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The use of acoustic sampling to estimate the dispersion and abundance of euphausiids, with an emphasis on Antarctic krill, *Euphausia superba*

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Abstract

Acoustic sampling has been used to investigate the ecology of Antarctic krill (*Euphausia superba*) and to provide information on dispersion and abundance necessary to manage their harvest. Population estimates based on multi-ship acoustic surveys have been used to set catch limits. More localized acoustic surveys have been conducted to study the response of land-breeding krill predators to local variations in their food supply. These and future surveys may result in additional controls on the fishery. In this context, the use of acoustics to survey euphausiids is reviewed and major sources of uncertainty are discussed. These issues are organized as they pertain to the two broad steps of acoustic surveys: (1) estimating the volumetric density of krill (measurement uncertainty) and (2) mapping krill distribution and estimating abundance (sampling uncertainty). Published by Elsevier Science B.V.

Keywords: SONAR; Active acoustics; Zooplankton; Euphausiids; CCAMLR

1. Introduction

Euphausiids have long been recognized as a critical element of the natural economy of the world's oceans (Sars, 1885; Brinton, 1962; Marr, 1962; Mauchline and Fischer, 1969; Mauchline, 1980). Early fishery biologists repeatedly stressed the importance of various species of euphausiids as food for exploited fish and whale stocks (Lebour, 1924; Hickling, 1927; Hjort and Rund, 1929). Norwegian whalers referred to the euphausiids found in large numbers in the stomachs of whales caught in the north Atlantic as *stor krill* (or large krill referring to *Meganyctiphanes norvegica*) and *smaa krill* (or small krill referring to *Thysanoëssa inermis*); the word "krill" is now used in reference to euphausiids in general (Mauchline and Fischer, 1969). Laws (1985) estimated that 190 million tons of Antarctic krill (*Euphausia superba*) were consumed annually by baleen whales in the Southern Ocean prior to their exploitation. It is estimated that current populations of whales, birds, pinnipeds, fish, and squid consume 250 million tons of Antarctic krill annually (Miller and Hampton, 1989a). Of the 85 species of krill, Mauchline and Fischer (1969) list nine of primary importance in terms of their distribution range and biomass: *M. norvegia, E. superba, E. pacifica, E. crystallorophias, T. inermis, T. raschii, T. macrura, T. longipes* and *T. inspinata*. They note that these species

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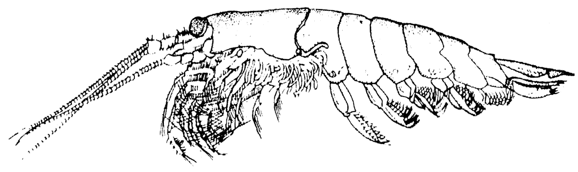

Fig. 1. Antarctic krill, *Euphausia superba* Dana, from Miller and Hampton (1989a).

constitute a large fraction of the plankton where they are found, and that their biomasses are largest at high latitudes. In addition to their numbers, the habit of euphausiids to form large swarms makes them particularly important as prey to marine vertebrates. After considering the large biomass of the Antarctic krill population, the extensive range of their geographic distribution, and their tendency to aggregate in swarms, Macintosh (1968) suggested that acoustic technology be used to locate areas of high krill density.

The ubiquitous nature of sound scattering layers throughout the world's oceans has been of interest to oceanographers since their discovery in the 1940s (Farquhar, 1977). During 1950s and 1960s, underwater acousticians and biologists gradually shifted their attention from describing the location, movement, and shape of these layers to determine their composition (see Barham's comments on p. 626 of Farquhar, 1977). The use of higher frequency transducers was initiated by several investigators to study volume backscattering from zooplankton (e.g. Barraclough et al., 1969; Bary and Pieper, 1971; Sameoto, 1976; Macaulay, 1978). Multi-beam (Ehrenberg, 1974, 1979) and multi-frequency (Holliday, 1980) systems were applied to the study of zooplankton which allowed the apportionment of volume backscattering into animal size classes. These developments led to the use of acoustic tools to describe specific ecological phenomena (e.g. Macaulay et al., 1984; Greene et al., 1988) which would be difficult or impossible to investigate using nets.

A large portion of the Antarctic krill population was acoustically surveyed in 1981 during a multi-nation, multi-ship experiment (Hemple, 1983; Miller and Hampton, 1989a). Abundance estimates derived from the survey, although plagued with technical problems and dated by 10 years, formed the basis of a management scheme adopted in 1991 to control the harvest of krill in the Atlantic sector of the Southern Ocean (Figs. 1 and 2). The management scheme incorporated a population model that included abundance estimates derived from acoustic surveys, as well as information

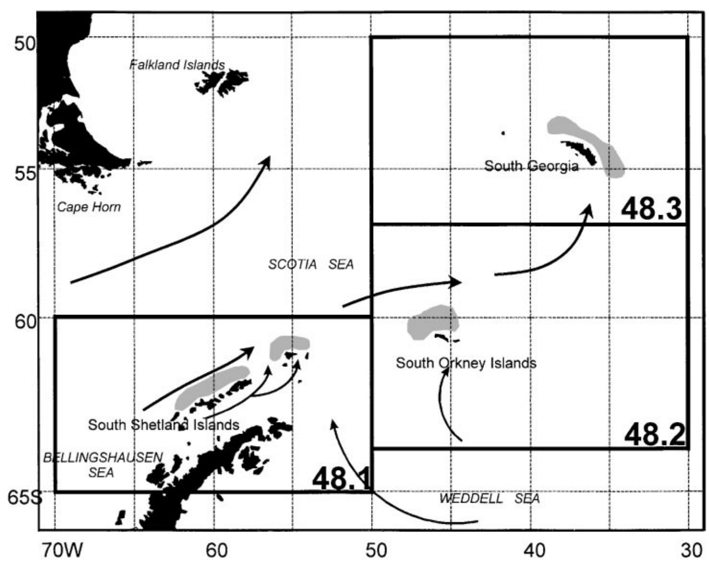

Fig. 2. Southwest Atlantic sector of the Southern Ocean where 85–95% of the annual krill harvest is taken. Bold boxes outline FAO statistical subareas 48.1 (South Shetland Islands), 48.2 (South Orkney Islands), and 48.3 (South Georgia). Shaded areas indicate the location of fishing grounds, and arrows indicate the general direction of surface currents.

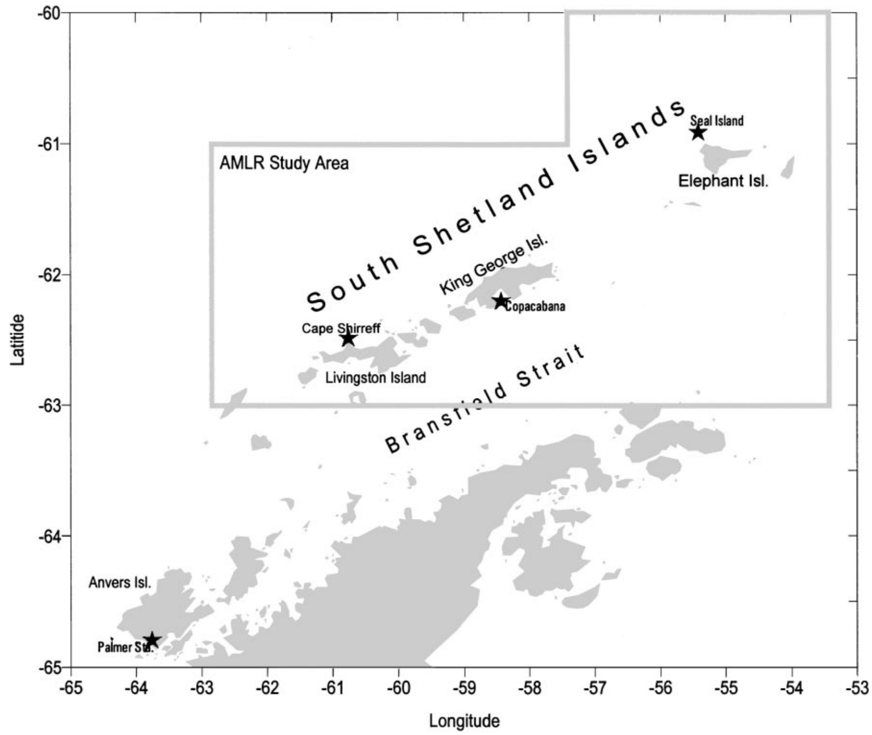

Fig. 3. The US AMLR program study area in the vicinity of the South Shetland Islands. The bold outline indicates the area within which surveys are conducted to describe the distribution and abundance of krill, their demographics, the position of hydrographic fronts and surface currents, and the distribution of phytoplankton biomass and productivity. The stars indicate the location of sites where the reproductive success and foraging behavior of land-breeding krill predators are monitored.

on the variability of vital rates (e.g. natural mortality, longevity, and fecundity) and recruitment (Butterworth et al., 1991, 1994, see also Nicol, 1989; Nicol and de la Mare, 1993, for reviews of the Antarctic krill fishery and its management). The model was set up to estimate the level of harvest that the krill population can sustain. Of equal concern is the potential effect of the harvest on vertebrate populations dependent on krill as prey (Mauchline and Fischer, 1969). In particular, attention has been drawn to colonies of land-breeding seals and penguins that are vulnerable to changes in the local availability of krill (Croxall, 1989). Acoustic surveys have been conducted in the vicinity of breeding sites as part of a larger effort to describe the effects of krill availability on predator performance (e.g. Hewitt and Demer, 1993; Veit et al., 1993b). It is expected that these studies will lead to refinements of the management scheme that will minimize the effects of localized krill harvest on adjacent land-breeding predators.

Management of the krill fishery is accomplished by agreement among members of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR); currently 29 nations, including the European Community, are members of the Commission established by CCAMLR or have acceded to the terms of CCAMLR. In support of CCAMLR, several national programs have employed the use of acoustic methods to assess the distribution and abundance of Antarctic krill (e.g. the US Antarctic Marine Living Resources (AMLR) program in the vicinity of the South Shetland Islands (Fig. 3), the British Antarctic Survey near South Georgia (Brierly et al., 1997), and the Australian Antarctic Division near Prydz Bay in the Indian Ocean sector of the Southern Ocean (Pauly et al., 1996)).

These surveys take advantage of a considerable body of work using acoustics to study euphausiids. In the following sections, we briefly review some of this work describing in more detail the 1981 survey, and then discuss uncertainties associated with acoustic measurements of krill density and those associated with extrapolating density to area estimates of distribution and biomass. We conclude with a discussion of the utility of using acoustic sampling to characterize krill aggregation patterns.

2. Acoustic studies of krill

Volume backscattering from layers composed of euphausiids has been measured by several investigators. Working in an inlet off the southeast coast of Vancouver Island, Bary and Pieper (1971) identified a ''midwater diffuse layer'' that migrated towards the surface at night as being composed of *E. pacifica*. Sameoto and Jaroszynski (1973) and Sameoto (1976) showed that acoustic scattering layers observed in the Gulf of St. Lawrence were composed of euphausiids, and that these layers moved towards the surface at night. Pieper (1979) described layers and swarms of euphausiids detected acoustically in the basins off the coast of southern California.

Extending this experience to the Southern Ocean, Cram et al. (1979) concluded that it was feasible to conduct large-scale surveys of Antarctic krill (*E. superba*) using high-frequency acoustic instruments. They also noted that, although there was a tendency for krill to rise towards the surface at sunset, swarms were observed near the surface at noon as well. Mathisen and Macaulay (1983) and Macaulay et al. (1984) used volume backscattering measurements to describe the morphology of aggregations of *E. superba* off Elephant Island, Antarctica. Several additional studies have employed volume backscattering techniques to study the distribution patterns of Antarctic krill (e.g. Witek et al., 1981; Everson, 1982; Guzman and Marin, 1983; Hampton, 1985; Klindt, 1986; Brinton et al., 1987; Everson and Murphy, 1987; Daly and Macaulay, 1988; Miller and Hampton, 1989b). Zhou et al. (1992) used volume backscattering measurements obtained from an acoustic Doppler current profiler (ADCP) to infer the dispersion of *E. superba* occupying coastal waters off the Antarctic Peninsula during the winter.

As a complement to measurements of volume backscattering strength, multi-beam and multi-frequency systems have been developed to aid in positioning animals in the acoustic beam, making behavioral observations, and determining size distributions. Dual beam and split beam systems can be used to measure the backscattering cross-sections of individual animals (Ehrenberg, 1974, 1979, 1989), providing that single targets can be resolved in the sample volume. Reuss and Jaffe (1992) and McGehee and Jaffe (1993) described a three-dimensional (3D) acoustic imaging system that can resolve backscattering into a 3D volumetric matrix, providing a means to delineate individual zooplankters and to unobtrusively observe their behavior. Cochrane et al. (1991) differentiated signals from silver hake (*Merluccius bilinearis*) and their euphausiid prey (*Meganyctiphanes norvegica*) by a color rendering of acoustic backscatter at 12, 50, and 200 kHz. Size distributions of zooplankton have been indirectly estimated by solving an inverse problem involving multi-frequency acoustical measurements and predicted backscattering strengths (Greenlaw and Johnson, 1983). The Multifrequency Acoustic Profiling System (MAPS) is an example of an implementation of this theory (Holliday, 1989) which employs twenty one discrete frequencies to provide zooplankton abundance estimates versus animal size and water depth.

Biological oceanographers have also begun to use acoustic tools to describe aspects of the natural history of euphausiids that would be difficult or impossible to investigate with direct sampling techniques. These descriptions suggest processes or tropic relationships that may have been previously unappreciated. Mathisen and Macaulay (1983) reported a set of observations on the dimensions, shape, density, and composition of a large swarm of Antarctic krill and how these features changed over several days. Macaulay et al. (1984) elaborated on these observations and suggested a mechanism for the formation, persistence and dissolution of super swarms. Greene et al. (1988) described high density layers of *M. norvegia* in the bottoms of submarine canyons off Georges Bank. They hypothesized that squid and fish populations found on Georges Bank may utilize the krill to sustain higher population levels than that which could be explained by secondary production on the bank. Daly and Macaulay (1988) described acoustic observations and net samples of *E. superba* and *T. macrura* at the ice edge zone in the Weddell Sea. They speculated that the pack ice is important to overwintering juvenile

E. superba, providing protection from predators as well as access to an abundant food source (ice algae).

3. BIOMASS-FIBEX surveys

An international program for the Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) was established after several years of planning sponsored by the International Council of Scientific Union's Scientific Committees on Antarctic Research (SCAR) and Ocean Research (SCOR) (BIOMASS, 1977; El-Sayed, 1988). Part of the program consisted of a large multi-national, multi-ship survey designed to improve knowledge of the distribution and abundance of Antarctic krill (First International BIOMASS Experiment — FIBEX, Hemple, 1983). Eleven ships from 10 nations conducted acoustic surveys over 2.88×10^6 km^2, or approximately 15% of the krill population's known geographical range (Miller and Hampton, 1989a). Six vessels conducted surveys in the west Atlantic sector of the Southern Ocean using a survey design consisting of randomly spaced parallel transects; four ships operated in the Indian sector using design of equally spaced parallel transects; and one ship operated in the Pacific sector conducting two surveys along single meridians in the western Pacific sector. All of the vessels used down-looking echo integration systems operating at 120 kHz, with the exception of two systems operating at 50 kHz and one system operating at 200 kHz. Acoustic targets were identified by net sampling. Preliminary analysis of the data was conducted at a workshop in 1981 (BIOMASS, 1981); the data were re-analyzed at another workshop in 1984 (BIOMASS, 1986). Estimates of sampling error include variations between transect means within a stratum and uncertainties regarding the dependence of target strength and weight on animal length. The following results are taken from the report of the second workshop (BIOMASS, 1986) as reprinted in Miller and Hampton (1989a):

Sector	Mean density (g/m^2)	Survey area (10^3 km^2)	Biomass (10^3 t)	Coefficient of variation (%)
Indian	1.97	2900	4510	19.7
West Atlantic	4.46	590	2650	14.0

They extrapolated these values over the geographic range of krill described by Macintosh (1973) and estimated the total standing stock to be 41 million tons. This estimate is considerably lower than the global standing stock they estimated by dividing the annual consumption by krill predators (250 million tons) by the highest published production/biomass ratio (2.3 from Allen, 1971) or 109 million tons. More recent evidence suggests that krill longevity is higher than that assumed by Allen (Nicol, 1990) implying a lower production/biomass ratio and an even larger discrepancy between survey estimates of biomass and estimates of standing stock derived from predator consumption. Miller and Hampton (1989a) listed several potential sources of error associated with the FIBEX surveys, the largest of which was bias in the assumed target strength of krill.

A series of experiments by Foote et al. (1990) and Wiebe et al. (1990) suggested that the target strength of krill used in the BIOMASS workshops was in error and that krill biomass was substantially underestimated (Everson et al., 1990). Trathan et al. (1992) re-analyzed the FIBEX surveys and estimated krill biomasses for the west Atlantic and Indian sectors to be 32710×10^3 and 8550×10^3 t, respectively; no estimate of the total standing stock was made. The west Atlantic biomass estimate was incorporated into a population model which formed the basis for establishing limits on the harvest of krill.

Another potential problem with using the BIOMASS-FIBEX surveys to scale the krill population model is that they may have been conducted at a time when krill biomass was substantially higher than its current level. Siegel et al. (1997) analyzed net catches of krill made in the Antarctic Peninsula area from 1977 to 1994 and concluded that krill density was much higher during the first half of the time period than in the second half. They noted that local krill density may vary by nearly two orders of magnitude and that the effects can persist for several years. Siegel and Loeb (1995) and Loeb et al. (1997) argued that krill surveys in the Antarctic Peninsula area are representative of the south Atlantic population, that variations in local krill density are the cumulative effects of variations in annual recruitment to the adult population, and that recruitment is affected by the extent of annual sea-ice development during the winter. In the context of an increasing temperature trend and a decreasing trend in sea-ice in the Antarctic Peninsula area (Jacobs and Comiso, 1997), Loeb et al. (1997) anticipate occasional years with strong krill recruitment, but a diminished krill population size relative to the late 1970s and early 1980s.

A new survey for krill in the Atlantic sector of the Southern Ocean has been proposed as a prerequisite to modifying the current management scheme for the krill fishery in this area (SC-CAMLR, 1996). The following section outlines major sources of biases and errors associated with the conduct of such a survey; these uncertainties are categorized as those associated with measurement and those associated with sampling. Approaches for quantifying these uncertainties are described where appropriate, and issues that need to be resolved are highlighted.

4. Sources of uncertainty

4.1. Estimating krill density (measurement uncertainty)

The largest potential bias in using acoustic techniques to estimate krill density is associated with the conversion of integrated echo energy to absolute numbers of krill reflecting sound (Miller and Hampton, 1989a). Ideally, a survey would obtain simultaneous measurements of volume backscattering strength and individual animal target strength, and estimate animal density as the quotient of the two. In practice, target strength measurements are difficult to obtain in the field, and a distribution of individual animal target strengths is assumed based on some morphological measure such as length.

Foote et al. (1990) noted that abundance estimates of Antarctic krill using acoustics were often much less than those obtained from estimates of predator demand. They suspected large errors associated with the definition of individual krill target strength, and conducted a series of experiments wherein they ensonified live krill aggregations in a cage at 120 kHz. The mean single-animal target strength of 30–39 mm krill was inferred from the aggregation backscatter to range from −81 to −74 dB. Everson et al. (1990) noted that these values were considerably lower that those calculated from previously used equations relating target strength to the physical size of krill (BIOMASS, 1986), and that the use of these equations resulted in gross underestimates of krill abundance (Fig. 4).

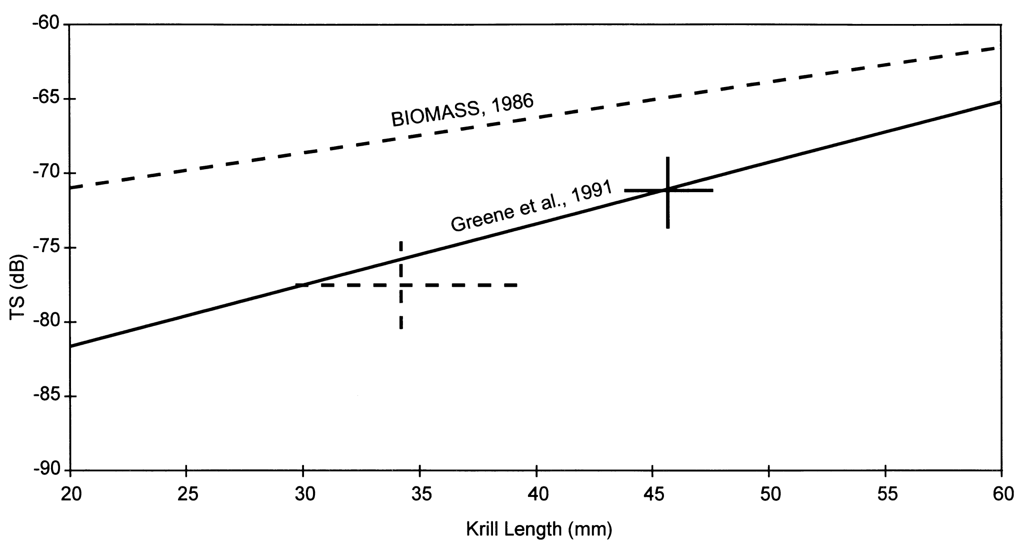

Fig. 4. Target strength of Antarctic krill at 120 kHz. The dotted line indicates the relationship used by BIOMASS (1986) when estimating krill densities from acoustic data obtained during a multi-national survey of Antarctic krill. The solid line was derived by SC-CCAMLR (1991) from a relationship between target strength and *ka* proposed by Greene et al. (1991) based on a series of measurements made by Greene et al. (1989) and Wiebe et al. (1990). The dashed cross indicates the range of measurements made by Foote et al. (1990) on caged krill; the solid cross indicates the range of in situ measurements made by Hewitt and Demer (1991, 1996) including both dorsal and lateral aspects.

Until recently, a fluid sphere model was used to characterize the target strength of krill (Greenlaw et al., 1980). Wiebe et al. (1990) ensonified several species of live, but tethered, zooplankton at 420 kHz and concluded that sound scatter from elongated animals is better described by a bent cylinder model (Stanton, 1989), and that target strength is proportional to the volume of an animal rather than its cross-sectional area. Using these data, Greene et al. (1991) modeled krill target strength at several frequencies and over a range of animal lengths. The Foote et al. (1990) data agreed with the Greene et al. (1991) model. Further corroboration was offered by Hewitt and Demer (1991) who reported a set of in situ target strength measurements using a 120 kHz split-beam transducer. For animals with an estimated mean length of 47.4 mm, the modal target strength was −69 dB, within 1 dB of the prediction by Greene et al. (1991). Foote et al. (1992) reviewed the status of work on the definition of krill target strength and presented a general prediction curve applicable to a range of acoustic frequencies, animal length, and body orientation. A group of scientists advising CCAMLR reviewed these and several unpublished studies on krill target strength and concluded that "a growing body of evidence suggests that the BIOMASS definition of target strength as a function of body length at 120 kHz consistently overestimates target strength," and that "measurements over a range of animal lengths imply a stronger dependence of target strength on length than that predicted by the BIOMASS definition;" they further derived a definition of krill target strength as a function of body length at 120 kHz from the more general Greene et al. (1991) expression and recommended its use in scaling measurements of volume backscattering strength to krill density (SC-CCAMLR, 1991, pp. 117–121).

Although the Greene et al. (1991) equation is a currently accepted estimator of krill target strength (Trathan et al., 1992), it does not explicitly account for body shape, physical condition, and orientation which have been noted by Stanton (1989) as important contributors to the target strength of an individual animal. Calculations made by several investigators (Greenlaw et al., 1980; Sameoto, 1980; Everson, 1982) indicate that orientation is the largest component of the observed variability in krill target strength. Progress in this area should consider several issues:

- Additional in situ measurements of target strength should be obtained over a range of animal lengths and animal condition including gender, sexual maturity, molt stage, and feeding condition in conjunction with high-resolution directed net sampling gear. Demer et al. (1999) demonstrated that the delineation of single targets could be improved during underway survey measurements by using target position information from multiple transducers. Application of the method has the effect of improving the measurement accuracy and precision by greatly reducing the occurrence of multiple targets in the sample volume being interpreted as a single target.
- The dependency of krill target strength on animal orientation should be investigated (Demer and Martin, 1996). One promising approach is to simultaneously photograph and acoustically ensonify a volume of water containing krill (McGehee et al., 1998). There may be a correlations between orientation and both vertical migration and maturity stage. Everson (1982) observed an 8 dB difference between the daytime and night-time volume backscattering strength of krill aggregations and attributed this to diel changes in orientation. Endo (1993) estimated that mature females would hover at a steeper angle than other krill, and as a result reflect approximately six times less sound.
- Although theoretical models of sound scattering by krill have incorporated various aspects of animal size and physiological condition, they have been verified only to a limited degree. The observed distributions of krill lengths, condition, orientation, and body shape can be input into theoretical models to predict the distribution of individual target strengths that would be expected from a natural aggregation of animals. Predicted distributions can be compared with observed distributions and the models adjusted or redefined as appropriate.

Apportioning volume backscattering strength to krill versus all other sound scatterers is also problematic (Martin, 1997). In the Elephant Island study area, three groups of organisms are responsible for most of the acoustic return observed in the epi-pelagic zone: micro-nekton (including several species of euphausiids and myctophids), non-gelatinous zooplankton (primarily copepods), and thaliaceans (salps). Although Antarctic krill are usually the dominate zooplankton scatterers at 120 kHz and their aggregations have distinctive morphologies, quantifying the error associated with various approaches is difficult. Directed net sampling has been used to help interpret echo returns from krill and other scatterers. Other solutions range from assuming that all reflections exceeding an arbitrary threshold are from krill to subjective decisions based on visual examination of echograms, using the difference in volume backscattering made simultaneously at multiple frequencies to separate krill echoes from other taxa (Madureira et al., 1993a,b; Brierly et al., 1997). Demer (1994) demonstrated that the difference in cumulative distribution of target strength measurements made on individual animals could be useful in distinguishing krill from salps. Foote (1993) comments that classification to species may not be possible, but suggests that discriminate analysis techniques using a variety of measured variables may provide the best solution.

The echo integration method assumes that the total backscattered energy is the sum of echoes from individual scatterers (Ehrenberg, 1973). This assumption may be violated in the case of high density zooplankton swarms. Complications may include multiple reflections of the returning echo, absorption of sound within the aggregation, and shadowing of one portion of the aggregation by another (MacLennan and Simmonds, 1992). The sensitivity of the method to this assumption may be investigated by comparing krill density estimated from acoustic return with that estimated from direct samples or photographs, over a range of aggregation shapes and densities.

The accuracy of measurements of both volume backscattering strength and target strength is very sensitive to system calibration (Foote, 1983). Experiments can be conducted to measure the variation of system gain with different instrument settings, environmental conditions, and calibration techniques (e.g. Demer and Hewitt, 1992). Such experiments can help define the minimum resolution of acoustic measurements that can be attained under field conditions.

As a final note, a distinction should be made between numerical density and biomass density. Estimates of krill biomass density are relatively insensitive to minor variations in the frequency distribution of length (Greenlaw et al., 1980; Hewitt and Demer, 1993). This is because the number of krill per kg decreases exponentially with increasing length at approximately the same rate as the predicted backscattering cross-sectional area of a single krill increases with increasing length. This implies that mean length may be used to calculate biomass densities without introducing substantial errors. If, on the other hand, numerical densities are desired (e.g. for studies of krill predator foraging behavior) then body length is critical to accurate estimates.

4.2. Estimating population abundance of krill and mapping their distribution (sampling uncertainty)

Investigators have used a variety of methods to estimate population abundance and its variance and to generate distribution maps (Simmonds et al., 1992). Johannesson and Mitson (1983) contoured acoustic density data and used the contours to define post-sampling strata boundaries for abundance estimation. Macaulay et al. (1984) assigned acoustic data collected along transects into blocks before averaging and summing over block area; variance was estimated using Williamson (1982) cluster sampling method. Macaulay and Mathisen (1991) used a mapping technique based on block kriging to generate distribution maps. The BIOMASS-FIBEX surveys were first analyzed by block and variance was computed by including a covariance term for observations within a block (BIOMASS, 1981). These data were later re-analyzed by considering each transect as a single sample of biomass density, assuming that the transects were parallel but randomly spaced, and developing expressions for the mean and variance that were weighted for variations in transect length (BIOMASS, 1986; Jolly and Hampton, 1990; Simmonds et al., 1992). No distribution maps were presented in either report. Others have followed Jolly and Hampton (1990) procedures for estimating abundance and its variance (Hewitt and Demer, 1993; Pauly et al., 1996; Brierly et al., 1997). These authors also gridded contoured transect data to produce distribution maps. Considerable interest, particularly among European fishery biologists, has been expressed in the application of geostatistical methods to estimate abundance and its variance from line-transect measurements of density, particularly without sacrificing the spatial relationships contained in the data set (e.g. Gohin, 1985; Guillard et al., 1987; Armstrong, 1990; Petitgas, 1990; Simard and Gerlotto, 1990; Foote and Rivoirard, 1992; Simard et al., 1993). Spatial structure in the data set is estimated from a semi-variogram which plots the correlation between areal density values by their spatial separation. This information can be used to check for differences in structure between strata, estimate the variance of the mean areal density, and interpolate areal density on a fixed grid prior to contouring (Simmonds et al., 1992).

The application of geostatistical techniques may allow better estimates of the variance of population abundance estimates and the creation of more realistic maps of the dispersion of krill throughout the survey area. Additional sources of uncertainty, however, remain to be quantified:

- *Diel vertical migration of krill*. At any one time, an unknown quantity of krill is above the vertical range of observation (10–250 m). Demer and Hewitt (1995) estimated that, on an average, 30% of the krill are above the transducer and therefore undetected during surveys conducted in the Elephant Island area. Possible approaches for assessing the amount of krill in the upper 10 m are the use of up-looking and/or side-looking towed transducers (Everson and Bone, 1986; Hewitt and Demer, 1996), vertically stratified net sampling, and remote self-contained acoustic systems (e.g. bottom-moored, buoy-mounted, or free drifting as described by Greene et al., 1989 and GLOBEC, 1991). Alternatively, descriptive models of vertical migration by krill may be formulated and used to adjust estimates of abundance and distribution maps (Demer and Hewitt, 1995).
- *Horizontal movement of krill*. Because krill have a circumpolar distribution it is reasonable to expect that only regional surveys, conducted with multiple ships, will not be substantially affected by movement of krill in and out of the survey area. Three water flows converge in the vicinity of the South Shetland Islands resulting in a hydrographic front north of the archipelago and introducing complexities in the general northeastward flow. Expected times of water residence range from 18 to 45 days with longer times predicted for the shelf surrounding the islands and shorter times north of the front and in deeper areas in Bransfield Strait south of the islands (SC-CCAMLR, 1994, pp. 267–293; Ichii and Naganobu, 1996). Additional complications arise when considering: (1) to what extent krill move with the mean flow of the water and (2) the spatial segregation of krill development stages (Siegel, 1988). One approach for quantifying the effect of krill movement on estimates of abundance is to deploy an array of bottom-moored ADCP instruments along transects perpendicular to the axis of general flow with the intention of resolving the movement of both water and krill. This information could then be used to improve survey simulations designed to quantify the effects of various aspects of survey design (e.g. transect spacing, direction of survey, duration of survey) on estimates of abundance.
- Krill surveys may also be biased if the animals react to the approach of the ship by adjusting their position and/or orientation. Possible approaches for assessing avoidance include the use of repetitive survey patterns to detect changes in the position and/or density of krill swarms, frequency analysis of echo returns from krill swarms to detect and quantify Doppler shift, and the use of moored acoustic systems to observe the change in distribution in reaction to the passage of a survey vessel.

5. Krill aggregation patterns

Like many organisms, krill are heterogeneously distributed. Quantitative data on the distribution patterns of krill are of interest for several reasons: (1) knowledge of spatial structure will help improve the reliability of survey designs, distribution maps, and abundance estimates; (2) linkage of predator foraging strategies with spatial aspects of the prey field will help better define prey availability; (3) descriptions of the dominant scales of krill distribution patterns will allow comparisons to be made with those of biotic and abiotic factors in the pelagic habitat postulated to affect the distribution of krill; and (4) quantitative descriptions of aggregation patterns will facilitate comparisons with other data sets to examine variations in patterns between regions and within a region over time.

Miller and Hampton (1989a) present a thorough review of observations of Antarctic krill aggregation patterns. Kalinowski and Witek (1982, 1985) suggested a hierarchical classification scheme of concentrations, patches within concentrations and swarms within patches. Swarms may be discrete aggregations, with dimensions of the order of tens of meters and densities of the order of 100 g/m^3, or dispersed layers, with dimensions of the order of tens to thousands of meters and densities of the order of 10 g/m^3. Discrete swarms may coalesce into super swarms (Macaulay et al., 1984), and extensive layers may break into irregular shapes. The distribution of swarm biomasses is highly skewed (Hampton, 1985) with as much as 95% of the biomass contained in only 5% of the swarms. Despite this variability, swarms appear to be the fundamental organizational unit (Watkins et al., 1986; Murphy et al., 1988); variability within swarms is much less than variability between swarms. Aggregating behavior has not been linked to any particular activity, although krill may feed more efficiently in dispersed swarms than when in tightly organized swarms (Hamner et al., 1983; Miller and Hampton, 1989a). Krill are also available to a wide variety of predators over a large range of scales because of the hierarchical nature of their distribution patterns (Murphy et al., 1988). Several investigators have generated quantitative descriptions of krill distribution patterns (Weber and El-Sayed, 1985; Weber et al., 1986; Morin et al., 1989; Macaulay, 1991).

There is a continuing need to describe the details and variability of krill aggregation patterns for the following reasons:

- This information is essential for planning efficient surveys as well as more fully understanding all aspects of krill biology. Descriptions of swarm dimensions, density and inter-swarm spacing can be generated from routine survey data. Seasonal, diurnal and spatial variability in these parameters can also be described.
- Aspects of krill distribution patterns that may be important to predators need to be described. Land-breeding predators have been shown to respond to the location and predictability of krill within their foraging range, the depth distribution of krill, the density of krill within layers, and diel changes in these patterns (Zamon et al., 1996; Logerwell et al., 1998; Croll et al., 1993) (Fig. 5). Aggregations of pelagic predators have been shown to be correlated with areas of high krill density (Hunt et al., 1992; Veit et al., 1993a; Reitsch and Veit, 1994). Foraging behavior of pelagic predators has also been shown to be responsive to the presence of krill (Veit et al., 1994).

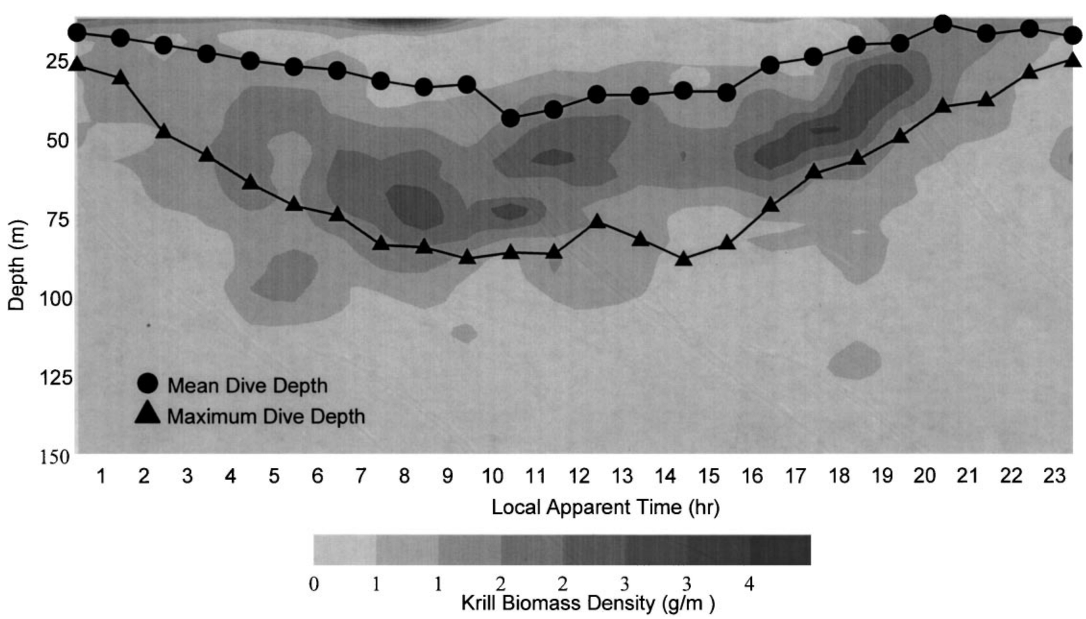

Fig. 5. Diurnal variation of Antarctic krill volumetric density and penguin foraging with depth (adapted from Croll et al., 1993).

- Testable hypotheses need to be developed regarding the effects of both biotic and abiotic factors on the spatial distribution of krill. Factors which may influence the distribution of krill include bathymetric features, water mass boundaries and frontal zones, phytoplankton biomass, species composition and production rates, predator foraging, and fishing. Possible approaches to the identification of dominate factors include correlative models (e.g. principal component analysis, step-wise regression, generalized additive models), scale comparisons (e.g. spectral analysis, autocorrelation), and process modeling (Levin et al., 1989; Levin, 1992).

6. Conclusions

Improved acoustic instrumentation has expanded the set of tools available to the biological oceanographer (Greene and Wiebe, 1990; Smith et al., 1992). In comparison to direct sampling with nets, relatively non-invasive techniques can be used to rapidly collect large amounts of high-resolution data over large areas. The techniques have enhanced the biological oceanographer's capabilities in at least three additional ways: (1) spatial structure in animal distributions can be simultaneously described over a range of scales; (2) temporal variability can be exposed with a time series of surveys that can be conducted in the time span required for a single net survey; and (3) ephemeral phenomena (in both time and space) can be detected and described.

Acoustic sampling has provided information used to manage the harvest of the Antarctic krill resource on two very different scales. The first is an estimate of the population abundance of krill along the Scotia Arc (including the South Shetland Islands, the South Orkney Islands, and South Georgia) in the southwest Atlantic sector of the Southern Ocean where 75–90% of the global harvest of krill is removed. This information, together with estimates of krill predator demand and the variability of krill population production, has been used to set a limit on the total harvest. More localized acoustic surveys have contributed to an understanding of the dependence of land-breeding predators on the availability of krill in the immediate vicinity of their breeding colonies. This understanding will ultimately lead to improvements in how the harvest limit is allocated among subareas of the fishery, and to additional management actions that minimize the effects of the harvest on predator production.

Before this information can be reliably used, however, several technical issues must be considered. In order to scale measurements of volume backscattering strength to animal densities, accurate measurements of the target strength on individual animals must be made. For these measurements, a calibrated instrument and a reliable method for delineating single animals in the acoustic sample volume are required. Instrument errors will still remain and must be quantified and included in the uncertainty associated with estimates of animal density. Alternately one may assume a mathematical model of TS, but this requires adequate knowledge of animal morphology, condition, and in situ behavior. Additional sources of uncertainty in estimating animal density include those associated with estimating taxonomic classification and the assumption of a linear relationship between volume backscattering strength and density. Sources of uncertainty in extrapolating animal density to survey abundance include those associated with the diel migration of krill in and out of the acoustic observation window, the horizontal movement of krill in and out of the survey area, and reaction by krill to the presence of a survey vessel.

One of the principal values of continuous sampling is the ability to infer animal dispersion patterns over a wide range of scales. This information will be useful for improving survey design, interpreting predator foraging strategies and defining prey availability, and investigating environmental influences on krill distribution.

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