeopardy the ability to regulate the krill fishery in order to minimize impacts on land-based predators. The results of our study clearly demonstrate that intensified exploitation of krill within Bransfield Strait and north of Elephant Island will likely result in increased

interactions between krill fisheries and baleen whales. Given that humpback and fin whales consume between 3 and 4 % of their body weight daily (Reilly et al. 2004), the impacts are likely to become measurable as whale populations increase towards pre-exploitation levels, the krill fishery expands, and krill stocks remain depressed or decline even more with climate warming (Atkinson et al. 2004).

Given the dramatic environmental changes in the Southern Ocean, either through human exploitation of whales (Tynan 1998), climate-driven changes in the ecosystem (de la Mare 1997, Moline et al. 2004, Clarke et al. 2007), and documented decline of krill populations (Atkinson et al. 2004) and the findings reported here, this area of the Southern Ocean should be carefully monitored. Data should continue to be collected to inform management about potential interactions between the krill fishery and whales. Our study showed that there are clear spatial associations between krill demographic patterns and foraging grounds of baleen whales in a region where the krill fishery historically operates. Ultimately, understanding the spatial ecology and behavior of whales will assist in better prediction of whale interactions with krill fisheries. This study presents a first step in making this a reality.

LITERATURE CITED

Ainley DG, Dugger KM, Toniolo V, Gaffney I (2007) Cetacean occurrence patterns in the Amundsen and southern Bellingshausen Sea sector, Southern Ocean. Mar Mamm Sci 23:287–305

Anselin L, Syabri I, Kho Y (2006) GeoDa: an introduction to spatial data analysis. Geogr Anal 38:5–22

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432:100–103

Buckland ST, Anderson DR, Burnham KP, Laake JL (1993) Distance sampling: estimating abundance of biological populations. Chapman & Hall, London

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Chapman EW, Hoffman EE, Patterson DL, Fraser WR (2009) The effects of variability in Antarctic krill (*Euphausia superba*) spawning behavior and sex/maturity stage distribution on Adélie penguin (*Pygoscelis adeliae*) chick growth: a modeling study. Deep-Sea Res II 57:543–558

Clarke A, Murphy EJ, Meredith MP, King JC, Peck LS, Barnes DKA, Smith RC (2007) Climate change and the marine ecosystem of the western Antarctic Peninsula. Philos Trans R Soc Lond B Biol Sci 362:149–166

Cotté C, Simard Y (2005) Formation of dense krill patches under tidal forcing at whale feeding hot spots in the St. Lawrence Estuary. Mar Ecol Prog Ser 288:199–210

Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. Mar Ecol Prog Ser 289:117–130

Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Mar Ecol Prog Ser 177: 115–131

Dalla Rosa L, Secchi ER, Maia YG, Zerbini AN, Heide-Jørgensen MP (2008) Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula. Polar Biol 31:771–781

de la Mare WK (1997) Abrupt mid-twentieth century decline in Antarctic sea ice extent from whaling records. Nature 389:57–60

ESRI (Environmental Systems Research Institute) (2007) ArcGIS geostatistical analyst. ESRI, Redlands, CA

Fach BA, Hofmann EE, Murphy EJ (2002) Modeling studies of Antarctic krill *Euphausia superba* survival during transport across the Scotia Sea. Mar Ecol Prog Ser 231:187–203

Färber-Lorda J, Gaudy R, Mayzaud P (2009) Elemental composition, biochemical composition and caloric value of Antarctic krill: implications in energetics and carbon balances. J Mar Syst 78:518–524

Ferguson JWH, Bester MN (2002) The treatment of spatial autocorrelation in biological surveys: the case of line transect surveys. Antarct Sci 14:115–122

Fiedler PC, Reilly SB, Hewitt RP, Demer DA and others (1998) Blue whale habitat and prey in the California Channel Islands. Deep-Sea Res II 45(8–9):1781–1801

Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. Mar Ecol Prog Ser 317:297–310

Friedlaender AS, Fraser WR, Patterson D, Qian SS, Halpin PN (2008) The effects of prey demography on humpback whale (*Megaptera novaeangliae*) abundance around Anvers Island, Antarctica. Polar Biol 31:1217–1224

Friedlaender AS, Lawson GL, Halpin PN (2009) Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. Mar Mamm Sci 25:402–415

Gaskin DE (1982) The ecology of whales and dolphins. Heinemann, London

Getis A, Ord JK (1992) The analysis of spatial association by use of distance statistics. Geogr Anal 24:189–206

Gille ST (2002) Warming of the Southern Ocean since the 1950s. Science 295:1275–1277

Goldbogen JA, Calambokidis J, Shadwick RE, Oleson RM, McDonald MA, Hildebrand JA (2006) Kinematics of foraging dives and lunge-feeding in fin whales. J Exp Biol 209:1231–1244

Heinemann D (1981) A range finder for pelagic bird censusing. J Wildl Manag 45:489–493

Hewitt RP, Demer DA (1993) Dispersion and abundance of Antarctic krill in the vicinity of Elephant Island in the 1992 austral summer. Mar Ecol Prog Ser 99:29–39

Hewitt RP, Watters G, Trathan PN, Croxall JP and others (2004) Options for allocating the precautionary catch limit of krill among small-scale management units in the Scotia Sea. CCAMLR Sci 11:81–97

Hill SL, Reid K, Thorpe SE, Hinke J, Watters GM (2007) A
compilation of parameters for ecosystem dynamics models
of the Scotia Sea–Antarctic Peninsula region. CCAMLR
Sci 14:1–25

Hyrenbach KD, Forney KA, Dayton PK (2000) Marine pro-
tected areas and ocean basin management. Aquat Con-
serv 10:437–458

Ichii T, Bengston JL, Boveng PL, Takao Y and others (2007)
Provisioning strategies of Antarctic fur seals and chinstrap
penguins produce different responses to distribution of
common prey and habitat. Mar Ecol Prog Ser 344:277–297

Ingram S, Walshe L, Johnston D, Rogan E (2007) Habitat par-
titioning and the influence of benthic topography and
oceanography of fin and minke whales in the Bay of
Fundy, Canada. J Mar Biol Assoc UK 87:149–156

Johnston JH, Wollman AA (1984) The humpback whale,
Megaptera novaeangliae. Mar Fish Rev 46:30–37

Jones CD, Ramm DC (2004) The commercial harvest of krill in
the southwest Atlantic before and during the CCAMLR
2000 Survey. Deep-Sea Res II 51:1421–1434

Kasamatsu F, Ensor P, Joyce GG (1998) Clustering and aggre-
gations of minke whales in the Antarctic feeding grounds.
Mar Ecol Prog Ser 168:1–11

Kaschner K, Watson R, Trites AW, Pauly D (2006) Mapping
worldwide distributions of marine mammals using a rela-
tive environmental suitability (RES) model. Mar Ecol Prog
Ser 316:285–310

Kawaguchi S, Nicol S, Taki K, Naganobu M (2006) Fishing
ground selection in the Antarctic krill fishery: trends in
patterns across years, seasons and nations. CCAMLR Sci
13:117–141

Laws RM (1977) Seals and whales of the Southern Ocean.
Philos Trans R Soc Lond B Biol Sci 279:81–96

Leaper R, Cooke J, Trathan P, Reid K, Rowntree V, Payne R
(2006) Global climate drives southern right whale (*Eubal-
aena australis*) population dynamics. Biol Lett 2:289–292

Legendre P, Legendre L (1998) Numerical ecology. Elsevier
Science, Amsterdam

Loeb V, Siegel V, Holm-Hansen O, Hewitt R, Fraser W, Trivel-
piece W, Trivelpiece S (1997) Effects of sea-ice extent and
krill or salp abundance on the Antarctic food web. Nature
387:897–900

Mackintosh NA (1965) The stocks of whales. Fishing News
Books, London

Marin VH, Delgado LE (2001) A spatially explicit model of the
Antarctic krill fishery off the South Shetland Islands. Ecol
Appl 11:1235–1248

Meredith MP, King JC (2005) Rapid climate change in the
ocean west of the Antarctic Peninsula during the second
half of the 20th century. Geophys Res Lett 32:L09604,
doi:10.1029/2004GL022286

Michaud J, Taggart CT (2007) Lipid and gross energy content
of North Atlantic right whale food *Calanus finmarchicus* in
the Bay of Fundy. Endang Species Res 3:77–94

Moline MA, Claustere H, Frazer TK, Schofield O, Vernet M
(2004) Alteration of the food web along the Antarctic
Peninsula in response to a regional warming trend. Glob
Change Biol 10:1973–1980

Mori M, Butterworth DS (2004) Consideration of multispecies
interactions in the Antarctic: a preliminary model of the
minke whale–blue whale–krill interaction. S Afr J Mar Sci
26:245–259

Murase H, Matsuoka K, Ichii T, Nishiwaki S (2002) Relation-
ship between the distribution of euphausiids and baleen
whales in the Antarctic (35° E–145° W). Polar Biol 25:
135–145

Murphy EJ, Thorpe SE, Watkins JL, Hewitt R (2004) Modeling

the krill transport pathways in the Scotia Sea: spatial and
environmental connections generating the seasonal distri-
bution of krill. Deep-Sea Res II 51:1435–1456

Nordhausen W (1992) Distribution and growth of larval and
adult *Thysanoessa macrura* (Euphasiacea) in the Brans-
field Strait region, Antarctica. Mar Ecol Prog Ser 83:
185–196

Ord JK, Getis A (1995) Local spatial autocorrelation statistics:
distributional issues and an application. Geogr Anal
27:286–306

Orsi AH, Whitworth T, Nowlin WD (1995) On the meridional
extent and fronts of the Antarctic Circumpolar Current.
Deep-Sea Res I 42:641–673

Panigada S, Zanardelli M, Canese S, Jahoda M (1999) How
deep can baleen whales dive? Mar Ecol Prog Ser 187:
309–311

Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet com-
position and trophic levels of marine mammals. ICES J
Mar Sci 55:467–481

Piatt JF, Methven DA (1992) Threshold foraging behavior of
baleen whales. Mar Ecol Prog Ser 84:205–219

Piatt JF, Wetzel J, Bell K, DeGange AR and others (2006) Pre-
dictable hotspots and foraging habitat of the endangered
short-tailed albatross (*Phoebastria albatrus*) in the North
Pacific: implications for conservation. Deep-Sea Res II 53:
387–398

Praca E, Gannier G, Das K, Laran S (2009) Modelling the
habitat suitability of cetaceans: example of the sperm
whale in the Mediterranean Sea. Deep-Sea Res II 56:
648–657

Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD and
others (2006) Techniques for cetacean–habitat modeling.
Mar Ecol Prog Ser 310:271–295

Reid K, Brierly AS, Nevitt GA (2000) An initial examina-
tion of relationships between the distribution of whales
and Antarctic krill, *Euphausia superb*a at South Georgia.
J Cetacean Res Manag 2:143–149

Reid K, Sims M, White RW, Gillon K (2004) Spatial distribution
of predator/prey interactions in the Scotia Sea: implica-
tions for measuring predator/fisheries overlap. Deep-Sea
Res II 51:1383–1396

Reilly S, Hedly S, Borberg J, Hewitt R, Thiele D, Watkins J,
Naganobu M (2004) Biomass and energy transfer to
baleen whales in the South Atlantic sector of the Southern
Ocean. Deep-Sea Res II 51:1397–1409

Reiss CS, Cossio AM, Loeb V, Demer DA (2008) Variations in
the biomass of Antarctic krill (*Euphausia superba*) around
the South Shetland Islands, 1996–2006. ICES J Mar Sci
65:497–508

Santora JA, Reiss CS, Cossio AC, Veit RR (2009) Interannual
spatial variability of krill influences seabird foraging
behavior near Elephant Island, Antarctica. Fish Oceanogr
18:20–35

SC-CCAMLR (Scientific Committee-Commission for the Con-
servation of Antarctic Marine Living Resources) (2008)
Report of the twenty-seventh meeting of the Scientific
Committee. CCAMLR Document SC-CCAMLR-XXVII.
CCAMLR, Hobart, TAS

Siegel V (1988) A concept of seasonal variation of krill
(*Euphausia superba*) distribution and abundance west of
the Antarctic Peninsula. In: Sahrhage D (ed) Antarctic
Ocean and resources variability. Springer-Verlag, Berlin,
p 219–230

Siegel V (2005) Distribution and population dynamics of
Euphausia superba: summary of recent findings. Polar Biol
29:1–22

Siegel V, Loeb V (1995) Recruitment of Antarctic krill *Euphau-*

sia superba and possible causes for its variability. Mar Ecol Prog Ser 123:45–56

Stevick PT, Aguayo A, Allen J, Avila IC and others (2004) Migrations of individually identified humpback whales between the Antarctic Peninsula and South America. J Cetacean Res Manag 6:109–114

Swenson NG, Howard DJ (2005) Clustering of contact zones, hybrid zones, and phylogeographic breaks in North America. Am Nat 166:581–591

Tarling GA, Klevjer T, Fielding S, Watkins J and others (2009) Variability and predictability of Antarctic krill swarm structure. Deep-Sea Res I 56:1994–2012

Thiele D, Chester ET, Moore SE, Sirovic A, Hildebrand JA, Friedlaender AS (2004) Seasonal variability in whales encounter in the Western Antarctic Peninsula. Deep-Sea Res II 51:2311–2325

Thompson AF, Heywood KJ, Thorpe SE, Renner AHH, Trasviña A (2009) Surface circulation at the tip of the Antarctic Peninsula from drifters. J Phys Oceanogr 39:3–26

Tobin PC, Bjørnstad ON (2003) Spatial dynamics and cross-correlation in a transient predator–prey system. J Anim Ecol 72:460–467

Trites AW, Christensen V, Pauly D (1997) Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. J Northwest Atl Fish Sci 22:173–187

Tynan CT (1997) Cetacean distributions and oceanographic features near the Kerguelen Plateau. Geophys Res Lett 24:2793–2796

Tynan CT (1998) Ecological importance of the Southern Boundary of the Antarctic Circumpolar Current. Nature 392:708–710

Warren JD, Santora JA, Demer DA (2009) Submesoscale distribution of Antarctic krill and its avian and pinniped predators before and after a near gale. Mar Biol 156:479–491

Watkins WA, Schevill WE (1979) Aerial observation of feeding behavior in four baleen whales: *Eubalaena glacialis, Balaenoptera borealis, Megaptera novaeangliae*, and *Balaenoptera physalus*. J Mammal 60:155–163

Whitehead HP, Carlson C (1988) Social behaviour of feeding finback whales off Newfoundland: comparisons with the sympatric humpback whale. Can J Zool 66:217–221

Williams R, Hedley SL, Hammond PS (2006) Modeling distribution and abundance of Antarctic whales using ships of opportunity. Ecol Soc 11:1. Available at: http://www.ecologyandsociety.org/vol11/iss1/art1/

Wilson C, Klinkhammer GP, Chin CS (1999) Hydrography within the central and east basins of the Bransfield Strait, Antarctica. J Phys Oceanogr 29:465–479

Woodward BL, Winn JP, Fish FE (2006) Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. J Morphol 267:1284–1294

Yen PPW, Sydeman WJ, Bograd SJ, Hyrenbach KD (2006) Spring-time distributions of migratory marine birds in the southern California Current: oceanic eddy associations and coastal habitat hotspots over 17 years. Deep-Sea Res II 53:399–418

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, Upper Saddle River, NJ

Zerbini AN, Andriolo A, da Rocha JM, Simões-Lopes PC and others (2004) Winter distribution and abundance of humpback whales (*Megaptera novaeangliae*) off North-eastern Brazil. J Cetacean Res Manag 6:101–107

Zerbini AN, Andriolo A, Heide-Jørgensen MP, Pizzorno JL and others (2006) Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. Mar Ecol Prog Ser 313:295–304