

Acoustic characterization of the three-dimensional prey field of foraging chinstrap penguins

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ABSTRACT: Few studies of diving predators have explicitly addressed the 3-dimensional nature of interactions between predators and prey at the spatial and temporal scales relevant to an individual predator's search behavior. Here, we present a new method for examining such interactions using the results from an acoustic survey of krill availability to foraging penguins. Analyses of fine-scale krill distributions within a $1852 \times 1852 \times 50$ m volume of ocean revealed substantial prey patchiness in all dimensions. Our survey detected the presence of at least 6 krill aggregations in the survey area. The surface distribution of penguins was associated with the edges of these aggregations and was non-randomly associated with krill densities above 0.1 krill m^{-3} in the 30 to 40 m depth layer. The latter association was masked when krill abundance was integrated over the entire water column. Given that mean daytime dive depths for chinstrap penguins fall between 30 and 40 m, our data suggest penguins may fail to detect or choose to pass by shallow, denser prey aggregations and successfully forage on deeper, more homogeneously distributed krill offering higher encounter probabilities per unit volume searched. These findings reveal biologically important features of prey patchiness that cannot be addressed within the limitations of a primarily 2-dimensional analysis of predator-prey distributions. We emphasize that if we hope to gain a predictive understanding of the foraging behavior of diving predators, then we must consider fine-scale, 3-dimensional patterns of prey patchiness when assessing the availability of prey to diving predators.

KEY WORDS: Antarctic krill · *Euphausia superba* · Chinstrap penguin · *Pygoscelis antarctica* · Foraging ecology · Patchiness · Fisheries management · Hydroacoustics

INTRODUCTION

It has been demonstrated that predator-prey interactions often play a fundamental role in determining the structure and dynamics of many freshwater and marine ecosystems (e.g. Brooks & Dodson 1965, Paine 1966, Estes & Palmisano 1974, Carpenter et al. 1987, Hairston & Hairston 1993). Perturbations of these interactions, such as a reduction in the abundance of top

predators and/or key prey species, can generate both direct and indirect effects on food web structure (Kerfoot & Sih 1987). The resulting trophic cascade of direct and indirect effects has been studied extensively in freshwater lakes (Carpenter et al. 1987) as well as in several marine benthic ecosystems (Mann & Breen 1972, Simenstad et al. 1978, Witman & Sebens 1992). In contrast, marine pelagic ecosystems have proven less amenable to controlled experimental investigation, and therefore it has been more difficult to predict the effects of changing predator and prey abundance on the food web dynamics of these ecosystems (Sherman et al. 1990).

One pelagic food web that has attracted considerable ecological and theoretical attention is that of the

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Southern Ocean surrounding the Antarctic continent (May et al. 1979, Nicol & de la Mare 1993). Although relatively remote, the pelagic ecosystem of the Southern Ocean has been subjected to some of the most intensive harvesting of top predators in recorded history (Laws 1985). The devastation of several finfish, seal, and baleen whale populations led to the formation of an international effort to manage and conserve living marine resources in Antarctica in 1981 (CCAMLR 1984). In addition to the focus on predator populations, another major component of this effort involves managing the harvest of Antarctic krill *Euphausia superba*. This patchily distributed epipelagic crustacean is the primary prey resource for many predators in the Southern Ocean ecosystem (Nicol & de la Mare 1993), and increased harvesting pressure by the krill fishery has the potential for generating effects that cascade throughout the food web.

While the population-level consequences of multi-trophic level fisheries on pelagic food web dynamics are extremely difficult to predict (May et al. 1979, Nicol & de la Mare 1993), they are likely to be mediated by the availability of prey to their natural predators. Prey availability itself is a function of predator foraging behavior and prey distribution at the spatial and temporal scales of a predator's foraging ambit (Holling 1959, Hunt & Schneider 1987). Therefore, in order to predict how changes in krill availability might impact regional predator populations in the Southern Ocean, the following 3 pieces of information are needed: (1) an estimate of the krill requirements for each predator population which is based on the foraging ranges and energetics of individuals in the population; (2) an estimate of how krill distribution and abundance changes over time and space, which includes natural variation in krill distributions as well as variation imposed by the commercial fishery; and (3) an estimate of how those changes in krill distributions affect prey availability to actively foraging predators. Although preliminary information for the first 2 items are available (e.g. CCAMLR 1991, 1992, Nicol & de la Mare 1993, Woehler 1995), little is known about the nature of krill availability and predator behavior in the context of a 3-dimensional environment. Methodological limitations make it extremely difficult to quantify both predator and prey distributions in such environments, although recent work by Piatt (1990) and Rose & Leggett (1990) are notable exceptions.

Here, we describe an innovative method for assessing krill availability to the chinstrap penguin *Pygoscelis antarctica*. The chinstrap penguin is the dominant predator on krill in the South Shetland Islands, a region of Antarctica where there is evidence that the krill fishery can have an impact on top predator populations. We discuss the implications of 3-

dimensional patchiness in prey distributions for fine-scale foraging behavior, and offer recommendations for how this particular acoustic method can be used to test hypotheses about which features of prey distribution have the greatest effect on prey availability to diving predators.

METHODS

Study site. Simultaneous field observations of krill and chinstrap penguins were made on 13 March 1991 near Elephant Island, South Shetland Islands, Antarctica (62° 09' S, 55° 00' W). The study site was directly east of a large colony (~25 000 breeding pairs) of chinstrap penguins located on Seal Island, an area known to contain krill aggregations and foraging chinstrap penguins on a regular basis.

Our study was conducted just inside the shelf-slope break north of Elephant Island. Water depth within the survey area ranged from 385 to 564 m, with a mean depth of 470 m. All data at this site were taken during daylight between 17:40 and 23:14 h Greenwich Mean Time (local time = GMT - 3 h) because chinstrap penguins forage primarily during daylight hours (Bengston et al. 1993).

Acoustic methods. We performed a fine-scale acoustic survey aboard the NOAA ship 'Surveyor' to determine the 3-dimensional distribution of krill within a 1852 × 1852 × 100 m deep volume of ocean. We collected data from a square survey grid centered on 61° 01.5' S, 54° 50' W by running 6 east-west and 6 north-south transects (Fig. 1). Each transect was 1852 m long. Due to the large size and limited maneuverability of the ship, the complete grid took slightly over 5 h to complete.

Acoustic data on krill abundance and size distribution were collected using a Simrad EK500 split-beam echosounder transmitting at 120 kHz (Knudsen 1990). The transducer had a beam width of 9.4° and was deployed on a towed body from the starboard side of the ship's fantail deck. The transducer was approximately 2 m below the sea surface and was transmitting at a rate of 1 ping s⁻¹. The ship towed the transducer at a speed of approximately 5 knots along the transect lines. Although the sea state was calm, no acoustic data were collected from 0 to 10 m away from the transducer because the echosounder had been configured for work in rough seas (i.e. data reports from <10 m were automatically blanked). However, because krill were not present in the engine cooling intakes (a regular occurrence when surface swarms of krill were present in an area), and because no seabirds were observed feeding at the surface during the survey, we believe that krill were rare in this depth layer

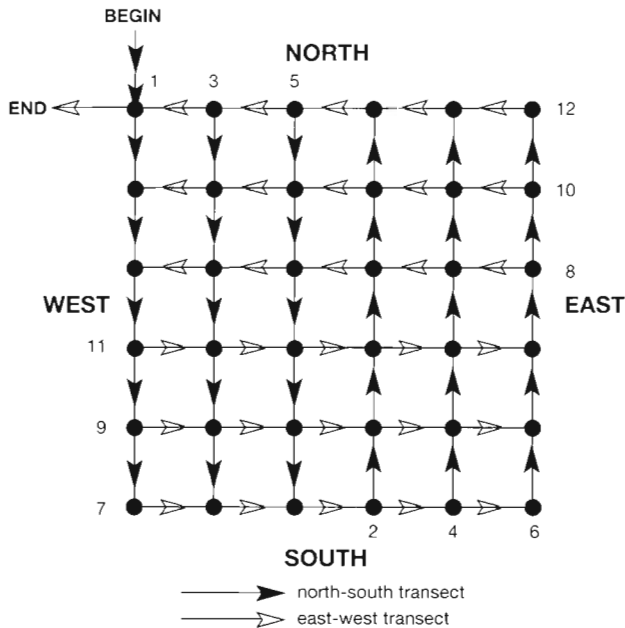


Fig. 1. Design of survey grid. Each transect line was 1852 m long; transects are numbered according to the sequence of execution. Acoustic data were integrated vertically into 10 m bins between 10 and 110 m from the transducer and integrated horizontally in 50 m report bins. Finest spatial resolution of krill aggregations was therefore limited to $50 \times 50 \times 10$ m deep sampling units. Surface observations of penguins along each transect were taken simultaneously with the acoustic data

Echo integration techniques were used to estimate the acoustic backscatter from krill (Knudsen 1990). Acoustic volume backscattering data were integrated vertically into two 20 m deep layers (10–30 and 30–50 m) and four 10 m deep (10–20, 20–30, 30–40, 40–50 m) layers for depths between 10 and 50 m from the transducer. Data were integrated horizontally every 20 pings, equivalent to approximately 50 m. Thus, the finest spatial resolution of this study was a $50 \times 50 \times 10$ m volume, and inferences from our data about the patchiness of krill distributions below that scale are not justified. For example, an extremely dense krill aggregation 10 m in diameter would not be distinguishable from equally abundant krill within a less dense but larger (e.g. 30 m diameter) aggregation (cf. Hamner 1984, O'Brien 1987).

The integrated acoustic data were reported as mean volume backscattering coefficients ($s_v = \text{m}^2 \cdot \text{m}^{-3}$). Volume backscattering coefficients were converted to estimates of krill abundance using the relationship:

$$\text{no. krill} = s_v / \bar{\sigma}_{\text{bs}}$$

where $\bar{\sigma}_{\text{bs}}$ is the mean backscattering cross section estimated using 2 independent methods.

The first method estimated $\bar{\sigma}_{\text{bs}}$ from net samples. Just prior to running acoustic transects, krill were captured

from all depths using a net towed obliquely across the survey area. We used the length distribution of these krill and the regression relationship from Greene et al. (1991) to predict a backscattering cross-section distribution (σ_{bs} distribution) and a mean backscattering cross section for krill. The net tow also confirmed that krill were the major source of acoustic backscatter.

The second method of estimation of $\bar{\sigma}_{\text{bs}}$ used the split-beam technique to make acoustic estimates of krill size distribution (Knudsen 1990, Greene & Wiebe 1990). The σ_{bs} distribution from acoustic targets was only recorded in the 10–20 m depth layer. Reliable σ_{bs} distributions from other layers were unavailable because the acoustic system could not resolve individual targets in an unbiased manner when targets were greater than 20 m from the transducer. Acoustic estimates of the σ_{bs} distribution agreed well with the σ_{bs} distribution predicted from the net samples (see Hewitt & Demer 1991 for explicit comparison).

Although we had 2 means to estimate $\bar{\sigma}_{\text{bs}}$, we used the $\bar{\sigma}_{\text{bs}}$ obtained from the net samples to convert volume backscattering coefficients into estimates of krill abundance. This method was chosen because it considered krill taken from the whole depth range sampled and not just from krill in the 10–20 m layer.

Using this $\bar{\sigma}_{\text{bs}}$, we obtained estimates of krill abundance for each layer and then ranked depth layers according to total estimated abundance of krill and according to the degree of krill aggregation. For this latter ranking, we used Lloyd's index of patchiness and Lloyd's index of mean crowding (Lloyd 1967). The index of patchiness is a measure of spatial aggregation that varies from zero (regularly spaced individuals) to one (randomly spaced individuals) and, theoretically, to infinity (infinitely aggregated individuals). It is the multiplier by which the actual densities experienced by individual krill within a sampling volume differ from the mean density expected from a completely random distribution of the animals. The index of mean crowding represents the mean number, per individual, of other krill found in the same sampling volume.

We also described krill patchiness using a novel index which assesses the relative contribution of different krill density levels to the total volume of each layer. We refer to the ratio of acoustic reports containing densities equal to or greater than $>10 \text{ krill m}^{-3}$ over the total number of acoustic reports for that depth layer as the 'relative volumetric contribution of the $>10 \text{ krill m}^{-3}$ density level to the layer's total volume'. For example, if 20% of all acoustic reports from a particular layer contain densities in excess of 10 krill m^{-3} , then the relative volumetric contribution of the $>10 \text{ krill m}^{-3}$ density level is 20%. Biologically, if one assumes we have a random sample of the volume, this means we estimate that 20% of that depth layer's total actual

volume contains more than 10 krill m^{-3} . Note that such an index can be used as an estimate of encounter probabilities with prey as a predator sweeps out a search volume through a given layer.

Penguin observations. A single observer (J.E.Z.) recorded all species of seabirds detected along each of the grid's transects according to methods of Tasker et al. (1984). Observations were taken within a 300 m wide bow-to-beam arc from the starboard side of the ship's flying bridge 17 m above the sea surface. Times of bird observations, along with bird behaviors, were recorded to the nearest minute. All observations were dictated into a voice recorder and later transcribed into a field notebook.

Data visualization and Monte Carlo analysis of penguin-krill spatial concordance. Two- and three-dimensional visualizations of krill abundance were generated using the SpyGlass Transform and IBM Data Explorer software packages (SpyGlass, Inc. 1991, IBM 1992). We used a nearest-neighbor cubed interpolation algorithm to grid the irregularly spaced acoustic data. The surface distribution of penguins was superimposed on 2- and 3-dimensional images of krill distributions in order to make a visual comparison of krill and penguin distributions. Recognizing the non-synoptic nature of the acoustic data, we only used these visual comparisons to help interpret our statistical analysis of spatial concordance between penguins and krill. Further interpretations from these visualizations should be carried out with great caution and with the recognition that the images may characterize the distributions of predators and prey, but do not represent a truly instantaneous snapshot of those distributions.

We tested for significant spatial concordance between the surface distribution of penguins and the distribution of krill at depth by using Monte Carlo techniques (Manly 1991). Simple parametric correlation analyses could not be used because data reports of krill abundance were known to be autocorrelated and we were unable to quantify this autocorrelation due to occasional missing data reports (Schneider 1990, Manly 1991). Although we had acoustic data down to a depth of 100 m below the transducer, only krill within the first four depth layers (i.e. 10 to 50 m) were used for the Monte Carlo analysis. We did this because 75 to 90% of chinstrap foraging dives are shallower than 50 m, and krill below 50 m were assumed to be too deep for the penguins to efficiently exploit (Lishman & Croxall 1983, Bengston et al. 1993). We also tested for spatial concordance between distributions of penguins at the surface and krill integrated over the whole 10–50 m depth layer.

Acoustic estimates of krill density were classified according to 3 *a priori* logarithmic density levels:

low/background densities (0 to 0.1 krill m^{-3}), moderate densities (0.1 to 10 krill m^{-3}), and high densities (>10 krill m^{-3}). A finer division of krill densities into more than 3 discrete density classes was not statistically feasible due to small sample sizes of penguin observations ($n = 14$; Snedecor & Cochran 1989).

Chinstrap penguins were classified as either present or absent rather than weighting observations according to the number of individuals observed within a group. Sightings of one or more penguins at different locations were assumed to be statistically independent for purposes of the Monte Carlo analyses. We used this conservative 2×3 classification scheme to avoid statistical problems that result from the fact that individual penguins within a group are not statistically independent of one another (Manly 1991, D. Deutschman & D. Schneider pers. comm.). This classification scheme is also consistent with the definition of spatial concordance already being used in seabird predator-prey studies (Obst 1985, Heineemann et al. 1989).

We expected that the chinstrap penguin, a specialist on krill, would be most closely associated with the highest krill densities available. We tested the null hypothesis that penguins are randomly distributed among krill density classes for each depth stratum, as well as for krill density integrated over 10 to 50 m. We compared the observed chi-square statistic for penguin-krill concordance with the chi-square distribution obtained from Monte Carlo simulations. The simulations randomized penguin presence/absence data over the krill density classes that were observed in the field. One thousand simulations were run for each of the depth layers examined.

RESULTS

Krill patchiness

An oblique net tow taken immediately prior to the acoustic survey captured mainly post-spawning female krill, confirming that *Euphausia superba* was the primary source of acoustic backscatter within the area. The net captured 108 krill, with an average length of 47.4 mm (equivalent to a $\bar{\sigma}_{\text{bs}} = 1.259 \times 10^{-7} \text{ m}^2$), ranging from 38 to 53 mm in length. The acoustic estimate of krill size distribution from the 10–20 m depth layer (Fig. 2) indicated that approximately 60% of the krill in this layer fell within the size range typically preyed upon by chinstrap penguins (30 to 55 mm standard length; Volkman et al. 1980, Croxall & Lishman 1987). Reliable acoustic estimates of size distributions from other depth layers were not available for reasons stated in the 'Methods'.

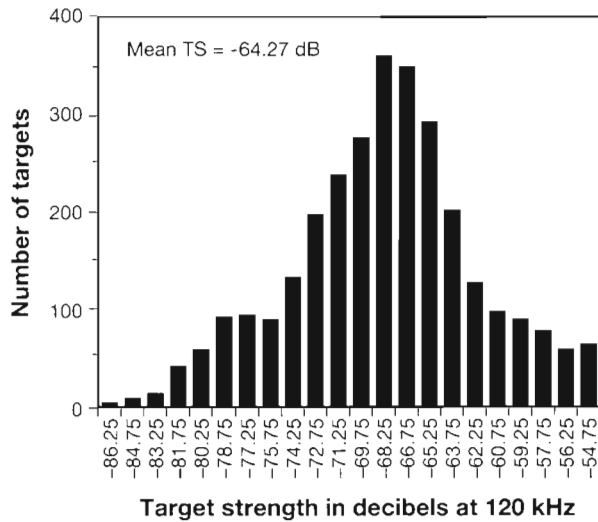


Fig. 2. Acoustic target strength distribution for krill in the 10–20 m depth layer. The echosounder detected a total of 2951 individual krill targets. An oblique net tow through the survey area confirmed that Antarctic krill *Euphausia superba* were the major source of acoustic backscatter

Krill were abundant but extremely patchy throughout the survey (Table 1). Three-dimensional visualization revealed the presence of 6 distinct krill aggregations within the southern-most half of the surveyed volume (Figs. 3 & 4). Peak krill densities within the aggregations averaged 173 krill m^{-3} , ranging between 20 and 635 krill m^{-3} . The highest densities occurred in the 10 to 20 m layer of the southeastern-most and central aggregations (Figs. 3 & 4).

Krill were more abundant and more highly aggregated in the 10–20 m depth layer than in other layers (Table 1). The relative volumetric contributions from different krill density classes indicated that the 30–40 m and 40–50 m depth layers contained higher volumetric proportions (30 and 45%) of above-background krill densities ($>0.1 \text{ krill m}^{-3}$) than did the 10–20 m and 20–30 m layers (15 and 13%; Fig. 5).

Table 1. *Euphausia superba*. Acoustic estimates of krill abundance and patchiness in different depth layers. Abundance estimates were computed using mean $\bar{\sigma}_{bs} = 1.259 \times 10^{-7} \text{ m}^{-2}$ (equivalent mean TS = -69 dB). Krill were most abundant and most aggregated in the 10–20 m depth layer. Krill were least abundant in the 20–30 m depth layer and least aggregated in the 40–50 m layer

	Depth layer			
	10–20 m	20–30 m	30–40 m	40–50 m
Mean density (\pm SD) in krill m^{-3}	7.89 (± 57)	4.74 (± 29)	5.79 (± 37)	7.17 (± 39)
Total krill per layer	2.70×10^8	1.63×10^8	2.00×10^8	2.46×10^8
Lloyd's index of patchiness	53	37	41	31
Index of mean crowding in krill m^{-3}	417	176	237	222
Rank by total krill per layer	1	4	3	2
Rank by Lloyd's index of patchiness	1	3	2	4

Penguin observations

A total of 80 chinstrap penguins were observed at 14 different locations during the survey. No penguins were seen in the northern-most third of the survey area where krill were virtually absent. Behavioral evidence and fecal discoloration of nearby icebergs indicated that the penguins counted during the survey were actively foraging on krill. A number of penguins ($n = 22$) were observed swimming very slowly with their heads underwater and looking downward; such behavior suggests that these birds were actively searching for prey in the water column. Furthermore, over 1000 chinstrap penguins were present on an iceberg located 4.6 km southwest of the survey area. This iceberg was visibly discolored by large amounts of pink (i.e. krill-dominated) feces that were known to be less than 3 d old. We therefore assumed that penguins counted during our survey were foraging intensively in the area.

Monte Carlo results

When comparing the observed penguin-krill distributions with the Monte Carlo analysis, we interpreted p-values of less than 0.05 for an observed χ^2 statistic as evidence of non-random spatial concordance between penguins and sub-surface krill in a particular density class. Monte Carlo analyses revealed that penguins were significantly associated with above-background krill densities in the deeper portion (30–50 m; $\chi^2 = 7.72$, $p = 0.02$) but not in the shallower portion (10–30 m; $\chi^2 = 4.22$, $p = 0.12$) of the water column. Further investigation revealed that this was due to statistically significant spatial concordance between penguins and krill densities of $>0.1 \text{ krill m}^{-3}$ in the 30–40 m depth layer ($\chi^2 = 16.57$, $p \ll 0.01$). There was no statistically significant spatial concordance between penguins and krill within the 40–50 m layer ($\chi^2 = 4.12$, $p > 0.12$) Concor-

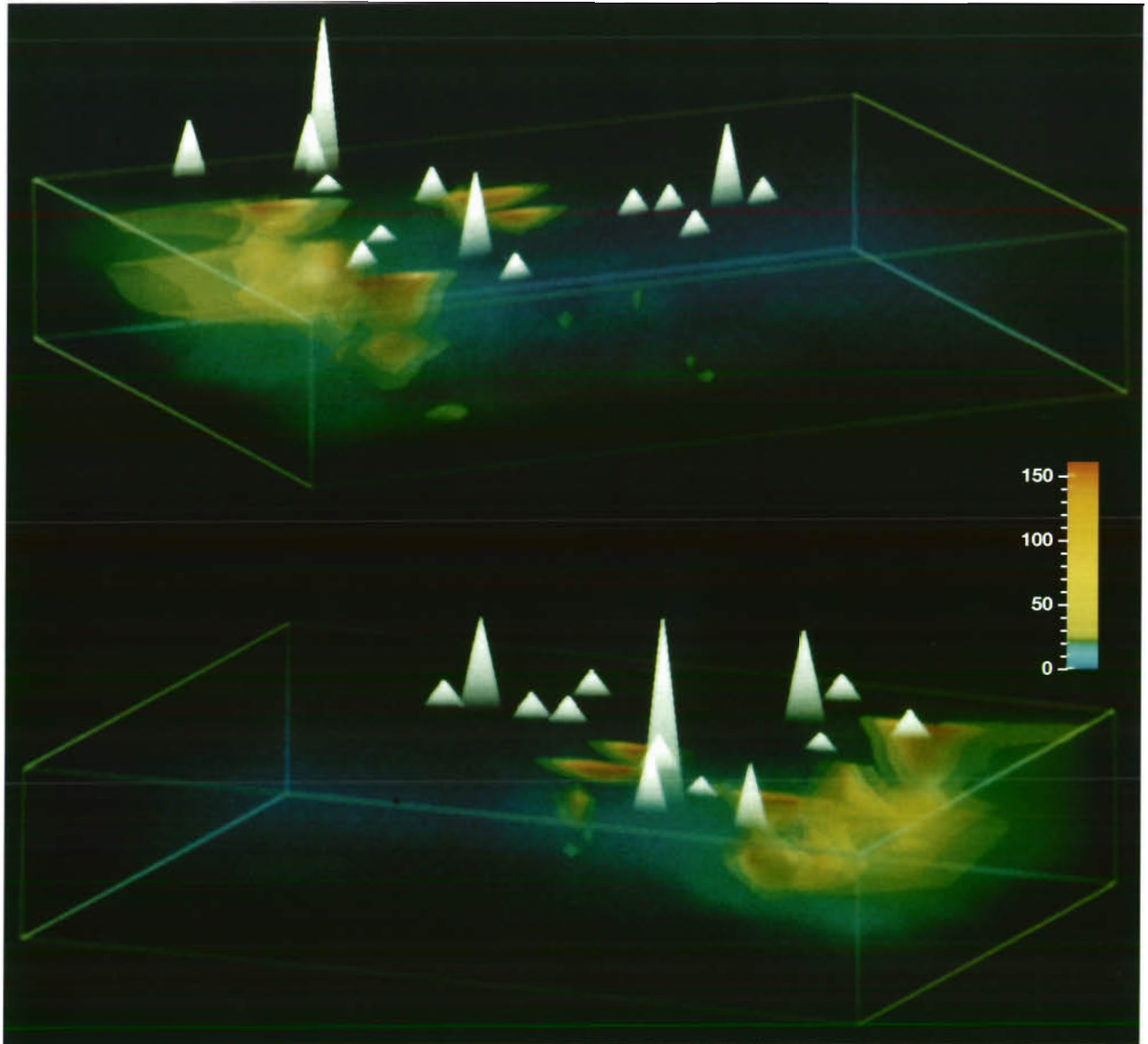


Fig. 3. *Pygoscelis antarctica*. Surface distribution of chinstrap penguins relative to the 3-dimensional distribution of krill. Acoustic data from a volume measuring $1852 \times 1852 \times 100$ m were visualized using the IBM Data Explorer software package. The upper-most corner of the top panel corresponds to the northwest corner of the survey. The lower panel is rotated 180° . At least 6 distinct krill aggregations were present during the survey. The highest recorded krill density was in excess of 600 krill m^{-3} . The locations of chinstrap penguins are indicated by white peaks on the surfaces of the 2 panels. The height of a peak is proportional to the number of penguins seen at each location. The highest peak represents 20 penguins; the lowest peaks represent 2 penguins. Note that krill in the lower half of the volume are deeper than 50 m, and were not included in the data analysis because they are likely to be out of the typical diving range of chinstrap penguins

dances were also non-significant ($p > 0.12$) in the 10–20 m and 20–30 m layers. Note especially that the existence of high krill-penguin spatial concordance in the 30–40 m depth layer was masked when krill density was integrated over the whole 10 to 50 m ($\chi^2 = 3.78$, $p = 0.15$).

DISCUSSION

The results of this study indicate that substantial fine-scale patchiness (scales of 10s to 100s of metres) exists for krill in both the vertical as well as horizontal dimensions. More importantly, however, our study indicates that a

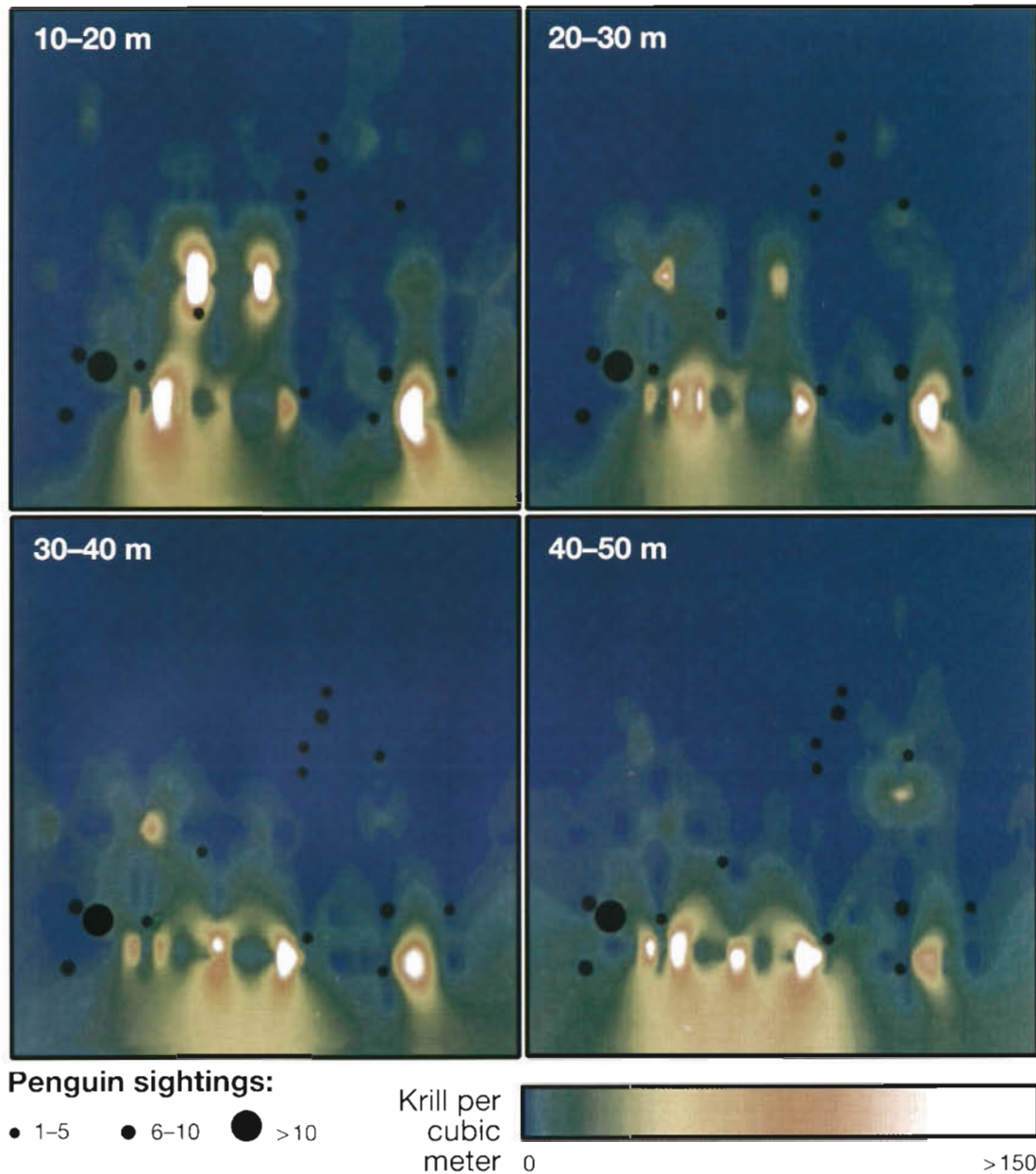


Fig. 4. *Pygoscelis antarctica*. Surface distribution of chinstrap penguins superimposed on krill distributions in four 10 m depth layers. Maps of krill distribution in each of the four 10 m thick depth layers were generated using the SpyGlass Transform software package (SpyGlass, Inc. 1991). The top left corner represents the northwestern corner of the survey grid. Surface penguin distributions were superimposed on the maps of krill distribution. No penguins were observed within the northern third of the survey area, where krill were virtually absent from the water column, and penguins seemed to be associated primarily with the edges of krill aggregations

2-dimensional approach integrating prey abundance over depth and over spatial scales of 1 km or more — which is typically the procedure used in line-transect surveys of predator-prey distributions — can mask statistically significant and ecologically meaningful correlations between diving predators and prey patches. In particular, our data show that encounter probabilities between predators and krill, as measured by the relative

volumetric contribution of different krill density levels, are different within different depth layers (Fig. 5). This depth-dependent heterogeneity in the prey field must be included when one is attempting to quantify how likely it is that an aggregation will be detected by predators, and how energetically profitable a given patch might be to exploit, particularly when searching and costs-of-descent are likely to play a role in determining

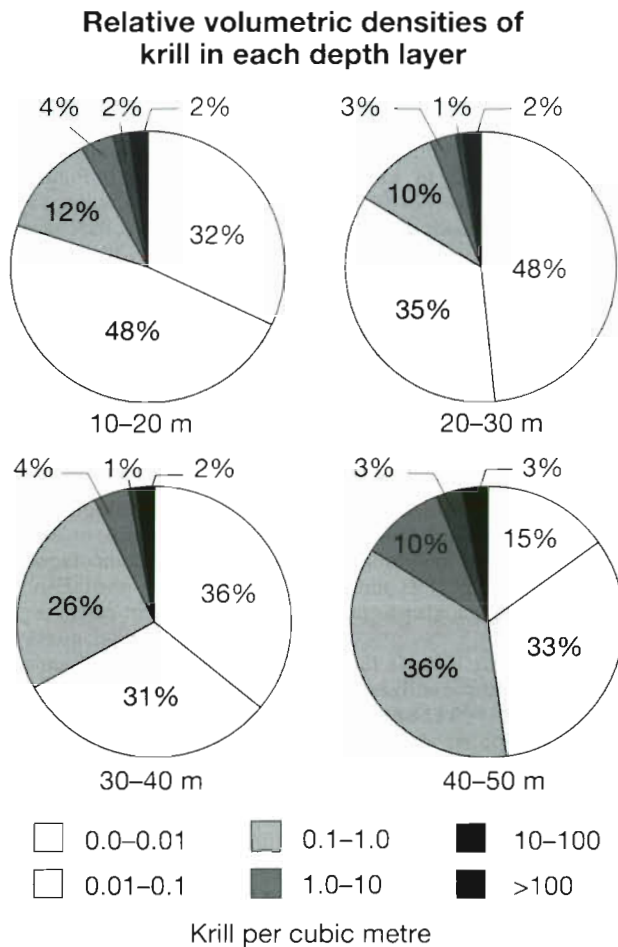


Fig. 5. *Euphausia superba*. Relative volumetric densities of krill in each 10 m depth stratum. Acoustic data reports of krill density along each transect were divided *a priori* into 6 density levels. For each depth layer, the number of acoustic data reports falling into each density category, divided by the total number of acoustic data reports for that depth layer, gave a rough estimate of what proportion of the water volume was occupied by different density levels. Our acoustic methods averaged krill densities within $50 \times 50 \times 10$ m sampling units and thus was unable to resolve differences in krill densities at spatial scales less than 50 m in horizontal dimensions and 10 m in vertical dimensions. This coarser resolution, however, does not affect the interpretation of distributional patterns above the resolution of our analysis. Note that the 30–40 m and 40–50 m depth layers have relatively higher proportions of their volume filled with the 0.1–10 krill m^{-3} density level (30 and 45%, respectively) than do the 10–20 and 20–30 m layers (15 and 13%, respectively)

energetic constraints of search-and-encounter phases of diving predators (e.g. Lovvorn et al. 1991, Burger et al. 1993).

Dive profiles from chinstrap penguins show that penguins from our study area exhibit mean daytime foraging dive depths of 31 m (Bengston et al. 1993). If we assume that penguins foraging at the time of our survey are also diving primarily between 30 and 40 m,

then we can begin to look for features of prey patchiness that distinguish this layer from the others and that are likely to influence the energetics of sub-surface foraging. Comparisons of krill abundance among the different depth layers lead us to hypothesize that penguins foraging between 30 and 40 m may be targeting the shallowest layer where the relative volumetric contribution of moderate to high krill density levels (>0.1 to 10 krill m^{-3}) is greatest (Fig. 5). The reason for this may be that the 30–40 m layer presents foraging penguins with better feeding conditions within this layer (i.e. higher average encounter probabilities per unit space) than in shallower layers (where krill are more abundant and more aggregated, but less likely to be encountered in an 'average' cubic metre).

The visualization technique presented in this paper reveals that the surface distribution of birds seems to coincide with the edge of prey patches, and that surface distributions of birds do not lie exactly above the densest area of a patch. Penguins, like other diving birds, are likely to prefer attacking a prey aggregation from the sides or from underneath to prevent the prey from detecting the initial attack or escaping via dispersal (Grover & Olla 1983, Hamner 1984, O'Brien 1987, J. Zamon unpubl.). For air-breathing predators to track schools between individual feeding dives, it would then be necessary for foraging individuals to maintain themselves as close as possible to the edges of the prey aggregation. Therefore the overall shape of the aggregation itself may have important consequences for the ability of a predator to track that aggregation. The observation that some pelagic prey tend to 'ball up' in small, rapidly moving spherical shapes when under attack may indicate that prey are attempting to minimize the surface area that is vulnerable to repeated attack (Grover & Olla 1983, O'Brien 1987). If the visualizations in Fig. 4 are reliable characterizations of real distributions, it is interesting to note that 10 of 14 groups of birds in our survey were within 100 m of the edge of a krill patch, and none of them were precisely on top of the patches. This spatial distribution of predators on the periphery of prey patches may be typical of air-breathing predators attempting to track and exploit a sub-surface prey patch, and may account for the fact that previous fine-scale studies have been unable to detect consistent, strong correlations between the highest densities of prey and the highest densities of specialist predators (Obst 1985, Hunt & Schneider 1987, Heinemann et al. 1989).

Repeated execution of grid-surveys over krill patches with foraging penguins present and over krill patches without foraging penguins would allow one to test the hypothesis that penguins forage only when krill in a particular volume of water exceed some *a priori* threshold density. For example, one could test

the generality of our preliminary observation that penguins are more spatially concordant with krill layers having greater volumetric proportions of >0.1 krill m^{-3} than with krill layers that have most of their volume consisting of krill densities <0.1 krill m^{-3} . These acoustic methods could also be used to determine whether or not foraging predators are consistently associated with aggregations of particular sizes (e.g. volumes) and shapes, independent of absolute prey density within the patch.

Commercial harvests of large, naturally occurring krill aggregations may affect local availability to krill predators. Without identifying specific features of krill aggregations that make them more or less available to foraging predators, it will not be possible to predict how altering prey patchiness will affect the predators' ability to locate and capture prey. Quantifying the availability of pelagic prey to diving predators is a complicated problem, and acoustic characterization of the prey field is one important step towards a fuller understanding of predator-prey interactions in the open ocean. Subsequent studies will need to integrate more extensive information on prey size distributions in different depth layers, on temporal changes in the spatial distributions of predator and prey, and on foraging patterns (e.g. dive profiles) of individual predators hunting within known prey distributions. Acquiring and interpreting such information will be critical to the successful understanding and management of marine pelagic ecosystems in general, and the Southern Ocean ecosystem in particular.

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