

Swarm characteristics of Antarctic krill *Euphausia superba* relative to the proximity of land during summer in the Scotia Sea

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ABSTRACT: We studied the relationship between the proximity of land and the distribution and swarming characteristics of Antarctic krill across the Scotia Sea in January and February 2003. Krill swarms identified with a Simrad EK60 (38 kHz, 120 kHz) echosounder were grouped into 4 categories according to distance from shoreline: 0 to 50 km, 50 to 100 km, 100 to 200 km and >200 km. Cross-sectional areas of swarms were significantly larger inshore, with a mean value of 120 m² in the 0 to 50 km zone compared to <80 m² further offshore. The packing concentration of krill within inshore swarms was also significantly greater, with an average density of 95 ind. m⁻³ compared to between 24 and 31 ind. m⁻³ elsewhere. A large proportion of the biomass was concentrated into a small number of large, dense swarms throughout the survey area, and this trend increased with decreasing distance from shore. The highest median number of swarms per km and krill acoustic biomass per km was found in the 50 to 100 km zone. However, a significantly greater number of large, biomass-rich swarms occurred in the 0 to 50 km zone compared to all other zones. Swarms in the 0 to 50 km zone were also significantly further apart. The majority of swarms were located in the upper 50 m during the daytime although they were marginally deeper in the night in offshore regions. Krill are likely to move between inshore and offshore environments continuously over their lifetimes. The change in krill behaviour between environments could be a response to local predatory threats over short spatial and temporal scales.

KEY WORDS: Acoustics · Southern Ocean · Distribution · Vertical migration · Predation · Seals · Penguins · Fishery

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INTRODUCTION

The pattern of swarming by krill has a strong influence on the distribution of their predators (Veit et al. 1993). Birds and mammals frequently aggregate where dense aggregations of krill are predictable and sustained (Croll et al. 1998) and especially large krill patches can have a disproportionate influence on the distribution of predators (Heinemann et al. 1989). Foraging often begins only when detected krill aggregations are above a threshold density (Zamon et al. 1996) although predators adjust their foraging behaviour in response to variability in krill density and distribution

(Mori & Boyd 2004). A thorough appreciation of the nature of patchiness in the krill prey field is an essential step to interpreting foraging behaviour in krill predators (Hunt et al. 1992).

There are both costs and benefits to swarming (Ritz 1994). It can assist in the location of food (Antezana & Ray 1983) or mates (Nicol 1984), decrease the individual cost of swimming through collective slipstreaming (Ritz 2000) and provide protection from predators (O'Brien 1987). However, the absolute numbers of krill in large swarms creates an internal microenvironment of waste products, reduced O₂, parasites, disease and lack of food (Hamner & Hamner 2000). Greatest atten-

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tion has been given to the protective benefits of swarming and there are numerous case studies of the interaction between predators and swarms (O'Brien 1987, Zhou & Dorland 2004, Cox et al. 2009).

Swarming is not the only means of reducing the threat of predation. Vertical migration to deeper parts of the water column also reduces risk, particularly in relation to surface-diving predators such as penguins and seals. The deeper layers are also darker, which reduces the visual acuity of both diving predators and planktivorous fish (e.g. mackerel icefish) and inhibits their ability to locate and capture prey (Aksnes & Giske 1993). Nevertheless, krill must occupy the surface layers for certain periods in order to feed, which cannot always be under the cover of darkness during the polar summer.

There is a great deal of interaction between the strong advective forces within the Southern Ocean and the life cycle of Antarctic krill (Nicol 2006). This is likely to result in krill travelling great distances during their lifetime (Thorpe et al. 2004, 2007). This journey will probably traverse both inshore and offshore environments (Atkinson et al. 2008) and will also involve interactions with seasonal sea-ice (Murphy et al. 2007). As well as being driven by the currents, Antarctic krill may also actively migrate between inshore and offshore environments at various stages of their life cycle, possibly in response to food availability or reproductive condition (Siegel 2000). Therefore, the stocks of krill in inshore and offshore environments are likely to be regularly mixed. This further implies that any difference in swarming behaviour and distribution between these environments probably reflects short-term responses by krill to local conditions.

The predatory impact of land-based predators on krill biomass can be large. Annual prey requirements of Antarctic fur seals and macaroni penguins on South Georgia alone are in the order of 11.9 Mt (range of 6.4 to 17.5 Mt, Boyd 2002). Recent published estimates of krill standing stock for the Scotia Sea (including South Georgia) range between 36 and 44 million tonnes (Trathan et al. 1995, Hewitt et al. 2004). The highest abundances of these predators are found between 60 to 120 km from land and decrease sharply at distances greater than 150 km from land (Reid et al. 2004). Therefore, it is likely that the nature of interactions between krill and its predators changes considerably moving away from land over small scales (<100 km).

A further dynamic element is the potential impact of harvesting by krill fisheries. These operate at a scale of 150 km and occur almost entirely within 100 km of land (Reid et al. 2004). Commercial harvests of krill aggregations have the potential to affect local availability to krill predators. This is of particular concern to the Commission for the Conservation of Antarctic

Marine Living Resources (CCAMLR), which manages the krill fishery and must balance the exploitation of the krill catch against the demands of the wider ecosystem, especially krill-dependent predator species. Identifying how krill biomass is distributed between swarms and the relative importance of different swarm types to fishery vessels and foraging predators is an aspect yet to be fully considered within the current management approach.

Recently, Tarling et al. (2009) categorised swarms into different types based on 7 swarm properties (depth, length, thickness, area, packing concentration, swarm acoustic biomass and distance to next swarm). Two main types of swarm were distinguished and the contribution each type made to the krill population was found to vary across the survey region. The survey covered a large area of the Scotia Sea, and included a number of areas where the fishery presently operates. The study also found that variation in swarm type distribution was predictable as a function of the body size and maturity of krill, the ambient level of fluorescence and level of light. Distance from land was not identified as a strong predictor of swarm type. However, the study focussed on mesoscale patterns (100 to 1000 km) whereas inshore-offshore clines are probably best resolved at smaller scales (1 to 100 km).

The intention of the present study is to describe krill swarming patterns and biomass in relation to one of the most important variables to a land-based predator, the distance it must travel from shore in order to reach its resource. This will enhance the interpretation of observed foraging patterns of krill-dependent predators such as seals and penguins. It will also provide valuable parameterisations, especially for models predicting optimal foraging patterns in krill predators. The results are also of direct relevance to the management of fisheries in this region, particularly in examining the relationship between swarm-biomass distribution patterns and fishing effort. Although it is accepted that distance from shore is only one of many influences on the swarming behaviour in krill, our observations of swarm features that alter along this cline provide some interesting insights into the behavioural ecology of krill.

MATERIALS AND METHODS

General survey details. The RRS 'James Clark Ross' undertook a survey (JR82) between 9 January and 16 February 2003 involving 8 transects within the region 65°S to 50°S and 30°W to 55°W in the Scotia Sea (Fig. 1). The survey area covered continental shelves, oceanic regions and major frontal zones. The majority of transects were transited at speeds between 5 and 10 knots (except for ice) with a ping rate of 1 to

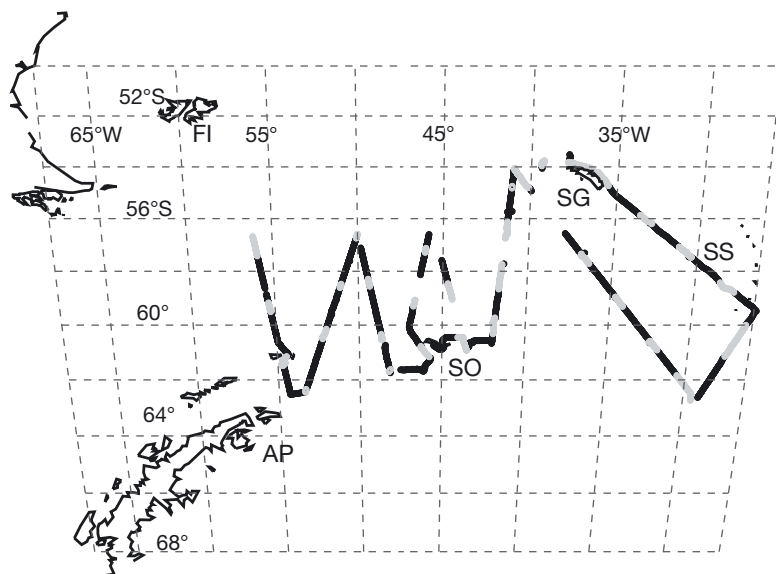


Fig. 1. Survey track highlighting the periods when acoustics were active and collecting acoustic data of sufficient analytical quality. Daytime sampling is indicated by black lines, night-time sampling by grey lines. FI: Falkland Islands, AP: Antarctic Peninsula, SO: South Orkney Islands, SG: South Georgia, SS: South Sandwich Islands

1.5 s and a pulse length of 1024 μ s. Krill were sampled either at fixed stations 60 nautical miles (n mile) apart, or en route, depending on when suitable swarms were located, using a rectangular midwater trawl (RMT8). Further details on net sampling strategy are given in Tarling et al. (2009).

Acoustic data. Volume backscattering strength (S_v re. 1 m^{-1} , dB) was collected using a SIMRAD EK60 echosounder with hull-mounted split-beam 38 kHz, 120 kHz and 200 kHz transducers. Acoustic system calibrations were undertaken at Stromness Bay (54°9.44' S 36°41.99' W on 17 February 2003), using the standard sphere method (Foote et al. 1987).

Acoustic processing. The raw acoustic data from the 38 kHz and 120 kHz sounders were processed using Sonardata Echoview v. 4.0. Filters were applied to exclude the surface-most 13 m and depths below the detected bottom (where applicable) and other 'bad data' resulting from interference or bad weather. Background noise levels were estimated and subtracted from both the 38 kHz and 120 kHz echograms using the method of Watkins & Brierley (1996). Smaller spikes were removed from the data by restricting the final swarm detection to those regions of the echogram where the 7×7 (pings \times samples, where the ping interval was 1.5 s and sample length 0.1867 m) convolution filtered data were above a threshold of -80 dB at 120 kHz. Subsequent analyses showed that this filter did not exclude any swarms delineated by the detection algorithms described in the next paragraph ('Swarm detection'). The S_v threshold used in the final

swarm detection was -70 dB at 120 kHz, as advised by Lawson et al. (2008a) based on estimates of the maximum distance that individual krill can remain in visual contact with each other. With a ping interval of 1.5 s and a standard cruising speed of 10 knots, the minimum spatial resolution was 7.5 m. There was some variation in each of these parameters depending on ice conditions and bathymetry.

Swarm detection: A swarm detection algorithm was applied to the 120 kHz echogram data using Sonardata Echoview 4.0 'School detection module', which employs a SHAPES algorithm (Coetzee 2000). The software was set to detect swarms with a minimum length of 15 m and thickness of 2 m (Table 1). Swarms were linked if they were <15 m apart horizontally or 5 m apart vertically. These parameters were selected partially to match the resolution offered by our acoustic data, and partially by reference to settings used in previous studies of

Antarctic krill and results obtained therein (Miller & Hampton 1989a,b, Sprong & Schalk 1992, Miller et al. 1993, Watkins & Brierley 2002, Woodd-Walker et al. 2003, Lawson et al. 2008b). Further details on the sensitivity of swarm detection to parameter and threshold settings are detailed in Tarling et al. (2009).

Table 1. Transducer specifications during cruise JR82 and pre-detection and swarm detection settings. Further settings and constants are given in Tarling et al. (2009). S_v : volume backscattering strength, S_a : correction coefficient

Specification	38 kHz	120 kHz
	transducer	transducer
Transducer type	ES38	ES120-7
Transducer depth (m)	5.00	5.00
Max. power (W)	2000	1000
Pulse duration (ms)	1.024	1.024
Ping rate (s^{-1})	1–1.5	1–1.5
Absorption coefficient ($dB km^{-1}$)	10.09	27.69
Transducer gain (dB)	24.19	22.43
S_a correction	-0.06	-0.42
Setting	120 kHz value	
Surface exclusion zone (m)	≥ 13	
Maximum permitted data range (m)	300 or sea bottom	
S_v threshold (dB)	-70	
Min. horizontal candidate (m)	10	
Min. vertical candidate (m)	0.5	
Max. horizontal linking distance (m)	15	
Max. vertical linking distance (m)	5	
Min. total swarm length (m)	15	
Min. total swarm height (m)	2	

Post-processing of detected swarms: After detection, the physical properties of the swarms were corrected for beam geometry and threshold effects. Swarms that were too small to be corrected by the school correction algorithm were removed (Diner 2001). Corrected swarms were positively identified as krill using the variable $\Delta S_{v120-38}$ dB window identification technique (CCAMLR 2009) and converted to abundance using the simplified stochastic distorted-wave Born approximation target strength model (SDWBA) (McGehee et al. 1998, Demer & Conti 2003, Conti & Demer 2006, CCAMLR 2009). Minimum and maximum $S_{v120-38}$ values for different size ranges of krill (identified from the net samples) were calculated using the SDWBA model, based on the distribution of 99% of the krill length frequencies estimated from a cumulative distribution function. Krill length frequency data were binned in 10 mm windows, rounded down to calculate the minimum limit, and rounded up to calculate the upper limit. The ranges used are detailed in Tarling et al. (2009), and are based on the CCAMLR recommended ranges (CCAMLR 2009). The simplified SDWBA was applied using fixed values for orientation N (11° , 4°) which represent the mean and standard deviation of the normal distribution of krill orientations relative to horizontal (0°), as defined by Demer & Conti (2005). The material properties of krill were based on those calculated/inferred for the CCAMLR synoptic survey in the Scotia Sea region at the same time of year as the present study (CCAMLR 2009).

For spatial analysis, the cruise track was split into 1 km resets, and averages and counts were computed within each reset. Some of these segments of acoustic data had to be discarded due to sampling problems such as bad weather. A reset was deemed valid if the GPS fixes in the acoustic data had no gaps larger than 50 m after the elimination of the bad acoustic data. Time of day and position were taken from the starting point of each reset. The distance to the nearest point on the shoreline (of any landmass, e.g. either the islands or the Antarctic Peninsula) was computed using a great circle algorithm implemented in the R package 'sp' (Ihaka & Gentleman 1996). Bottom depths were taken from the GEBCO_08 grid (version 20091120, www.gebco.net) closest to reset midpoints.

The data were split into night- and daytime observations, in order to check for diel effects. This split was done according to the local time of sunset and sunrise, with data accepted as 'daytime' if it was recorded between sunset and sunrise. Because the data was recorded during the Antarctic summer, it follows that 'daytime' data encompasses most of the data (Fig. 1).

Data were subsequently divided according to estimated distance to the shoreline into the following

zones: 0 to 50, 50 to 100, 100 to 200 and >200 km. The choice of these zones match those of an accompanying study by Cresswell et al. (2009), where krill swarming and vertical migration behaviour is predicted to change over this cline as a function of the different levels of land-based predation and food availability. In referring to these zones, we use the terminology inshore/offshore to describe proximity to any landmass. Our definition only reflects distance away from shore and should not be confused with on-shelf and off-shelf, which is a bathymetric categorisation. We detail the bathymetric ranges of the 4 zones in Fig. 2 as background information.

The distance between swarms was calculated from the midpoints of each krill swarm using the same algorithm as for calculation of distances to shoreline. Swarm acoustic biomass was expressed as the nautical area scattering coefficient (NASC, $m^2 n \text{ mile}^{-2}$) and the concentration of krill within swarms in terms of mean volume backscatter. All averaging and statistical analyses were undertaken in the linear domain ($s_v m^{-1}$). Conversion from acoustic to absolute numbers of krill was carried out using the predictions of the SDWBA model described at the beginning of this section ('Post-processing of detected swarms').

Statistical differences in swarm properties and distribution between zones were tested for using a combination of a Mann-Whitney rank sum test and a Kruskal-Wallis 1-way ANOVA on rank test within the SIGMASTAT 2.03 software package.

RESULTS

A total of 4274 resets of 1 km were successfully completed across the entire survey area, distributed between the 4 zones as follows: 429 resets in the 0 to 50 km zone, 645 in the 50 to 100 km zone, 955 in the 100 to 200 km zone and 2245 in the >200 km zone. A total of 11 723 swarms were identified across all zones: 582 swarms in the 0 to 50 zone, 2239 in the 50 to 100 km zone, 3090 in the 100 to 200 km zone and 5812 in the >200 km zone. Seventy percent of swarms were detected during the day and 30% at night. We examined how time of day affects the distribution of swarms and then controlled for these effects before further examination of the swarm's physical properties relative to the proximity of land.

Day versus night swarming patterns

Both the number and the acoustic biomass (NASC) of detected swarms per km were significantly lower during the night than the day across the whole survey grid

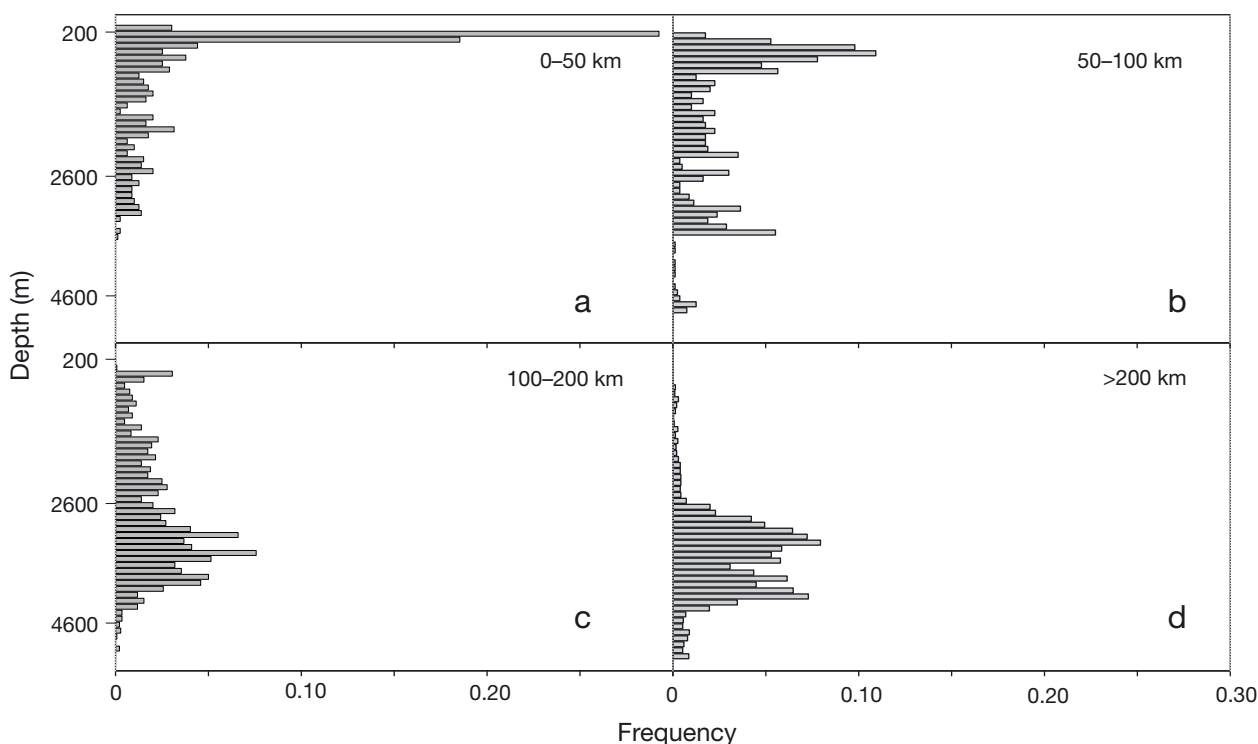


Fig. 2. Frequency distributions of depth of resets within the 4 land-proximity zones: (a) 0–50, (b) 50–100, (c) 100–200 and (d) >200 km

(Mann-Whitney rank sum test: NASC: $p < 0.001$; swarm numbers: $p < 0.001$). In fact, only about 1 in 3 of each 1 km reset surveyed during night-time contained swarms at all, whereas >44 % of daytime cells contained at least 1 swarm (Fig. 3).

Our approach was to separate the day and night data sets and focus mainly on the daytime data to minimise this potential bias in our analyses. We return to the issue of the depth distribution of swarms relative to time of day in a later section ('Vertical distribution of krill swarms').

Physical properties of krill swarms

Swarm area. Krill swarms were significantly larger in cross-sectional areas (m^2) in inshore zones (<100 km from land) compared to zones further offshore (Mann-Whitney rank sum test, $p < 0.001$) (Fig. 4). The vast majority of swarms had an area of between 10 and 100 m^2 . However, the major difference between zones was observed in the greater proportion of swarms with areas above 1000 m^2 in inshore areas. As a result, the median cross-sectional area was around 120 m^2 in inshore regions and below 80 m^2 further offshore (>100 km, Table 2).

Swarm volume backscattering strength (S_v). The average S_v of swarms was significantly greater in

inshore compared to offshore zones (Kruskal-Wallis 1-way ANOVA on ranks: $H = 190.91$, 3 df, $p < 0.001$) (Fig. 5). The S_v of the majority of swarms was between -65 dB and -69 dB. However, there was proportionally greater numbers of swarms with average S_v values in excess of -55 dB in inshore regions.

Inter-swarm distance. Typical inter-swarm distances differed significantly between zones (Kruskal-Wallis 1-way ANOVA on ranks: $H = 160.122$, 3 df, $p < 0.001$) (Fig. 6). Most notably, median inter-swarm distance in the 0 to 50 km zone (194 m) was around 60 % larger than in all other zones (~ 100 m). Fig. 6 shows that inter-swarm distances were log-normally distributed. The peak was comparatively broader in the 0 to 50 km zones as a result of the number of swarms with inter-swarm distances >100 m being proportionally larger.

Swarm acoustic biomass (NASC). The NASC per swarm decreased significantly moving from inshore to offshore (Kruskal-Wallis 1-way ANOVA on ranks: $H = 276.08$, 3 df, $p < 0.001$), with the median swarm acoustic biomass in the 0 to 50 km zone being more than twice that in the >200 km zone (50.7 and 20.6 $\text{m}^2 \text{ n mile}^{-2}$ respectively, Table 2). This is to be expected given that both the area and S_v of swarms is greatest in inshore areas, and resulted in overall acoustic biomass peaking in the 0 to 50 km zone. Five percent of swarms had an acoustic biomass in excess of 10 000 $\text{m}^2 \text{ n mile}^{-2}$

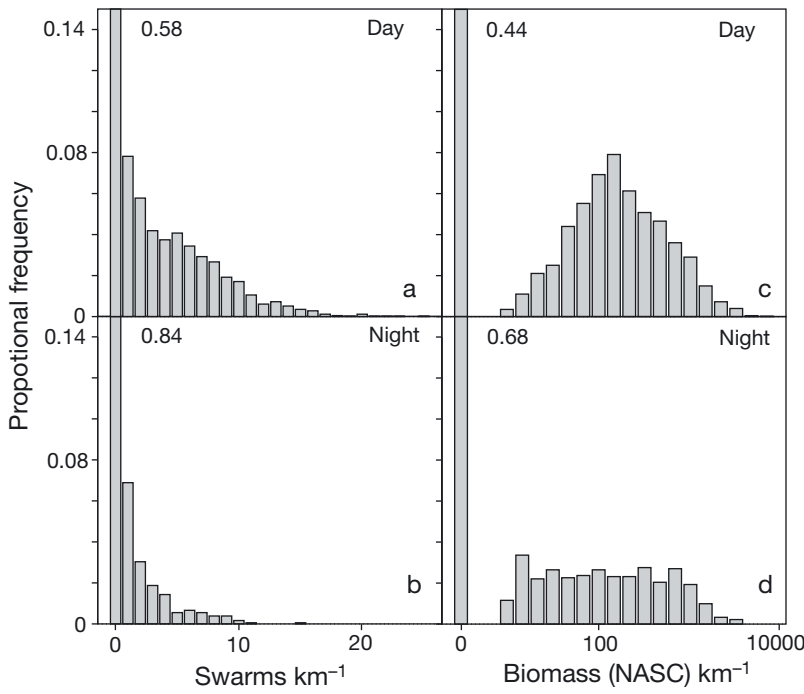


Fig. 3. Frequency distribution of swarms per km by (a) day and (b) night, and acoustic biomass (NASC) per km by (c) day and (d) night across the entire survey grid. Value on the top left of each graph represents the proportional frequency of 0 values (off-scale). NASC: nautical area scattering coefficient

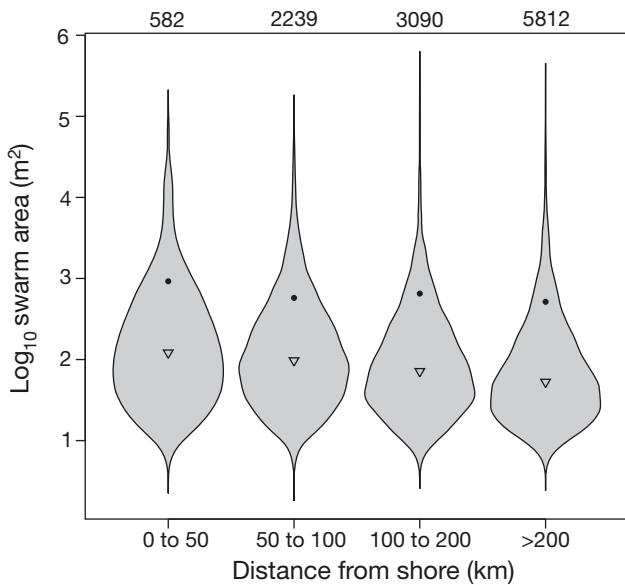


Fig. 4. Frequency distribution of log swarm area in different land-proximity zones. Inverted triangles: median, dots: mean, values. Frequencies in each respective zone were scaled such that the total area amounts to 1. The total number of swarms within each zone is indicated at the top of each plot

Table 2. Summary statistics for swarms and for 1 km resets in the 4 zones. Statistics are for daytime data only. Values are presented as 25 % quartile/median/75 % quartile. NASC: nautical area scattering coefficient; n mile: nautical mile

Zone	Swarm properties				Spatial properties				
	Density (dB)	Cross-section (m ²)	Distance between swarms (km)	Depth (m)	Length (m)	Height (m)	Acoustic biomass (NASC, m ² n mile ⁻²)	Swarms km ⁻¹	Acoustic bio-mass km ⁻¹ (NASC, m ² n mile ⁻²)
0–50 km	–67.0/–64.5/–58.8	43/121/396	0.076/0.194/0.551	42.9/73.7/117.8	31/52/99	3.3/6.9/13.5	15/51/298	0/0/2	0/0/275
50–100 km	–66.8/–65.0/–61.8	39/97/290	0.054/0.115/0.238	31.4/48.5/67.8	31/52/98	3.1/5.9/10.9	15/33/106	0/2/6	0/149/735
100–200 km	–67.3/–65.6/–62.3	31/72/208	0.046/0.096/0.195	23.5/34.7/50.1	27/45/82	2.8/5.0/9.3	13/25/90	0/1/5	0/62/550
>200 km	–67.6/–66.0/–63.1	24/53/155	0.052/0.106/0.223	24.0/33.4/44.0	25/41/77	2.4/4.1/7.6	11/21/58	0/1/4	0/12/206

in the 0 to 50 km zone compared to <1% in all other zones (Fig. 7). This is further seen in the relative contribution of individual swarms to total zone acoustic biomass. In the 0 to 50 km zone, swarms with an acoustic biomass in excess of $10\,000\text{ m}^2\text{ n mile}^{-2}$ contributed

46% of total zone acoustic biomass, while the contribution was 21, 6 and 28% in the 50 to 100, 100 to 200 and the >200 km zones respectively.

Horizontal distribution of krill swarms

Swarm numbers per km. There were significantly more swarms per km in the 50 to 100 km zone than in any other zone (Kruskal-Wallis 1-way ANOVA on ranks: $H = 106.43$, 3 df, $p < 0.001$), with a median of 2 swarms km^{-1} compared to 1 swarm km^{-1} in both the 100 to 200 km and the >200 km zones, and 0 swarms km^{-1} in the 0 to 50 km zone. As shown in Fig. 8, however, the number of swarms encountered per km was quite variable. For instance, the maximum number of swarms was 18 km^{-1} in the 0 to 50 km zone and 26 km^{-1} in the 100 to 200 km zone. Furthermore, the proportion of 1 km sections containing no swarms at all ranged from 31% in the 50 to 100 km zone to 51% in the 0 to 50 km zone.

NASC per km. The median NASC per km in the 50 to 100 km zone was significantly higher than in any other zone (Kruskal-Wallis 1-way ANOVA on ranks: $H = 113.96$, 3 df, $p < 0.001$) with a median value of $149\text{ m}^2\text{ n mile}^{-2}$ compared to 62 and $12\text{ m}^2\text{ n mile}^{-2}$ in the 100 to 200 and the >200 km zones, respectively. Although the median value in the 0 to 50 km zone was 0, meaning that over half the resets contained no krill swarms at all, this zone also had the highest NASC per km, indicating that when krill was present, it occurred at very high levels of acoustic biomass (Fig. 9).

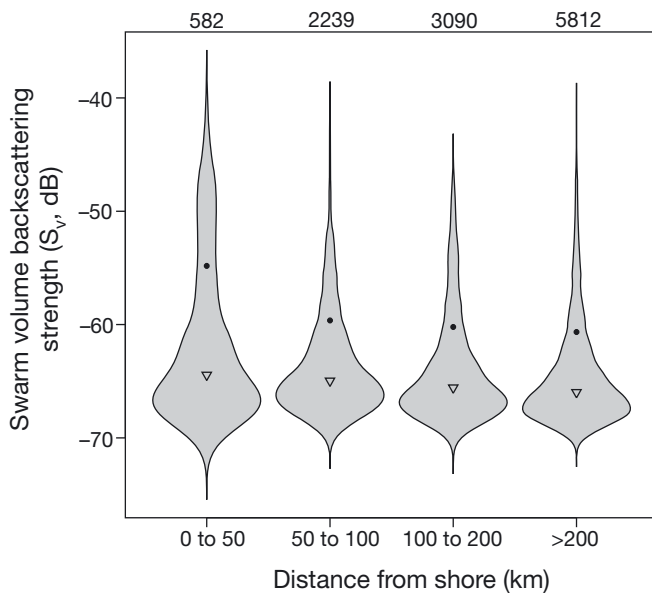


Fig. 5. Frequency distribution of volume backscattering strength (S_v , re. 1 m^{-1} , dB) in different land-proximity zones. Inverted triangles: median, dots: mean, values. Frequencies in each respective zone are scaled such that the total area amounts to 1. The total number of swarms within each zone is indicated at the top of each plot

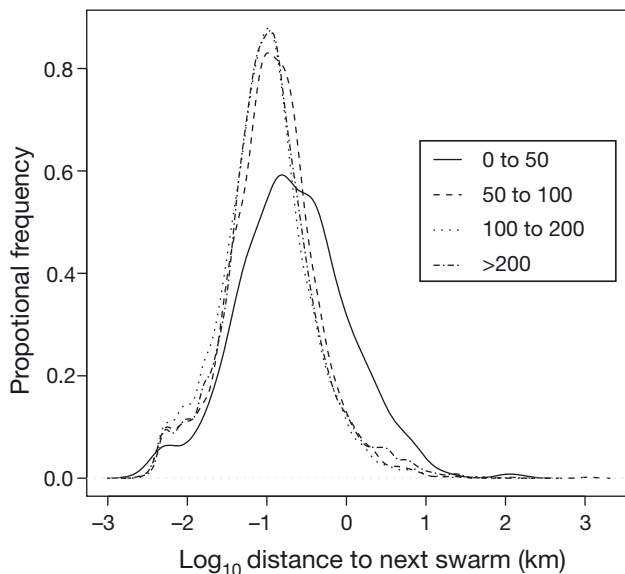


Fig. 6. Frequency distribution of inter-swarm distances in different land-proximity zones. Frequencies in each respective zone were scaled such that the total area beneath the curve amounts to 1

Vertical distribution of krill swarms

The majority of krill swarms were confined to the upper 50 m during the daytime in zones that were >100 km from shore (Fig. 10a). Closer than 100 km, there was a progressive spreading of swarms through the water column, such that a much greater fraction of swarms was found in the deeper parts of the water column. Hence, whereas 3% or less of swarms occurred deeper than 100 m in the offshore zones, the percentage increased to 8 and 34% in the 50 to 100 and the 0 to 50 km zones, respectively. Depths above 13 m were largely excluded as a result of surface-noise contamination.

Although we earlier (see ‘Results — Day versus night swarming patterns’) pointed to the potential bias in night-time data, it is instructive to examine this data set with respect to depth as a comparison to daytime distributions (Fig. 10b). One of the major differences between day and night was the apparent movement of the main centre of acoustic biomass to the upper part of

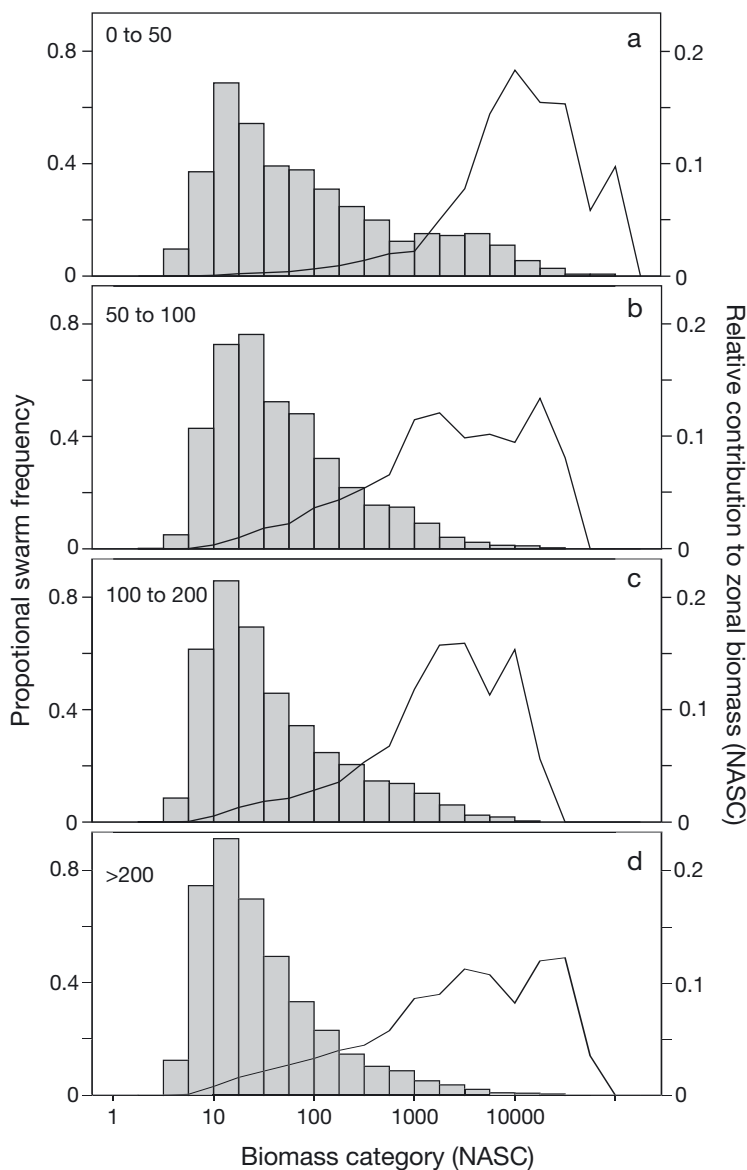


Fig. 7. Contribution of swarm frequency (bars) and swarm acoustic biomass (lines) to total zone acoustic biomass (NASC, $\text{m}^{-2} \text{ n mile}^{-2}$) in the 4 land-proximity zones: (a) 0–50, (b) 50–100, (c) 100–200 and (d) >200 km. NASC: nautical area scattering coefficient; n mile: nautical mile

the water column (0 to 50 m) in the inshore zones (<100 km from shore) at night. The most likely explanation is the diel vertical migration (DVM) of the population to the surface during night-time (normal DVM). However, contrasting with that pattern is an apparent reverse DVM in the zones further than 100 km from shore, with the population spreading to deeper parts of the water column during the night: 16% of swarms were found below 100 m during the night-time as opposed to <3% during the day. Also notable was bimodality in certain night-time depth distributions,

with one part of the population located in the upper water column and the other deeper than 100 m.

Swarm packing concentrations and acoustic biomass

Table 3 gives swarm packing concentrations (ind. m^{-3}), and swarm biomass density (g m^{-3} , g m^{-1}) values typically seen across the zones surveyed in the present study. The in-shore zone (0 to 50 km) had the highest average swarm density of 95 ind. m^{-3} , which equated to 41 g m^{-3} (Table 3). Average swarm densities in the outer zones (>50 km from shore) were between 24 and 31 ind. m^{-3} (14 to 17 g m^{-3}). Swarm biomass density ranged between 0.6 and 1823 g m^{-3} across all zones, although values $>500 \text{ g m}^{-3}$ occurred in <0.4% of swarms. Swarm sum biomass ranged between 4.6 and $4\,528\,821 \text{ g m}^{-1}$.

DISCUSSION

There were significant differences in the distribution and characteristics of swarms across the Scotia Sea in relation to the proximity of land during summer 2003. In particular, we found that large proportions of krill acoustic biomass inshore (0 to 50 km from land) were packed into a small number of large, acoustically dense swarms. Inshore swarms were also likely to be deeper than those further offshore. Both characteristics suggest that the krill were responding to predatory threat, although other factors such as food availability and the physical properties of the water column may also contribute to this pattern.

Horizontal distribution of swarms

We found that the majority of krill acoustic biomass resided in a relatively small number of swarms, with >50% of acoustic biomass occurring in <1% of swarms. Large swarms were particularly common in the 0 to 50 km zone. The acoustic density of inshore swarms was also significantly greater than that of offshore swarms. A further interesting aspect of the 0 to 50 km zone was that the median acoustic biomass within 1 km resets was 0, yet the zone also had the highest average acoustic biomass per km. By compari-

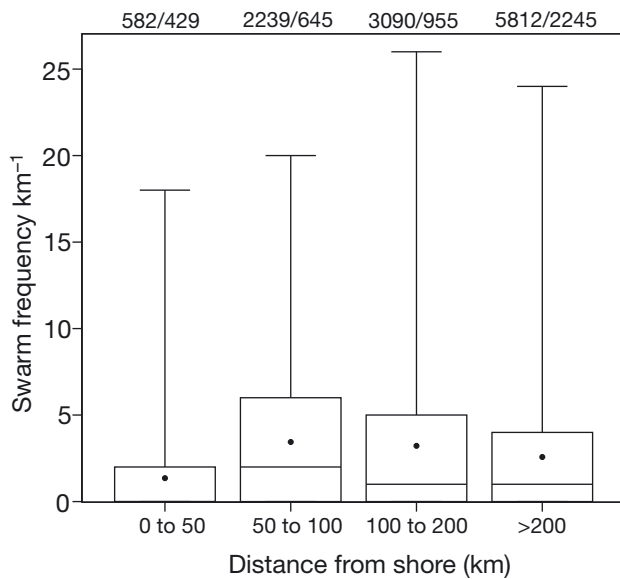


Fig. 8. Distribution of swarms per km in different land-proximity zones. Boxes extend from lower to upper quartile, with median shown by a horizontal bar. Whiskers extend to maximum values. Dot represents average number of swarms per km observed in each zone. Numbers at the top of each plot indicate total number of swarms and number of 1 km resets respectively

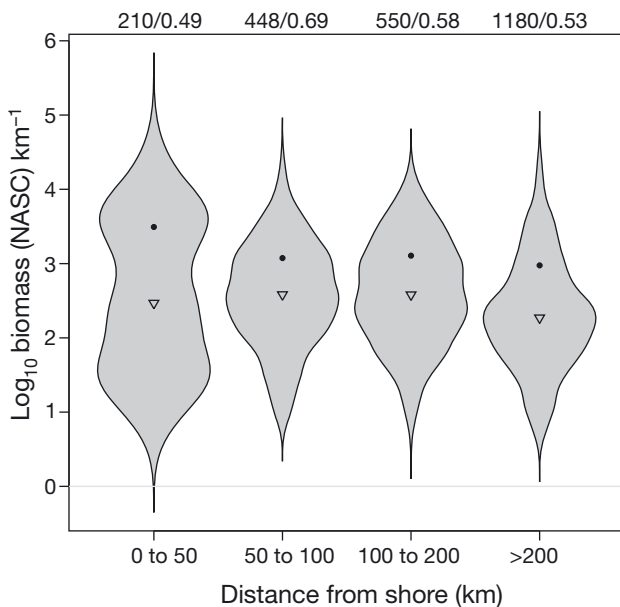


Fig. 9. Frequency distribution of log acoustic biomass per km in different land-proximity zones. Data is restricted to those resets that contain krill. Inverted triangles: median, dots: mean, values. Frequencies in each respective zone were scaled such that the total area amounts to 1. Numbers at the top of each plot indicates respectively the total number of resets and the proportion of resets containing krill in each zone

son, zones further offshore had a much closer match between the median and the mean acoustic biomass per km. This indicates that krill swarms in the inshore zone were not only larger and acoustically denser, but also more patchily distributed than further offshore.

The uneven distribution of biomass between swarms has been previously reported in a number of acoustic studies (Miller & Hampton 1989b, Hewitt & Demer 1993, Murray et al. 1995, Ross et al. 1996, Lascara et al. 1999, Pauly et al. 2000, Lawson et al. 2008b). Nevertheless, the present study is the first to report that the degree to which this distribution becomes uneven increases with proximity to land. Predation from land-based air-breathing predators is probably the largest source of mortality during the summertime in the Scotia Sea (Boyd 2002). Increasing swarm density provides better surveillance capacity and the denser or more integrated the school, the faster the propagation of an escape response through aggregation (O'Brien 1987). Zhou & Dorland (2004) found that krill aggregated more densely in the presence of predators. Cox et al. (2009) showed that the topography of the swarm edge (the roughness) altered depending on the proximity of predators. Predators are cognitively constrained in being able to track individuals that are visually indistinguishable (Krakauer 1995) and capture rates decrease as group size increases (Landeau & Terborgh 1986).

Studies into interactions between krill and its predators have stressed the importance of especially large patches to foraging behaviour (Heinemann et al. 1989, Veit & Hunt 1991, Veit et al. 1993). Veit et al. (1993) reported that birds and seals bypassed smaller aggregations of krill in anticipation of finding a larger one later on. Although large swarms may be visible from greater distances than small swarms, this may be counteracted by the resultant larger-scale patchiness, which makes the probability of interception by a randomly searching predator less likely. In general, it is assumed that predation risk increases with the local density of aggregations, since predators are attracted by groups (Hofmann et al. 2004). However, in inshore regions, the main predation threat is from penguins and seals, which only have a small search radius and difficulties in detecting distant groups of prey or feeding aggregations of other predators (Hunt et al. 1992). Forming into large, dense swarms may therefore be the best strategy for krill to avoid detection when inshore.

We found that the 50 to 100 km zone contained the most swarms per km, whereas the 0 to 50 km zone had the highest acoustic biomass (NASC) per km. Trathan et al. (2003) found that bathymetry was a consistent predictor of krill abundance, with abundance being greatest nearest the shelf break, whereas Lawson et al. (2008b) found the highest biomass in regions close to land during winter and autumn. In East Antarctica

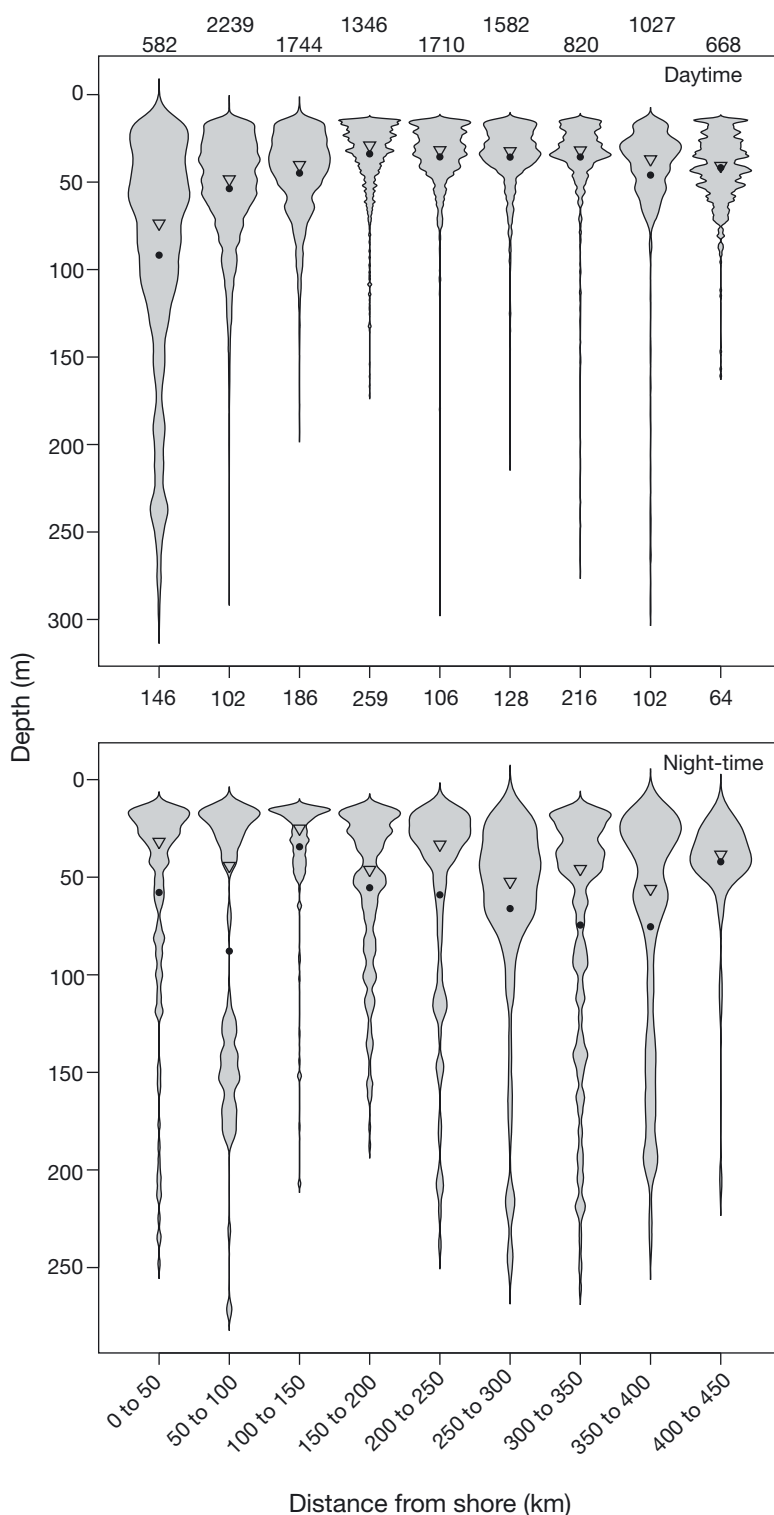


Fig. 10. (a) Daytime and (b) night-time vertical distribution of swarms with respect to distance from shore. Zones were sub-divided into 50 km intervals to a maximum 450 km from the shore. Frequencies in each respective 50 km interval were scaled such that the total area amounted to 1. Inverted triangles: median, dots: mean, values. The total number of swarms within each zone is indicated at the top of each plot. Note that some areas within the 0 to 50 km zone were shallower than 300 m

(80 to 150° E), Pauly et al. (2000) found that krill aggregations were most frequently encountered in the shelf break region, where the summer ice edge, 1000 m isobaths and the Antarctic slope front coincided.

Continental shelf and shelf-edge environments in the Southern Ocean are frequently associated with semi-permanent phytoplankton blooms (Korb & Whitehouse 2004, Pollard et al. 2007), which are ideal feeding environments for krill.

Meanwhile, predator species show a decrease in density with increasing distance from colonies (Hunt et al. 1992). The shelf-edge zone may therefore provide an ideal compromise between food availability and predator avoidance. Nevertheless, shelf-edge environments also contain strong current flows (Meredith et al. 2003a,b) and krill may find it difficult to retain position within such environments (Cresswell et al. 2007). Atkinson et al. (2008) compared krill biomass across continental shelf and oceanic regions in the Atlantic sector of the Southern Ocean and found that, although krill density was 1.65 times higher over shelves, they contained only 13% of the total krill stock in the sector, with the remainder occurring over deep oceanic areas. They concluded that while growth rates are higher in productive shelf regions, the ocean provides a refuge from shelf-based predators (Atkinson et al. 2008).

Vertical distribution of swarms

In all zones, the majority of krill swarms were found in the upper 100 m. Lascara et al. (1999) similarly found that the vertical distribution of oceanic krill in summer was skewed towards the surface, with only 25% of biomass deeper than 50 m and hardly any biomass below 100 m. Nevertheless, we found that the vertical distribution pattern changed closer to shore, with a spreading of the population through the water column such that almost 34% of the population was found deeper than 100 m in the 0 to 50 km zone. Residing deeper in the

Table 3. Equivalent average swarm densities between acoustic and absolute units using the simplified stochastic distorted-wave Born approximation (SDWBA) target strength model (McGehee et al. 1998, Demer & Conti 2003, Conti & Demer 2006, CCAMLR 2009). Target strength values were calculated on a region-specific basis according to the length-frequency distributions of the krill population. Three major regions were distinguished on this basis: southwest Scotia Sea (SW), northeast Scotia Sea (NE) and South Georgia (SG). Target strengths (dB) calculated with the SDWBA model were applied to determine swarm packing concentrations (ind. m⁻³) as follows: SW: -74.6607, NE: -74.4974 and SG: -74.448. Swarm biomass density (g m⁻³) was calculated by multiplication of ind. m⁻³ by the following factors: SW: 0.27480, NE: 0.69565 and SG: 0.800814. Swarm biomass density was multiplied by swarm cross-sectional area to give swarm sum biomass (g m⁻¹). Only daytime data were used in these calculations

Zone	Volume backscattering strength (S _v re. 1 m ⁻¹ , dB)	Packing concentration (ind. m ⁻³)	Biomass density (g m ⁻³)	Sum biomass (g m ⁻¹)
0–50 km	-54.82	95.03	41.11	40094.49
50–100 km	-59.64	31.17	15.38	8143.30
100–200 km	-60.21	27.26	14.03	12331.80
>200 km	-60.66	24.22	16.85	10374.69

water column is a classic strategy to reduce the predation threat from visually foraging predators and is also likely to be a particularly effective strategy against air-breathing diving predators. Eighty percent of Antarctic fur seal and macaroni penguin dives are shallower than 40 to 60 m (Croxall et al. 1985, 1988) and these predators are also less likely to travel more than 100 km away from their colony. Hunt et al. (1992) found that 75% of Antarctic fur seals and macaroni penguins at sea occurred 18 to 56 km away from land. The threat of surface-based predation may explain why krill in inshore regions were more likely to reside deep in the water column. This threat is lower in offshore regions, which may allow the krill here to occupy shallow depths throughout the diel period. While we interpret the vertical behaviour of krill to be dependent on the predators, the reverse is also likely to be true. For instance, Staniland & Boyd (2003) found that fur seals perform more deep daytime dives when on-shelf compared to off-shelf.

By night-time, almost all krill swarms in the inshore region were found in the upper 50 m, which is consistent with a classic DVM pattern. If krill occupy deep, unproductive layers in the daytime, their high energetic requirement necessitates a migration into the productive surface layers during the night-time to feed. DVM is observed in many zooplankton species and is sometimes thought of as a relatively fixed behaviour controlled by the light cycle (Ringelberg 1995). However, Cresswell et al. (2009) predicted distinct selective advantages to those krill capable of altering depth in relation to predation risk over short time scales. The present study gives evidence of

krill reacting to predator disturbance through spreading through the water column. Zamon et al. (1996) showed that penguins will target the layer where the relative volumetric contribution of moderate to high krill density levels is greatest. Escape from this threat would be achieved through moving either up or down the water column, which may drive the observed vertical spreading of krill.

Further evidence of the relative flexibility of krill migration is seen offshore, where swarms adopt a deeper position in the water during night-time than during the day. Such reverse DVM has been previously reported in Antarctic krill by Godlewski (1996), but it is unclear as to the exact cause and/or benefit of this behaviour in the present context. One potential explanation is that feeding activity increases during

night-time and swarms sink when constituent individuals become satiated (sensu Tarling & Johnson 2006). Alternatively, such swarms may be comprised of individuals that are moulting in a synchronised manner (Buchholz 1991), and so have a reduced swimming capacity (Thomasson et al. 2003).

Nevertheless, we found that both swarm numbers and acoustic biomass were apparently lost from the water column during night-time. This was probably because either some swarms had dispersed and fell below our threshold detection level or had migrated above the depths visible to our echosounder. It is therefore possible that the numbers of swarms in the deeper layers remained approximately the same both day and night, but that the deep night-time swarms became relatively more important as a result of the loss of swarms above the echosounder.

Swarm packing concentrations and acoustic biomass

We mainly expressed the acoustic density and biomass of krill swarms in terms of the acoustic units S_v (dB) and NASC (m⁻² n mile⁻²) respectively. Converting from acoustic units to absolute krill numbers is very sensitive to target strength models, which are under continual development (CCAMLR 2009). Providing results in terms of acoustic units allows conversions to be made as and when further target strength models are published. In our own conversion (Table 3), we used the simplified SDWBA model (McGehee et al. 1998, Demer & Conti 2003, Conti & Demer 2006).

We found that the density of biomass within swarms ranged between 0.6 and 1823 g m⁻³ across all zones, with the highest average levels (41 g m⁻³) being found inshore. These values are broadly in line with previous acoustic studies within this sector of the Southern Ocean. Ricketts et al. (1992) found average densities of 33 g m⁻³ and Kalinowski & Witek (1985), 72 g m⁻³. Las-cara et al. (1999) reported densities of between 150 and 500 g m⁻³. It is to be noted that such acoustically estimated densities are well below estimated densities of visually observed krill schools, where values of up to 15 000 g m⁻³ have been reported (Hamner & Hamner 2000).

Harmonising swarm biomass estimates between methods remains a major challenge in krill science.

Implications for fisheries management

We found that swarms in offshore regions were more frequently encountered but contained relatively low acoustic biomass and packing concentrations of krill. Inshore, swarms were more sparsely distributed but contained greater amounts of krill acoustic biomass. From the perspective of a fishing vessel, although swarms would be commonly found offshore, the yields from fishing such swarms would be relatively low. Inshore, a much greater effort would be required in searching for swarms but, once located, the yields per swarm will be relatively high. These findings agree with those of Hill et al. (2009), who found that areas suitable for krill exploitation were more common in shallower water (i.e. closer to shore) than in deeper water (i.e. further offshore). The study by Hill et al. (2009) was based on a re-analysis of acoustic data from a series of simultaneous cruises carried out in the Scotia Sea in 2000 (Hewitt et al. 2004). Hill et al. (2009) also examined fishery data for the past 10 yr and found that the majority of reported catches were taken in inshore regions. This may result from a combination of the abundance of on-shelf krill and the ease of access from mooring locations that provide shelter and stable anchorages for processing.

The management of the krill fishery in the Southern Ocean by CCAMLR takes an ecosystem approach, aiming to balance the requirements of the target species, the wider ecosystem and the fishery itself. Further development of this management strategy may include spatial restrictions on harvesting, particularly a limit on the level of fishing in inshore areas where krill predators are most affected. Whether or not such a limitation would be detrimental to the fishery will depend on a number of factors, including the exact size and density thresholds for profitable fishing of swarms and the effect of small-scale swarm distribution on searching

times. We recommend that focusing on patterns of swarm structure and distribution provides a powerful means by which to inform these management decisions.

CONCLUSIONS

Quantifying the availability of pelagic prey to diving predators is a complicated problem and acoustic characterisation of the prey field is one important step towards a fuller understanding of predator-prey interactions in marine environments (Zamon et al. 1996). Overall, we found that krill were patchier and less available to predators inshore (< 50 km from land). They reached peak acoustic biomass in the 0 to 50 km zone, though the highest number of swarms per km was found in the 50 to 100 km zone. Veit et al. (1993) concluded that the distribution of krill predators was disproportionately influenced by a few large swarms of krill. It is these large swarms that are also of most interest to krill trawlers (Mangel 1988). Both predators and trawlers are therefore likely to focus on the same regions and this potential conflict must be managed effectively in future krill-fishery policy.

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