An initial examination of relationships between the distribution of whales and Antarctic krill *Euphausia superba* at South Georgia

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ABSTRACT

The distribution of whales and krill in two survey boxes north of South Georgia was examined by comparing sightings and underway acoustic data collected as part of a multi-disciplinary research cruise carried out during January/February 1998. A total of 222 cetaceans of 10 species was recorded with the southern right whale (*Eubalaena glacialis*) and humpback whale (*Megaptera novaeangliae*) the two most frequent. The largest aggregation of cetaceans (21 southern right whales, 16 fin whales (*Balaenoptera physalus*), 4 sei whales (*B. borealis*), 1 humpback whale and 8 hourglass dolphins (*Lagenorhynchus cruciger*) occurred close to the largest single aggregation of krill. The level of association between baleen whales and krill was examined at a number of spatial scales. There was a positive relationship between whale abundance and mean krill density at the largest spatial scale examined (80×100km). At progressively smaller scales the relationship weakened, due mainly to the increased frequency of areas of high krill density where whales were not recorded. In particular, whales were absent from inshore areas (up to 300m depth) that had higher mean krill densities compared with areas where whales were recorded. To thoroughly compare krill and whale distribution, particularly at smaller scales, will require information on krill swarm structure and density, as well as more information on the behaviour and feeding requirements of whales. Such information may also be crucial to understanding the role of scale-dependence in potential interspecies competition among krill-feeding marine predators.

KEYWORDS: WHALES; FEEDING; EUPHAUSIIDS; SOUTH GEORGIA; ANTARCTIC; HABITAT

INTRODUCTION

Most Southern Hemisphere mysticete whale species undertake extensive latitudinal migrations from their tropical breeding grounds to feed in the more productive waters south of the Antarctic Polar Front in summer (Brown and Lockyer, 1984; de la Mare, 1997; Tynan, 1998) where Antarctic krill (*Euphausia superba*) is a key food resource (e.g. Mackintosh, 1965). At the island of South Georgia (54.5°S, 37°W), large breeding colonies of krill-dependent seals and seabirds attest to a usually high abundance of krill in the surrounding waters (Croxall and Prince, 1980; Croxall *et al.*, 1984; Boyd, 1993); historically this region was an important feeding ground for whales (Hardy, 1967). From 1904 to 1965, however, South Georgia was the focus of a commercial whaling operation that killed over 175,000 animals, and now whale numbers there, as throughout the Southern Ocean as a whole, are much reduced (perhaps to about 35% of initial numbers, Laws, 1977).

Environmental changes in Antarctica (de la Mare, 1997) and expansions in populations of other krill predators, probably in response to the so-called 'krill surplus' left following the removal of whales (Laws, 1985; Murphy *et al.*, 1988; Croxall, 1992 but see also Fraser *et al.*, 1992) may affect the rate of recovery and the equilibrium population level of some whale species (Murphy and King, 1997). Since whales have individual energy requirements associated with their large size (e.g. Brodie *et al.*, 1978), there is the potential for some competition for krill between whales and other krill dependent species even with whale populations considerably below pre-exploitation levels. The form of this competition would be highly dependent, *inter alia*, upon the scales over which different species (and fisheries) operate, especially when considering pelagic predators (whales) and land-based species (e.g. penguins and seals) which are constrained to return to a central place to feed their young (Murphy *et al.*, 1988). As a result of their relatively low numbers and paucity of distributional data, whales have previously been excluded from analysis of the role of krill-dependent predators in the South Georgia marine environment (e.g. Croxall *et al.*, 1984; 1985). However, given their large *per capita* food requirements, whales have considerable potential for impact on local prey resources. Therefore, the spatial distribution of resource utilisation by whales around South Georgia may have important implications for both competition with other krill predators and for fisheries management.

The aims of this paper are to use data collected as part of a multi-disciplinary cruise held during January/February 1998 to begin to: (1) describe the species composition and distribution of cetaceans around South Georgia; (2) compare their relative density in relation to krill distribution; and (3) examine how this relationship varies over a range of spatial scales.

MATERIALS AND METHODS

Survey design

Each year since 1995, British Antarctic Survey has conducted a series of detailed biological and oceanographic observations to the north of South Georgia and in particular have used acoustic techniques to estimate krill biomass. The surveys at South Georgia are preceded by a large-scale transect (Trathan *et al.*, 1997) from northeast of the Falkland Islands, across the Maurice Ewing Bank and the Antarctic Polar Front to the northwest of South Georgia. At South Georgia, survey effort is concentrated within two defined 80×100km boxes that span the continental shelf break to the northeast and northwest of the island. Within each of these boxes, 10 randomly-spaced parallel transects are surveyed during daylight hours over a five day period (2 transects per

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day run in opposite directions). The surveys are conducted from RRS *James Clark Ross*, and in 1998 took place between 17 January and 5 February.

Estimating krill density

A calibrated hull-mounted *Simrad* EK500 scientific echosounder operating at 38 (7° beam angle) and 120kHz (9° beam angle) was used to detect krill in the top 250m while underway along each survey transect. Echo energy was integrated over 100s intervals which, at a nominal survey speed of 10 knots, provided mean volume backscattering strength data (MVBS) with a spatial resolution along the transect of approximately 0.5km. Antarctic krill were distinguished from other acoustic targets on the basis of the difference in echo intensity at the two echosounder frequencies, krill being identified as those targets where $MVBS_{120kHz}$-$MVBS_{38kHz}$ fell between 2 and 12dB (Madureira *et al.*, 1993). Krill density (g m^{-2} wet weight) per 0.5km integration interval was calculated by scaling the 120kHz echo intensity by a Target Strength (TS). Acoustic data collection and processing was performed using custom-written software (Socha *et al.*, 1996; Watkins and Brierley, 1996) on a Unix workstation.

Whale distribution

Marine predator observations were conducted by two observers from the bridge (height of eye 17m above sea level) on the large scale transect and along each of the 10 transects within the South Georgia survey boxes. Primary observations of all predator species (birds and seals) were made in a 100m×100m box located 100m directly ahead of the vessel. In addition, all cetaceans (species and numbers) observed in a 180° arc forward of the vessel up to about 2.6km (Leaper *et al.*, 1999) were recorded and included in this analysis. As sighting angle and distance were not recorded, standard line-transect estimates could not be calculated (e.g. see Hiby and Hammond, 1989) and thus estimates of cetacean density are expressed as number of whales per unit vessel track. Observations were entered into a hand-held computer that automatically appended a time (synchronised to the ship's time). This was used to provide a position for each observation through reference to the on-board GPS. Estimation of cetacean density was consistent between transects because survey effort was the same on all transects within the two core boxes and the same two observers recorded all cetacean sightings. The likelihood of sighting a cetacean is influenced *inter alia* by sea state (which is primarily wind dependant). The mean wind speed (corrected for the movement of the ship) was therefore calculated for each transect as one way of attempting to examine potential biases in the sightability of cetaceans.

Relationships between whales and krill

The relationship between baleen whale numbers and krill density was examined at four scales of increasingly fine spatial resolution (see Fig. 3) using regression analysis.

Scale 1. By survey box

The total number of whales observed on transect in each 80×100km survey box was compared with the mean krill density for that box. Mean krill density for each transect was calculated as the mean of all 100s intervals along it, and density for each survey box was calculated as the mean of all ten individual transects surveyed within that box (Jolly and Hampton, 1990; Brierley *et al.*, 1997).

*Scale 2. By day (80km ×*ca *20km)*

Krill density was enumerated by day (as the mean of two 80km transects) and compared to the total number of whales observed along transect that day.

*Scale 3. By depth zone by day (*ca *40km ×* ca *20km)*

Krill density and whale abundance from each day's transect pair were partitioned with reference to bathymetry into on- and off-shelf components. Since the survey boxes were centred on the shelf break, each box nominally included equal on- and off-shelf areas. However, because the shelf break meanders, the two areas are not actually equal. Data collected from water shallower than 300m were considered as on-shelf, whereas data from water deeper than 500m were designated off-shelf: data from the zone between 300 and 500m (typically less than 7.5km along transect) were considered to lie within a transition zone, and were discarded (in practice there was only a single baleen whale in this zone).

*Scale 4. By depth zone by transect (*ca *40km ×* ca *5km)*

Krill density and whale abundance were compared within individual transects after each transect had been divided into on- and off-shelf components (following the same criteria as for scale 3).

Adjusted r^2 (r^2_{adj}) values were calculated for log-log relationships between total number of baleen whales and the mean krill density within each cell at each scale (a cell being a box, transect pair, part transect pair or part transect). Adjusted r^2 was used because it is independent of sample size which varied here as a function of the scale under examination.

RESULTS

Whale sightings

A total of 222 cetaceans from 10 species was recorded in 53 sightings during approximately 90 hours of observations throughout the cruise (see Table 1). The single largest aggregation of cetaceans occurred in the extreme south east of the area covered by this cruise and involved 21 southern right whales (*Eubalaena australis*), 16 fin whales (*Balaenoptera physalus*), 4 sei whales (*B. borealis*), 1 humpback whale (*Megaptera novaeangliae*) and 8 hourglass dolphins (*Lagenorhynchus cruciger*).

The largest single sighting comprised a pod of approximately 70 long-finned pilot whales (*Globicephala melas*) which, along with all sperm whale (*Physeter macrocephalus*) observations, was made near the Antarctic Polar Frontal Zone. There were three encounters with odontocetes in each survey box, all except one of which were in the offshore region (Fig 1).

The most frequently observed mysticete species were the southern right whale (47 individuals in 19 encounters) and the humpback whale (20 individuals, 8 encounters). Sixteen fin whales, 8 sei whales and 4 minke whales (*Balaenoptera acutorostrata*) were also seen. Most of the southern right whales were recorded offshore in the eastern survey box, although seven individuals were seen close inshore near the north west coast of the island (outside the defined box survey areas) (Fig. 2).

The sea state was generally between Beaufort scale 3-5 and there was no difference between survey boxes (one-way ANOVA $F_{1,18} = 0.82$ *n.s.*); the number of whales recorded on each transect was independent of wind speed/sea state (ANOVA $F_{1,18} = 1.19$ *n.s.*).

Table 1

Summary of cetacean sightings near South Georgia from RRS *James Clarke Ross* during the period 17 January to 5 February 1998.

Species	Total number	Number of encounters	Max. group size
Southern right whale, *Eubalaena glacialis*	47	19	15
Minke whale, *Balaenoptera acutorostrata*	4	4	1
Sei whale, *Balaenoptera borealis*	8	3	4
Fin whale, *Balaenoptera physalus*	16	1	16
Fin/sei whale, *Balaenoptera* spp.	3	2	2
Humpback whale, *Megaptera novaeangliae*	20	8	7
Unidentified baleen whale, *Balaenopteridae* spp.	7	5	2
Sperm whale, *Physeter macrocephalus*	5	2	4
Hourglass dolphin, *Lagenorhynchus cruciger*	27	4	8
Killer whale, *Orcinus orca*	8	2	7
Long-finned pilot whale, *Globicephala melas*	70	1	70
Southern bottle-nosed whale, *Hyperoodon planifrons*	7	2	6
Total	222	53	

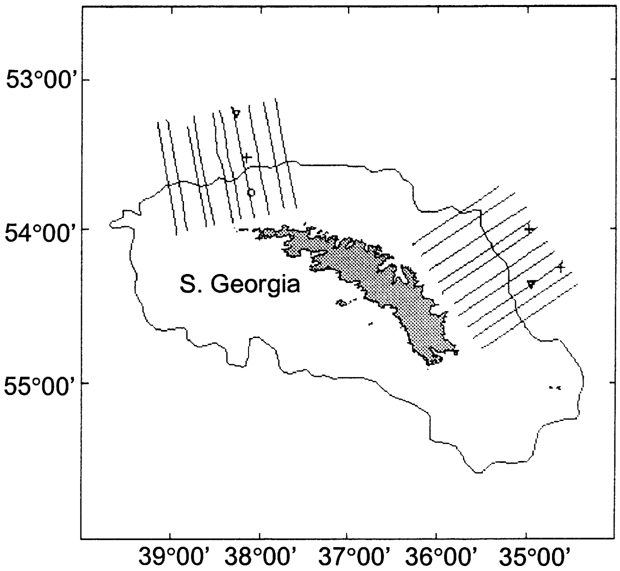

Fig. 1. The distribution of sightings of killer whale (∇), Southern bottle-nosed whale (+) and hourglass dolphin (○) around South Georgia during January and February 1998. The 500m isobath is shown in each survey box.

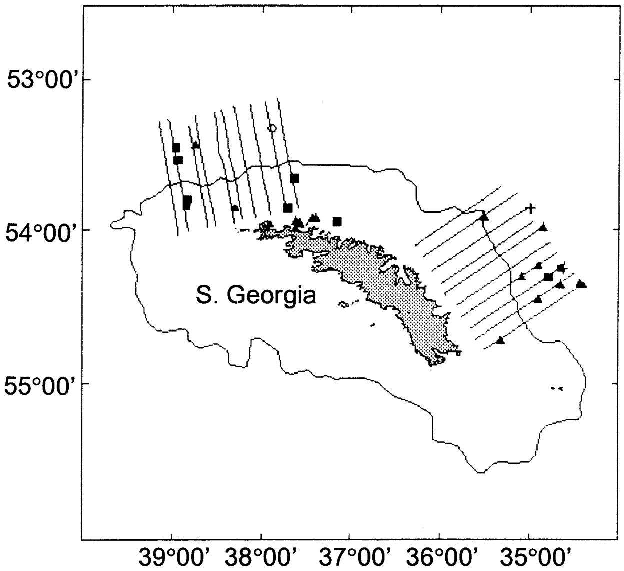

Fig. 2. The distribution of sightings of fin whale (∇), sei whale (+), minke whale (○), humpback whale (■) and southern right whale (▲) around South Georgia during January and February 1998. The 500m isobath is shown in each survey box.

Krill density

The mean krill density in the eastern survey box (151.0 g m^{-2}, SD = 29.7) was significantly greater than in the west (21.4 g m^{-2}, SD = 4.2) and krill were generally more abundant on-shelf than off-shelf (Table 2). The Table also reveals a wide range of densities within transects.

Relationship between baleen whales and krill

At the largest scale (80×100km), the distribution of whales and krill was directly related, with the greater density of whales (0.09 whales km^{-1}) in the eastern survey area where krill density was greatest. In contrast, only 0.03 whales km^{-1} were recorded in the western box where mean krill density was significantly lower. Since there were significant differences between mean krill densities in the eastern and western survey areas, all further comparisons at finer scales were made only within boxes. On a day by day (80×20km) basis (scale 2, $n = 5$), there was a positive relationship between krill and whale distribution within both survey boxes, with more whales recorded on those days when more krill were detected acoustically. The relationship at this scale was stronger in the western box ($r^2_{adj} = 55.0$) than in the eastern box ($r^2_{adj} = 18.6$; Fig. 3a). At scale 3 (40×20km, $n = 10$), in the western box the highest whale numbers occurred in the inshore regions at either end of the box and these coincided with the highest krill densities ($r^2_{adj} = 12.6$);

Table 2

Mean acoustic estimate of krill density (g m^{-2}) on the inshore and offshore region of each core box transect. See methods for definition of krill density and division of transect into onshore and offshore components.

	West			East	
Transect	Onshore	Offshore	Transect	Onshore	Offshore
1	103.0	3.4	1	127.8	89.0
2	94.2	2.7	2	156.6	161.5
3	27.9	5.6	3	106.1	51.4
4	10.7	4.6	4	73.1	85.3
5	8.1	5.4	5	251.6	125.4
6	41.0	3.3	6	417.4	69.2
7	18.3	2.7	7	145.4	115.2
8	31.1	1.9	8	198.4	497.6
9	86.0	2.2	9	97.7	52.5
10	87.5	7.0	10	133.5	12.9

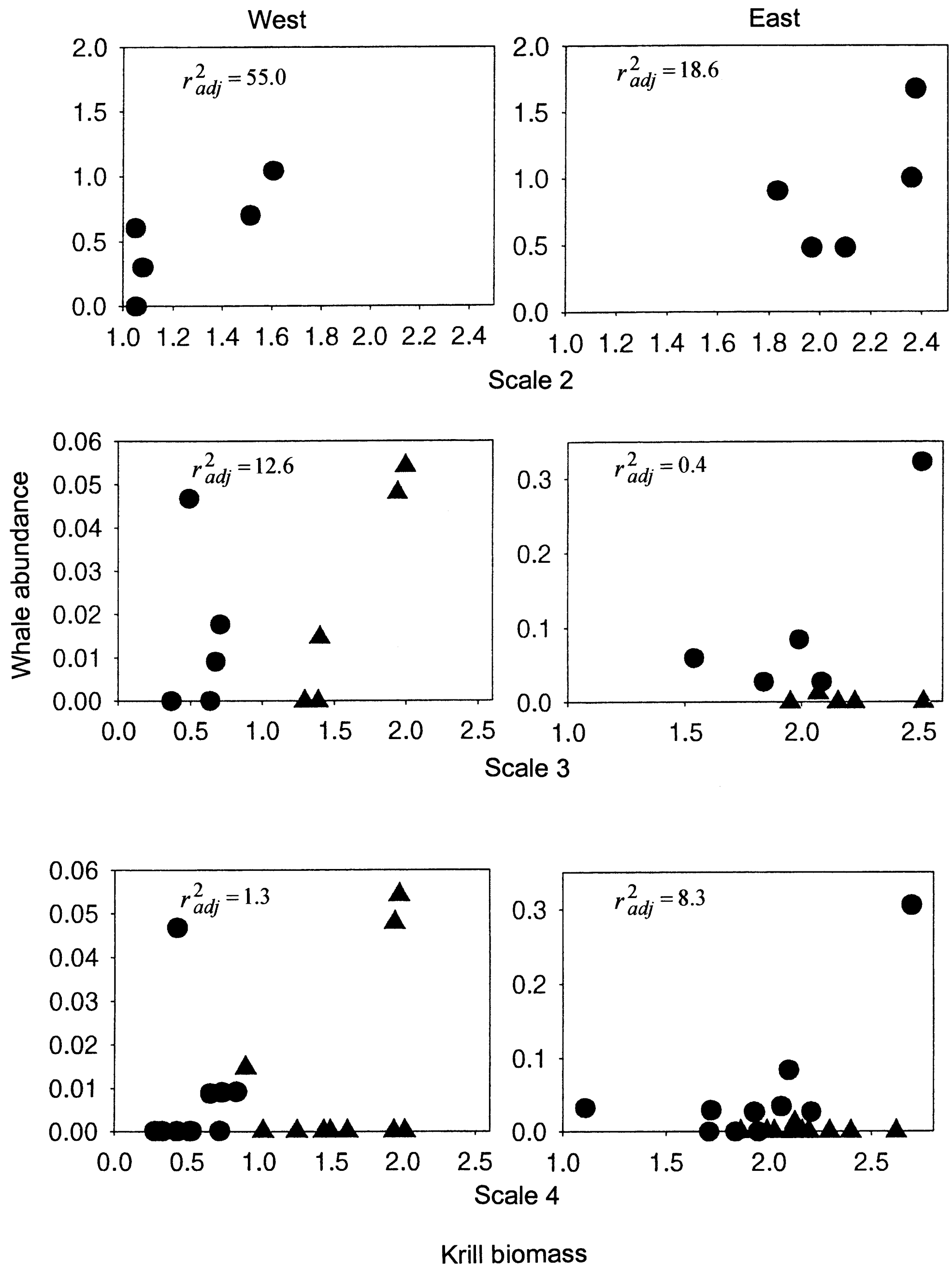

Fig. 3. The log-log relationship between krill biomass and whales at different spatial scales, see methods for definition of scales, at scales 3 and 4; ▲ denotes onshore, ● offshore.

in the east, although whale and krill maxima coincided, there were some large concentrations of krill inshore around which no whales were recorded, and the relationship was much weaker ($r^2_{adj} = 0.4$; Fig. 3b). At the smallest (40×5km) scale (4, $n = 20$) the largest whale numbers coincided with the highest krill densities in both boxes, however, there was an increased number of cells in which krill biomass was relatively high yet no whales were recorded. As a consequence, the strengths of correlation between whale count and krill density were further reduced at this fine scale in the west ($r^2_{adj} = 1.3$) although there was a slightly improved relationship in the east ($r^2_{adj} = 8.3$; Fig. 3c).

DISCUSSION

General distribution

There are few data available on whale numbers and distribution from South Georgia other than those associated with the whaling period. Comparison between species composition from this small-scale survey and other data sources, such as the International Whaling Commission/International Decade of Cetacean Research cruises which concentrate effort in the marginal ice-zone (Punt *et al.*, 1997), are limited by differences in habitat, timing (over decades), season, location and duration. In recent years, Moore *et al.* (1999) also found the southern right whale to be the most frequently encountered species during a cetacean survey around South Georgia in February 1997.

Data limitations

One potential problem with surveys designed to record sightings of a variety of predators is that, particularly in areas of high density of one species/predator type (e.g. seabirds), sightings of others (e.g. large whales in a different region of the search area) may be missed. However an examination of this issue by Leaper *et al.* (1999), who compared the results of cetacean sightings from dedicated cetacean observers with simultaneous observations from the multi-species predator observers used in this study, suggested that the cetacean observations made by the 'predator' observers were suitable for analysis of relative abundance and distribution.

Practical limitations on this multi-disciplinary survey precluded the collection of standard line-transect data. Such data, particularly if used in conjunction with newly-developed spatial modelling approaches (e.g. Hedley *et al.*, 1999), would provide a more powerful tool for examining relationships between the distribution of predators and their prey. Where possible, future studies should utilise this methodology.

A general difficulty in comparing the sighting and krill abundance data is that the latter are essentially collected in a 'cone' directly along the trackline. The cetacean sightings may thus be some distance (up to 2-3km) away from the direct density estimates of krill, which may be problematic if the distribution of krill is highly patchy. The range in krill densities along individual tracklines shown in Table 2 shows that this requires further investigation if detailed small-scale comparisons of krill density and predators are to be made.

Relationships at various scales

At the largest scale, observations of more baleen whales in the survey box where krill density was highest conforms to basic expectations that predator distribution will be linked directly to prey abundance (Stephens and Krebs, 1986; Tynan, 1998). This has been found in several areas of the world. For example, Fiedler *et al.* (1998) noted the importance of the distribution of two euphausiid species to the distribution of blue whales in the California Channel Islands. Piatt and Methven (1992) found a strong correlation between seasonal changes in capelin (*Mallotus villosus*) density and baleen whale numbers over several years in a relatively large-scale coastal system in Newfoundland. Similar to our results, Kann and Wishner (1995), working in the Gulf of Maine (northwestern Atlantic), found high numbers of North Atlantic right whales (*Eubalaena glacialis*) in areas of high biomass of their major prey item, the copepod (*Calanus finmarchicus*), although there were also areas of similarly high copepod biomass where whales were not present. These and a number of other studies suggest that at fairly large spatio-temporal scales, a positive relationship between whales and their prey is relatively easy to detect.

However, although the relationship between whale numbers and krill density remained positive in both survey boxes over all scales examined (with the largest whale numbers generally occurring in the regions of highest krill density) in our analysis the overall strength of the relationships decreased with increasing spatial resolution.

A similar pattern of decreasing correlation with increasing spatial resolution was also found in a large scale study of krill and two dependent krill predators, Antarctic fur seals (*Arctocephalus gazella*) and macaroni penguins (*Eudyptes chrysolophus*), around South Georgia (Hunt *et al.*, 1992); the maximum level of correlation occurred at different spatial scales and was higher for macaroni penguins ($r = 0.8$) than for Antarctic fur seals ($r = 0.52$).

It is, in fact, generally more difficult to detect spatial coherence between predators and their prey at smaller scales (Ritchie, 1998), especially in dynamic marine ecosystems (e.g. Schneider and Piatt, 1986; Hunt *et al.*, 1992; Veit *et al.*, 1993).

The increased frequency of cells containing relatively high mean krill biomass but no whales at increasingly fine spatial resolution may simply be a function of the relative differences in the numbers and distribution of krill and whales. However, if this was the complete explanation then one would expect the spatial distribution of these high krill/no whales cells to be random throughout the survey boxes. In fact, particularly in the eastern survey box, such cells occur mainly in the inshore region. It may be that these inshore regions are not a favoured habitat for feeding whales, either because of the physical topography of the area or as a result of interference competition from other krill predators feeding closer to land-based colonies. There are many examples of baleen whales feeding in other coastal environments (e.g. Piatt and Methven, 1992) and indeed the inshore regions of the western survey box were favoured by the small number of whales recorded. There are also a number of studies that show that the distribution of whales may also be influenced by social aggregation behaviour (e.g. Kasamatsu *et al.*, 1998), particularly in breeding areas (e.g. IWC, 2000c); however, in a non-breeding area, prey is likely to be the major factor influencing these social aggregations. It also remains a possibility that the whales have simply yet to locate these inshore krill. Clearly there are a number of hypotheses, which are not mutually exclusive, that may explain why the small-scale distribution of whales, or any predator, may show only a weak correlation with its prey.

An important factor to consider is that whilst whales seek to exploit areas of high prey biomass, this biomass may be perceived at a number of scales. To a whale, the fundamental exploitable unit of krill is probably related to some function of swarm size and density, rather than the number of individual krill in an area (Murphy *et al.*, 1988). Although at large scales, mean krill biomass appears to be an adequate measure of prey available to whales, identifying relationships at smaller scales may require data on the detailed structure and density of krill swarms. The role of high-density prey patches has been shown to be of particular importance to the North Atlantic right whales (see IWC, 2000b). Small-scale process oriented studies focussing on prey acquisition may reveal the nature of krill targeted by foraging whales and thereby indicate more appropriate measures of krill abundance than mean krill biomass for comparison with whale density (IWC, 2000a).

Correlations between predators and prey are generally stronger for prey that forms discrete patches (e.g. capelin) than for krill, which forms patches of variable dimensions (Hunt *et al.*, 1992). Therefore, by restricting the analysis to krill swarms above some threshold of size or energy density the level of apparent concordance may be improved. At all scales, understanding the physical processes involved in the advection and aggregation of prey in will be essential for interpreting the patterns of prey availability and hence whale distribution (Tynan, 1997; Fiedler *et al.*, 1998; IWC, 2000a). Cetacean abundance is known to vary inter-annually at South Georgia (Harmer, 1931) and data on such changes in the abundance and distribution of whales, especially in relation to changes in krill, may reveal key information about the foraging strategies of whales.

Inter-specific competition

The aggregation dimension of both predators and prey may have a direct influence on the correlation between their relative distributions (Rose and Leggett, 1990); simplistically this suggests that predators select prey according to the spatial scale at which they themselves operate. Since krill at times forms large, dense aggregations, while at other times it exists in more dispersed layers, interactions with its predators occurs over a range of spatial scales (Murphy *et al.*, 1988) The level of potential inter-specific competition between krill predators is therefore determined by the level of overlap in the scale at which the predators exploit krill. Although whales require dense aggregations of krill for energy efficient feeding, smaller predators, such as penguins, may be able to exploit much more diffuse areas of krill. This use of areas of different prey densities may act to limit direct interference competition between predators. Given the very high level of spatio-temporal variability in the distribution of prey in a dynamic marine environment, such small-scale coherence may not be detectable at any particular point in time and space. It is possible that the very variability in the spatial structure of krill, allowing a diverse range of predators to exploit it at different scales, is inconsistent with a high level of spatial coherence between krill and a single predator species.

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