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Use of moored acoustic instruments to measure short-term variability in abundance of Antarctic krill

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Abstract

Upward-looking acoustic Doppler current profilers (ADCPs) (300 kHz) and echosounders (125 kHz) were deployed on moorings at South Georgia to measure abundance of Antarctic krill continuously over several months. Echoes from krill were identified using the theoretical difference in echo intensity at 300 and 125 kHz and scaled to krill density using target strengths appropriate for krill in the region: krill size was determined from diet samples from furseals and penguins foraging near the moorings. A method using water flow past the moorings was developed to convert time-based acoustic observations of krill to area-based abundance estimates. Flow past the stationary moorings was treated analogously to motion along-track of a research vessel through a nominally stationary body of water during a conventional survey. The moorings thus provide a Eulerian view of variation in krill abundance. This is ecologically instructive for South Georgia, where krill are generally passive drifters on currents and where temporal fluctuations in abundance have significant consequences for krill-dependent predators. Moorings were positioned on routine research vessel survey transects, and validity of the mooring method was assessed by comparison of mooring and vessel observations. Krill density estimates from the moorings were not statistically different from vessel estimates in adjacent time periods. A time series of krill density from a mooring revealed step-changes that were not seen during short-term vessel surveys. Moorings deliver data over time scales that cannot be achieved from research vessels and provide insight on environmental factors associated with variation in krill abundance at South Georgia. Mooring data may aid ecosystem-based management.

Introduction

Pelagic systems are variable over numerous scales of space and time (Haury et al., 1978; Murphy et al., 1988). Understanding the causes and consequences of this variability is an essential step toward understanding pelagic ecosystem function. At South Georgia, in the Atlantic sector of the Southern Ocean (54°S, 37°W), the food web is centered on Antarctic krill (*Euphausia superba*), and temporal variability in local abundance of krill has major impacts on ecosystem function there. Acoustic surveys of krill abundance at South Georgia have revealed significant variation between years (over 2 orders of magnitude, from 2 to 150 g m^{-2} wet mass, between 1994 and 1998; Brierley et al., 1999b). Years of low mean krill density (about < 10 g m^{-2}) result in significantly reduced reproductive success for krill predators such as Antarctic furseals and Gentoo penguins (Croxall et al., 1999) and poor condition of the commercially important Mackerel icefish (Everson et al., 1997). Understanding, and ultimately being able to predict (Brierley et al., 1999a), variability in krill abundance at South Georgia will be necessary before robust ecosystem-based management strategies for the region can be implemented.

South Georgia is remote and experiences often hostile weather conditions. Logistic and financial constraints restrict the time over which data on the pelagic ecosystem can be gathered using conventional ship-based approaches. Although exist-

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ing summer data (almost no winter data exist) show apparent year-to-year variation in krill abundance at South Georgia, few data are available on variation within years, and the possibility that apparent interannual variability is a temporal alias of shorter-term, intra-annual variation cannot be discounted. In fact, on the few occasions when more than one research cruise per year has made measurements at the island, marked within-year variations in krill abundance have been detected (for example 2 g m^{-2} wet mass in October 1997 versus 21 g m^{-2} in January 1998; Brierley et al., 1999b). Data from predators breeding ashore at South Georgia suggest that krill availability can vary significantly throughout the course of the breeding season (for example, significant changes in the foraging behavior of Antarctic furseals have been detected; Mori and Boyd, 2004), but a lack of corroborating independent at-sea observations has prevented direct verification of this. Evidence from elsewhere around Antarctica suggests that local krill abundance can change substantially within seasons (McClatchie et al., 1994; Siegel et al., 1998). Understanding the scale, timing, and causes of such variation is key to understanding, managing, and conserving the South Georgia pelagic marine ecosystem. Low krill abundance at the peak of the predator breeding season, for example, could have far graver ecosystem consequences than would krill scarcity during midwinter, and these two scenarios would have different implications for krill fishery management in an ecosystem context (Constable et al., 2000). Present at-sea sampling regimens cannot resolve such short-term differences in krill abundance, however, and it has been impossible so far to link predator breeding performance indices to krill abundance (i.e., to describe functional responses of predators to varying prey availability) because of the mismatch between the time scales of the vessel surveys (~2-week duration) and the breeding season (4 to 5 months) (Reid et al., 2005). Furthermore, it has not yet been possible to determine the causes of short-term changes in krill abundance at South Georgia. The krill population at the island is not self-sustaining, and it has been suggested that abundance changes partly due to fluctuations in the position of the Sub-Antarctic Circumpolar Current Front (SACCF) that acts as a conveyor belt transporting krill to South Georgia from the Antarctic Peninsula (Hofmann et al., 1998; Murphy et al., 1998; Thorpe et al., 2004). The SACCF is a dynamic feature that retroflects around the eastern tip of South Georgia. When it meanders toward the northern shelf, it may deliver krill to the island, in which case increases in krill abundance should be associated with the arrival of water with the properties (temperature and salinity) of the SACCF. To date, lack of contemporaneous oceanographic and krill abundance data have prevented this hypothesis from being tested empirically.

We deployed moorings at South Georgia to measure krill abundance and oceanographic parameters continuously and so gain insight on possible variations in abundance, and causes thereof, that could not be achieved with conventional ship-based sampling. Use of moorings to investigate temporal variability in pelagic ecosystems is not new (e.g., Cochrane et al., 1994; Fischer and Visbeck, 1993; Tarling, 2003), and a forward look at priorities for zooplankton research (Marine Zooplankton Colloquium 2, 2001) identified the use of remote sensing tools such as acoustic moorings as key to future studies of zooplankton hotspots. To our knowledge, however, previous mooring-based studies have not attempted to scale the point observations they gather to account for variability in water flow past them. In regions where current velocity is not uniform, scaling for flow will be important because, to take an extreme example, a period of apparent sustained high acoustic backscatter (planktic biomass) could be due to a single discrete aggregation in an otherwise empty background remaining stationary over the mooring: in that case the view from the mooring would be of continually high abundance, whereas the more widespread regional view would be of generally low abundance. In the case of krill, which are characterized by extremely patchy distributions (most biomass is in compact, high-density swarms), setting mooring-based observations in a wider context is particularly important (for example, predators cannot be expected to forage for our convenience directly over moored instruments), and we need to understand both temporal and spatial variation in abundance (Trathan et al., 1993).

In this article, we report a method we have developed that uses the rate of water flow past the mooring to scale time-based observations of krill abundance. Analysis of data from what we have called "virtual survey transects" enables quantitative biomass estimates to be calculated. We describe analysis of data from a mooring deployed off shelf at South Georgia between November 2004 and January 2005 to illustrate our method. The method has potential wide application for studies of planktic ecosystems.

Materials and procedures

Acoustic surveys are conducted routinely to estimate abundance of pelagic species such as herring, pollock, and krill (Simmonds and MacLennan, 2005). During these surveys, calibrated echo intensity data are recorded from pings transmitted downwards into the water column at regular intervals (typically 1 s) at one or more frequencies (typically 38, 120, and 200 kHz) from a research vessel progressing along predefined survey transects (typically at 10 knots). Each ping is time- and position-stamped (using GPS) and provides the volume backscattering coefficient (s_v, m^{-1}) for regular depth bins (the size of which depend on the rate at which the echosounder samples the echo wave) down the water column. Further averaging down the water column or integrating along track leads to volumetric (e.g., mean volume backscattering strength [MVBS], S_v, dB re 1 m^{-1}) or areal (e.g., nautical area scattering coefficient [NASC], s_A, m^2 n.mi^{-2}) measures of sound scattering that can be scaled using target strength (TS, dB re 1 m^2) to provide various measures of animal abundance. Target strength at a given frequency usually varies as a function of animal size, and physical samples of the target species have to be obtained to determine size (usu-

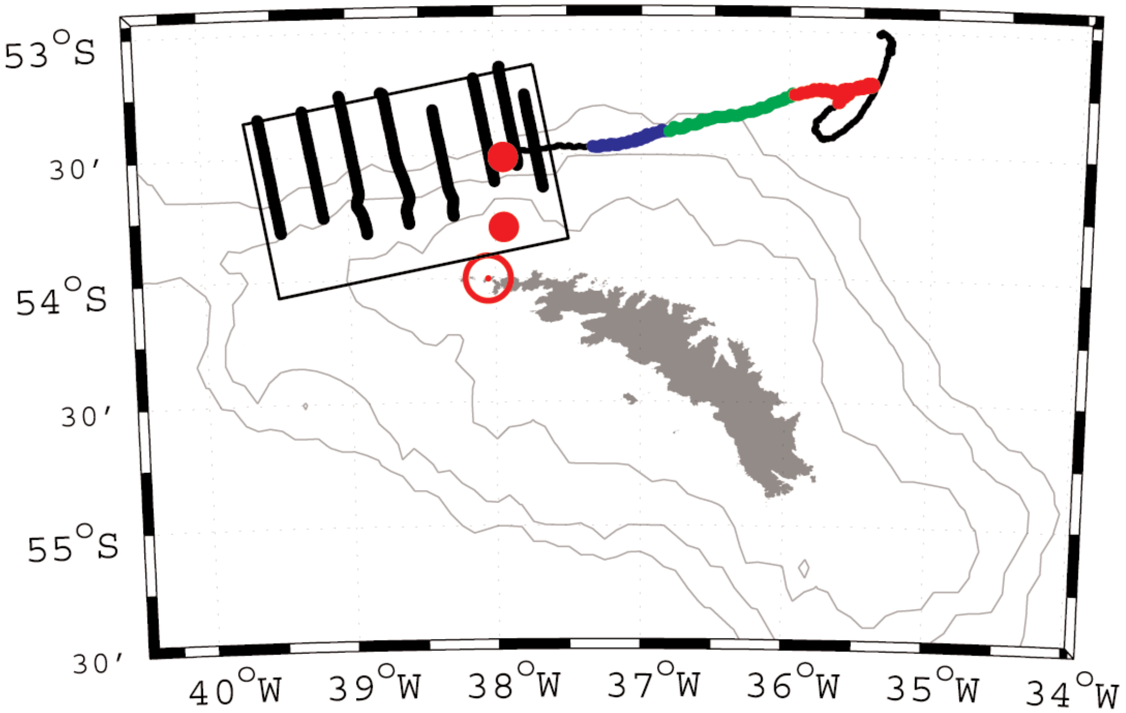

Fig. 1. Map showing South Georgia and the surrounding bathymetry (200-, 1000-, and 2000-m depth contours), the locations of the on- and off-shelf moorings (solid red dots), the bounds of the British Antarctic Survey western core box and portions of survey transects in water deeper than 200 m (only the 4 easternmost transects were considered in the ship-based analysis reported here), and the location of Bird Island (red circle) where predator diet sampling took place. The progressive vector plot (PVP) of water flow over the off-shelf mooring (in the 100- to 108-m depth horizon) for the duration of the deployment considered here is also shown (colors highlight portions of track during 3 separate density phases: red beginning; green middle; blue end: black sections are outwith analyses reported here). Although we show the entire PVP, we do not mean to imply that we think we can extrapolate to determine the exact historical trajectory over the whole period: this is oceanographically a very dynamic region (Murphy et al., 2004). Rather we include the entire vector to provide a relative indication of the variation in water flow at the mooring site throughout the observation period. The variability that is apparent reinforces the need to scale temporal observations for spatial variability.

ally achieved by net sampling). Net sampling also provides information on the species identity of acoustic targets: identifying the targets that cause echo returns is an essential step in determining single-species biomass estimates that are not biased by inclusion of echoes arising from other species. Substantial progress has been made recently in the use of echo intensities collected simultaneously at multiple frequencies from the same sampling volume for species identification (and sizing), and in some cases it is no longer essential that net samples be obtained (Horne, 2000; Watkins and Brierley, 2002). To determine krill abundance estimates from moorings, mooring equivalents of each of the above steps have to be completed. The way in which we implemented these steps is described below.

Mooring location—Two moorings were deployed at on- and off-shelf locations to the northwest of South Georgia (Fig. 1) from RRS *James Clark Ross*. Moorings were first deployed in October 2002 and have remained more or less continually in place (for brief periods, usually about 1 day at approximately 4-month intervals, they have been recovered for data download, battery replacement, and servicing). On- and off-shelf locations were chosen because previous acoustic surveys had shown that krill abundances were different in the 2 zones (Trathan et al., 2003), and oceanographic conditions in the 2 regions are not uniform (Brandon et al., 2000). Both locations were within a box ("western core box") that was surveyed routinely as part of ongoing British Antarctic Survey (BAS) core research (Brierley et al., 1997) and, as far as possible (where bathymetry allowed), moorings were placed on standard survey transects within the box. The survey box itself was positioned to include foraging areas used routinely by air-breathing krill predators that breed ashore at Bird Island on the western tip of South Georgia, the location of a long-term BAS predator monitoring program (Croxall et al., 1999). This methods paper reports analysis of data collected by the offshore mooring during a deployment between November 2004 and January 2005. Full analysis of the complete time series will be presented elsewhere.

Mooring design and instrument configuration—The design of the 2 moorings was essentially the same, with the exception that the anchor tether for the off-shelf mooring was longer. Moorings were anchored with ballast weights (railway wheels)

Fig. 2. Photographs showing (a, upper panel) the mooring buoyancy float and instruments (ADCP right, WCP left, Argos beacon top, radio and light beacons bottom; the CTD is beneath the float and hence not visible) and (b, lower panel) both moorings on the afterdeck of RRS *James Clark Ross* (the off-shelf mooring is on the lefthand side, and has substantially more tether in the square basket than does the on-shelf mooring). The instrument floats, railway-wheel ballast, and acoustic releases are lying beneath the A-frame.

to the seabed via acoustic releases, with the instrument packages floating a nominal 200 m below the sea surface. The seabed was at approximately 1300 m depth at the off-shelf location (requiring a 1100 m tether), and at approximately 300 m on-shelf (100 m tether). During the deployment considered here, the off-shelf mooring was at a depth of 226 m. Each mooring included a single-beam echosounder (ASL Environmental 125 kHz Water Column Profiler [WCP]), an acoustic Doppler current profiler (ADCP; RDI Workhorse 300 kHz), and a conductivity/temperature/depth logger (CTD; Seabird SBE37). The instruments were mounted in cylindrical apertures in a high-density syntactic foam flotation buoy (1.7 m diameter × 0.6 m depth; mass in air 636 kg; buoyancy 347 kg; CRP Group Ltd.) (Fig. 2), the size of which was determined by the buoyancy required to float the instruments and to maintain them in a stable position, without oscillation, in the current-swept environment off South Georgia (average prevailing current speed ~10 cm s^{-1}). The ADCP and WCP were oriented to sample vertically upwards, and sampled from just above the mooring to the sea surface. Configurations for the ADCP and WCP during the deployment reported here are given in Table 1. These configurations were typical, and provided the highest-frequency data acquisition over the planned duration of the deployment that the manufacturers' specifications suggested available battery power and memory capacity could support. The CTD sampled just beneath the flotation buoy and recorded measurements every 4 minutes. In addition to the sampling instruments, the moorings were equipped with strobe lights and Argos beacons that helped us find them at the surface during recovery.

Analysis of water column profiler backscatter data—The ASL Environmental WCP is a single-beam echosounder that has been developed from an instrument originally designed to measure draft of sea ice keels. It has an 18° 3-dB beam width. The WCP recorded echo intensity on a 0 to 255 linear scale. We converted these data to mean volume backscattering strength (S_v, dB re 1 m^{-1}) using an active version of the SONAR equation for distributed targets (Urick, 1983):

$$S_v = 20\log N - G - \mathrm{OCV} - \mathrm{SL} + (20\log R + 2\alpha R) - 10\log(\tau\psi c/2)$$

where R is range (m), N is the recorded WCP count, OCV is the transducer receiving response (open circuit voltage, dB re 1 V/μPa), SL (source level, dB re 1 μPa) is the transmitted signal intensity, α is the absorption coefficient (dB m^{-1}), c is sound velocity (m s^{-1}) (α and c were calculated using temperature and salinity values logged by the mooring CTD), ψ is the equivalent 2-way beam angle (0.01172 steradians), τ is the pulse length (s), and G is the receiver gain (dB). OCV and SL are instrument-specific constants and were provided by the manufacturer. The gain function G was determined using measured time varied gain (TVG) curves provided by the manufacturer. Limitations in the WCP electronics meant that that gain function did not quite conform to the standard 20log$R$, and we determined G using a 6-term range-dependent polynomial model of the manufacturer's measurements. The WCP was calibrated with reference to echo intensities recorded from a standard target during a calibration exercise in Stromness Bay, South Georgia (WCP at ~10 m depth).

Analysis of acoustic Doppler current profiler data—The RDI Workhorse Sentinel ADCP is used widely for oceanographic and bioacoustic research. It has 4 beams, each with a 3.9° 3-dB beam width, which are oriented with a slant 20° off vertical. The ADCP recorded echo intensity on a 0 to 255 automatic gain control (AGC) count scale. We converted AGC to

Table 1. Instrument configurations for the water column profiler (WCP) and acoustic Doppler current profiler (ADCP).

Instrument	Frequency	Sampling rate	Range bin	Pulse length	Blank after transmit
WCP	125 kHz	1 ping every 2 min	0.5 m	600 µs (= 8.72 m @ 1453 m s^{-1})	0 m
ADCP	300 kHz	7 ping ensemble every 4 min	8.0 m	560 µs (= 8.13 m @ 1453 m s^{-1})	1.76 m

S_v using the version of the SONAR equation presented by Deines (1999):

$$S_v = \mathrm{C} + 10\log[(T_x + 273.16)R^2] - \mathrm{L}_{\mathrm{DBM}} - \mathrm{P}_{\mathrm{DBW}} + 2\alpha R + \mathrm{K}_c(E - E_r)$$

where R is the (slant) range to the sample bin (m), C is a sonar-configuration scaling factor (that includes the system-source level, transducer directivity, transducer efficiency, and the Boltzmann constant that is applied to scale thermal noise to an absolute level; 143.5 dB for the Workhorse Sentinel), T_x is the temperature at the transducer (° C), $\mathrm{L}_{\mathrm{DBM}}$ is 10log (transmit-pulse length) (m), $\mathrm{P}_{\mathrm{DBW}}$ is 10log(transmit power) (dB re 1 W), α is the absorption coefficient (dB m^{-1}), K_c is a beam-specific sensitivity coefficient (supplied by the manufacturer), E is the recorded AGC, and E_r is the minimum (background) AGC recorded. We used beam-averaged data because the 4 beams together give a better signal-to-noise ratio than individual beams and provide information from a larger sampling volume.

Preparation for acoustic identification of krill—The moorings were equipped with acoustic devices (ADCP and WCP) operating at 2 frequencies so that a frequency-difference technique could be used to identify echoes arising from krill and discriminate them from echoes from other targets. The proportion of sound energy backscattered from a target at a given frequency is a function of numerous physical properties of the target, including size, shape, orientation, and the ratios of the density of the target to the density of seawater and of sound velocity in the target to sound velocity in seawater. Different targets (e.g., plankton types such as euphausiids, copepods, and salps) may backscatter different proportions of energy because they have different physical properties (e.g., euphausiids are larger than copepods and denser than salps). Over a range of frequencies, different plankters have characteristic scattering responses, such that species can often be distinguished on the basis of their dual- or multifrequency "fingerprint." At South Georgia, where plankton species diversity is quite low, and where the majority of krill biomass is usually contained in high-density swarms, this approach has proved effective (Brierley et al., 1998b; Madureira et al., 1993), and automated dB-difference based (S_v120 kHz – S_v38 kHz) identification of krill echoes agrees very closely with traditional visual echogram scrutiny and netting-based krill identification (Watkins and Brierley, 2002).

S_v data from both the ADCP and WCP were loaded into SonarData Echoview software to enable them to be processed together, as follows. First, regions of bad data (times when instruments were pinging on deck before deployment and descending to their moored depths; depths in "blank after transmit" and near-surface dead zone; periods of interference) were marked and excluded from further analysis. The depth range sampled effectively by the mooring during this deployment was approximately 20 to 210 m. Second, TVG-amplified background noise was removed from each dataset (Watkins and Brierley, 1996). Third, the WCP data were resampled (averaged in the linear domain) on to a depth/time grid corresponding to the sampling resolution of the ADCP (8 m × 4 min), enabling frequency differences from equivalent time periods to be determined.

Krill length-frequency—We sampled krill in the vicinity of the mooring using a rectangular midwater trawl with a square 8-m^2 mouth opening (RMT8) just before mooring deployment (n = 157, mean length = 44.2 mm). Krill were also obtained from diet samples of Antarctic furseals and Macaroni penguins breeding ashore at Bird Island (n = 478, mean length = 52.6 mm). Both of these species forage in the vicinity of the moorings. It has been shown previously (Reid and Brierley, 2001) that sizes of krill in predator diet samples are representative of the regional krill population length-frequency distribution, and thus that they can be used to infer acoustic target strength (TS).

Ventral-aspect TS of krill at 125 and 300 kHz—Conventional ship-based acoustic surveys detect animals from above with downward-facing echosounders that sample echoes arising from the animals' dorsal surfaces. Conversely, the instruments on our moorings sample from beneath and detect sound scattered back from the ventral surface. We used the Demer and Conti (2003) stochastic distorted-wave Born approximation (SDWBA) model to determine ventral aspect 125- and 300-kHz TS for krill with the length-frequency distributions (from net and predator samples) apparent during the deployment. The model was evaluated with a generic krill shape comprising 14 cylinders (following McGehee et al., 1998) and an empirically determined standard deviation of the phase variability of (√ 2)/2 radians (Demer and Conti, 2003).

Demer and Conti (2005) inferred that krill typically adopt a mean orientation 15° (tail down) off the horizontal (SD 5°). The WCP was oriented vertically upwards and so, using the Demer and Conti (2003) model coordinate system (head 180°, tail 0° or 360°, dorsal surface 90°, ventral surface 270°), would impinge on typical krill at a mean of 285° (± 5° SD). The ADCP has 4 beams (20° slant) which serve to broaden the range of angles at which krill might be viewed to 265° to 305° (± 5° SD). Variation of TS by angle is shown for the length-frequency dis-

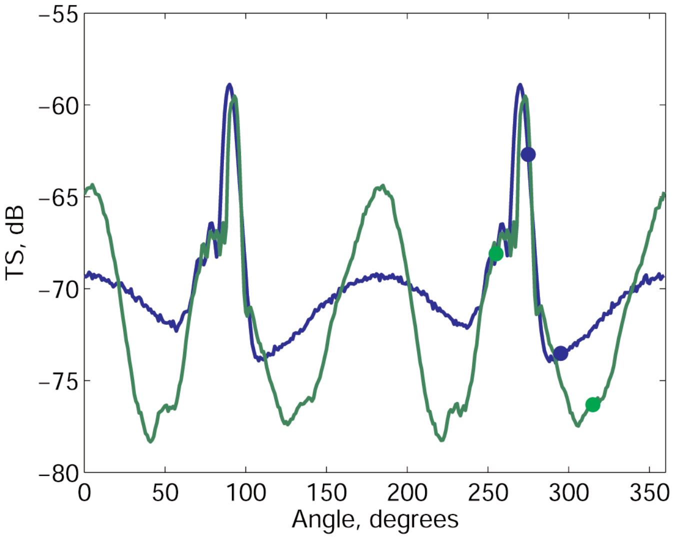

Fig. 3. Target strengths at 125 kHz (WCP, blue line) and 300 kHz (ADCP, green line) for krill (averaged over the length-frequency distribution detected by net just before the mooring deployment) as a function of angle. The extreme bounds of the sections of the curves corresponding to the limits of the ranges of ventral aspect angles viewed from the moorings are marked with filled circles.

tribution of krill from the net sample in Fig. 3. We calculated the average TS at 125 and 300 kHz over appropriate angular ranges for each instrument (Table 2). We also calculated the maximum and minimum differences in echo intensity at 125 and 300 kHz over these ranges, and used this difference range in Echoview to generate a mask to select those 8 m × 4 min acoustic data bins within the range believed to contain krill.

Construction of virtual survey transects—An important parameter in the calculation of krill density from a shipboard acoustic survey is the length of the survey transect sampled. This is used to scale the observed krill density values to the unit area of water sampled, and ultimately to calculate a regional mean density (Jolly and Hampton, 1990). To calculate robust mean density estimates from the moorings, the rate of flow past the mooring has to be considered. We used the ADCP velocity measurements to determine flow. The north and east velocity components for bin 14 (depth 100-108 m) were used to construct progressive vector plots (PVP) with the Matlab Fathom toolbox (available for download from the website of the author, David L. Jones, Department of Marine Biology and Fisheries, University of Miami, FL, USA, at http://www.rsmas.miami.edu/personal/djones/, accessed Jan. 30, 2006). These plots provide a Lagrangian display of Eulerian measurements and can be considered analogous to the cruise track of a research vessel conducting an acoustic survey through a nominally stationary body of water. The 100- to 108-m depth range was chosen as approximately the midpoint of the observational range (~200 to 20 m) and because data quality was consistently good in this bin (> 25% good). This depth is also at approximately the center of the distribution range of krill swarms at South Georgia in daylight (Godlewska, 1996; Taki et al., 2005) and, as such, water movement at this depth interval is likely to be representative of the conditions encountered in situ by most krill sampled at the island. We could find no evidence of sheer above the offshore mooring, and there was no significant variation in velocity with depth over the range where % good remained high (bins 1 to 16): for observations at midday on alternate days throughout the deployment ($n = 20$), mean velocity at bin 14 was 11.0 cm s^{-1} (SD 7.2) and the mean over all bins was 10.3 cm s^{-1} (range 9.2-11.4 cm s^{-1}). Our choice of depth for PVP construction is unlikely to have biased our conclusions. In locations where sheer is strong, however, it may be advisable to determine a mean velocity over the entirety of the depth range occupied by the organism of interest, and use this mean to construct the PVP.

Water velocities are determined by ADCPs using echoes from particles in the water (including plankton) on the assumption that the particles are drifting passively and that particle motion is due entirely to the motion of the water. If the particles are moving independently of the water, then particle motion may bias inferred water velocity. It has been shown, for example, that fish movement can bias velocity measurements (Plimpton et al., 1995), and indeed ADCP data have been used to infer fish motion (Demer et al., 2000). To determine if krill motion might bias our estimation of water velocity (and thus our virtual survey transects) we extracted velocity measures from within 20 krill swarms (detected during daylight) chosen at random throughout the deployment and from empty water immediately adjacent to each swarm and conducted paired *t* tests to see if differences could be detected.

The PVP data were transformed to equivalent latitude and longitude coordinates relative to the position of the mooring

Table 2. Target strengths (TS per individual krill) at each of the survey frequencies and observation angles, and frequency differences indicative of krill, averaged over the krill length-frequency distribution determined by net sampling before the mooring deployment.

Instrument	Frequency, kHz	Angular range degrees	TS mean dB	TS max dB	TS min dB	Krill ID range (S_v low to S_v high) dB
ADCP	300	255-315	–67.21	–59.52	–77.48	–14.77 to +14.53
WCP	125	275-295	–69.29	–62.70	–74.05	
EK60	120	Dorsal aspect	–74.20	–71.28	–78.19	+3.10 to +8.72
EK60	38	Dorsal aspect	–79.54	–74.38	–86.91	

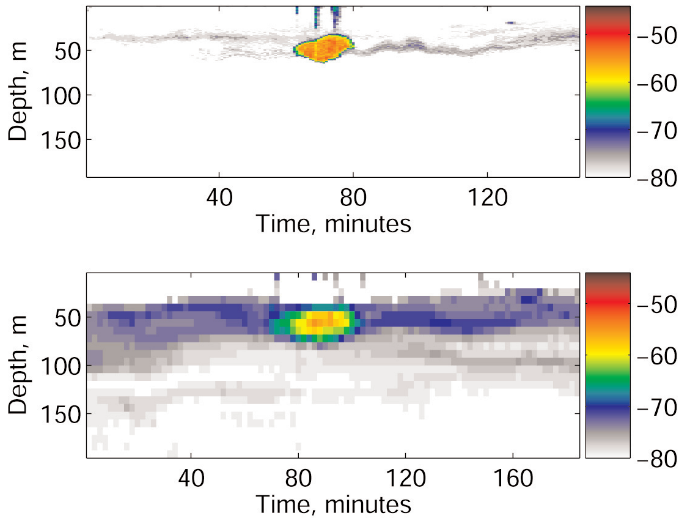

Fig. 4. Echograms showing a krill swarm detected simultaneously by the WCP (upper panel) and ADCP (lower panel). Color bar shows mean volume backscattering strength (S_v), dB. The swarm was identified as krill on the basis of the difference in echo intensity between frequencies. Note the finer resolution in the WCP echogram due to the more frequent time and depth sampling. Time 0 = 16:30 Z, Dec. 9, 2004.

using the Geographic Calculator (v. 3.09), a Universal Transverse Mercator projection and zone 24 S / 42°W to 36 °W (see Fig. 1). These latitude and longitude data were loaded in to Echoview as if they were a ship's GPS data, and linked by time to backscatter data.

Calculation of krill density from mooring data—Echo integration (in Echoview) of echoes identified on the basis of their frequency difference as arising from krill enabled NASC values attributable to krill to be determined at regular (we chose 30-minute) intervals throughout the deployment. The dB difference filter identified 26.7% of integration cells as containing krill (these cells contained 93.3% of all backscattered echo energy). Echoes from krill were scaled to krill density (g m^{-2}) using the target strength appropriate for each instrument for the length-frequency of krill sampled by predators during the mooring deployment (separate density estimates were calculated at 125 and 300 kHz: $\text{TS}_{\text{predators}}$ 300 kHz = –43.83 dB kg^{-1}, $\text{TS}_{\text{predators}}$ 125 kHz = –44.92 dB kg^{-1}), generating time-series of krill density at 30-minute intervals throughout the deployment. Diel vertical migrations were apparent in most echograms at dawn and dusk (approximately 06:00 and 23:00 Z for the middle of this deployment) and between these times, during hours of darkness, much of the plankton was lost to the near-surface deadzone that it was not possible to sample acoustically (Ona and Mitson, 1996). Data from these periods were therefore discarded from further analysis. For each daily period (06:00-23:00), individual half-hour krill density values were multiplied by the flow distance for that half-hour period: flow distance was calculated using spherical trigonometry from the ADCP-derived GPS position for the start and end of each interval. The daily mean krill density was then determined as [sum(density × distance)]/[sum(distance)]. This is exactly equivalent to the treatment of ship survey data to calculate mean transect density (Jolly and Hampton, 1990). Longer-term means for multiple daily periods were calculated as the mean of days within the period, weighted by the sampling distance for each day: again this is equivalent to the Jolly and Hampton (1990) method for calculating strata means from data from several transects.

Calculation of krill density from ship data—Acoustic surveys were conducted by RRS *James Clark Ross* along the standard BAS core box transects (Fig. 1) using a calibrated Simrad EK60 echosounder operating at 38 and 120 kHz (hull-mounted transducers, downward facing) before mooring deployment and after mooring recovery. Krill were identified on the basis of the expected dB difference between dorsal aspect echoes at 38 and 120 kHz (see Table 1) (Demer and Conti, 2005). Echo integration was used to generate 120-kHz NASC values for krill at 137-m intervals along track (137 m was the mean flow distance past the mooring in a half-hour interval) over the depth range equivalent to that sampled by the mooring (20 to 210 m). Data were excluded from portions of the transect landward of the 210 m depth contour because we have seen previously that mean krill densities on-shelf are different from densities off-shelf (e.g., Trathan et al., 2003): calculation of ship-based density estimates from on- and off-shelf data would not facilitate a like-with-like comparison with the off-shelf mooring. NASC data (120 kHz) from the ship survey before the mooring deployment were scaled to krill density using a dorsal aspect target strength appropriate for the krill length-frequency determined from the net sample (TS_{nets} 120 kHz = –42.76 dB kg^{-1}); data from the ship survey after the mooring deployment were scaled using the TS appropriate for the predator-derived length-frequency distribution ($\text{TS}_{\text{predators}}$ 120 kHz = –43.71 dB kg^{-1}; no net sampling was conducted during the postmooring ship survey). We calculated 120 kHz TS values from the TS-to-krill length relationship given by Demer and Conti (2005) that is a polynomial approximation of the SDWBA model output. Krill densities from each 137-m interval were used to generate weighted transect and box means using the method of Jolly and Hampton (1990).

Assessment

Mooring acoustic observations—The mooring deployment considered here was from Nov. 25, 2004, to Jan. 10, 2005. The ADCP logged data throughout this period, but a battery failure caused the WCP to stop on December 20. Krill identification using the dual-frequency technique was possible for a 26-day period. During that time, numerous krill swarms were detected in the water above the mooring (Fig. 4). The maximum mean volume backscattering strengths detected by the ADCP (4-beam average) and WCP were in the order of –46.5 dB, equating to a krill numerical density of roughly 150 animals

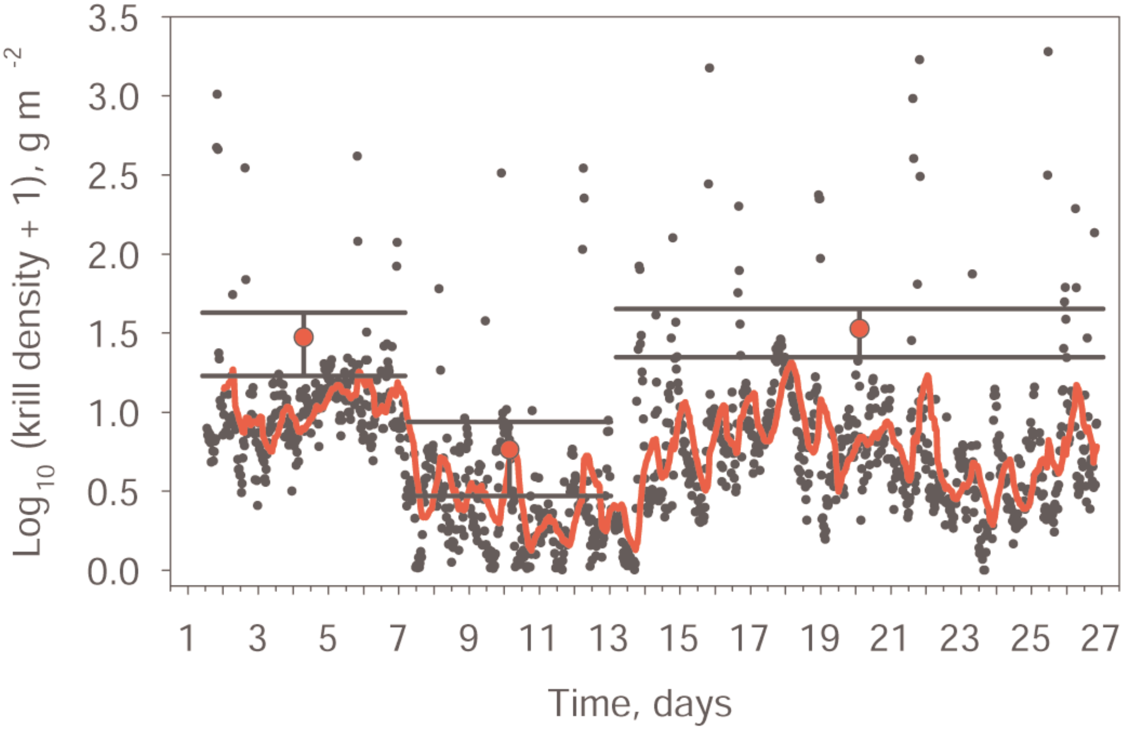

Fig. 5. Time series of ($\log_{10}$) krill density from the WCP, a 24-point moving average (of the log), and means (red circles, ± 1 SD error bars) for the 3 distinct density periods (first 6 days, middle 6 days, final 14 days). Day 1 starts 00:00 Nov. 25, 2004. The range of individual half-hour density values is high, as is usual for acoustic surveys of krill density, and much of the biomass is contained within relatively few high-density swarms.

per m^3. These values are below saturation (no values of 255 were recorded), and the dynamic ranges of both instruments were thus adequate for evaluating krill swarms with the packing density prevailing during this deployment.

Mean flow velocity (at 100-108 m) during the deployment was 7.6 cm s^{-1}, leading to a mean sampling distance of 137 m for a 30-minute interval, but velocity was not constant and sampling distance ranged from 5 to 403 m. This variation illustrates well why backscatter values need to be scaled by sampling distance to calculate unbiased mean density estimates. This is further illustrated by the meander in the PVP in the period after the WCP battery failed (black line, Fig. 1). Although flow velocity varied throughout the deployment, we could find no evidence for differences in velocity within krill swarms compared with empty water, and thus have no reason to believe that the presence of krill biased our inferred sampling distances. Within the 20 swarms (mean ADCP echo intensity –55.9 dB, mean depth 87 m, depth range 53 to 150 m), mean velocity was 11.6 cm s^{-1} (range 3.3 to 21.9 cm s^{-1}). Outside the swarms, at the same depth, mean velocity was also 11.6 cm s^{-1} (range 2.3 to 30.3 cm s^{-1}). Paired sample t tests failed to detect any significant difference in velocities within and outside swarms ($n = 20$; pre-swarm versus in swarm $P = .44$; in swarm versus post-swarm $P = .35$), and it thus seems unlikely that the presence of krill swarms would have biased our estimates of sampling distance.

The time series of krill density (from the WCP) for the 26-day period is presented in Fig. 5. A 24-point running mean through this time series (12-hour intervals) has a clear daily cyclicity, with low nighttime values punctuating generally higher daytime values. This is in part a consequence of krill migrating upwards into the surface dead zone at dusk and downwards away from the surface at dawn. There may also be a tidal component to this variability (maximum power in the time series is at 14.8 hours): previous studies have reported an impact of tidal flow on euphausiid aggregation (Cotte and Simard, 2005). The time series also shows prominent step-changes after 6 days (Nov. 30) and 12 days (Dec. 6) that divide it into 3 distinct density periods. Using the flow vectors over the mooring each day to construct daily (daylight only) virtual transects and to weight daily mean density estimates in a manner analogous to that advocated by Jolly and Hampton (1990) for conventional survey transects, weighted mean krill densities for each period were calculated as 29.7 g m^{-2} (SD 12.8), 5.8 g m^{-2} (SD 2.8), and 33.6 g m^{-2} (SD 11.3), respectively, using WCP data.

Comparison of WCP and ADCP backscatter—Successful implementation of a dual-frequency species identification technique requires that data at both frequencies are accurate. Calibration data for the WCP were collected with the standard target technique used routinely to calibrate ship's scientific echosounders (Foote et al., 1987), but calibration was conducted near surface (10 m) and not at the ~200-m operating depth, and depth may influence calibration (Dalen et al., 2003). The slanted beams of the ADCP are difficult to calibrate using standard target techniques, and we relied on data from the manufacturer, ambient temperature information, and the Deines (1999) equation to determine backscatter from the ADCP. Given our a priori uncertainty in calibration, we conducted a regression analysis to compare the krill densities determined from the ADCP measures of backscatter to those from the WCP. Considering all 1216 30-minute observation periods throughout the deployment,

$$\text{ADCP density} = 0.79\ \text{WCP density} + 28.89\ (r^2\ 0.76,\ P < .0001)$$

Confidence limits (95%) for the slope and intercept are 0.77 to 0.82 and 25.71 to 32.09, respectively. Substituting the WCP mean krill density (21.18 g m^{-2}) into the regression equation gives a ratio of ADCP density to WCP density of 2.15:1, which equates to a 3.3 dB difference between instruments. This difference, as expressed at the level of density, is a function not only of instrument calibration (change in depth from 10 to 200 m might cause a ~0.5 dB change in WCP calibration, cf. Dalen et al., 2003) but also of target strength (in turn a function of krill length-frequency and orientation). As such, a between-instrument difference of just 3.3 dB is very pleasing, especially since we might expect the ADCP to detect more krill swarms (hence more biomass) anyway because it is sampling a broader total area than the WCP (4 beams each 20° off vertical versus a single vertical beam) and might detect swarms that pass outside the WCP sampling volume.

Comparison of mooring and ship—The moorings make measurements of krill at single points in the ocean. To have confidence that mooring-derived time series of krill abundance are representative of changes over a broader area—an area, for example, that might be relevant to foraging predators—we need to examine mooring observations in context with more widespread (yet temporally restricted) observations. Conventional ship-based acoustic surveys provide such data. Krill density in the South Georgia western core box is assessed by surveys of 10 transects each 80 km long and on average 10 km apart. At a survey speed of 10 knots, 2 such transects can be surveyed per day in daylight. Surveys are conducted in daylight only to avoid negative bias that would otherwise be caused as krill migrate to the near-surface zone at dusk (this zone is not sampled by the ship's echosounder) (Demer and Hewitt, 1995). We used standard protocols (e.g., Brierley et al., 1997, 1999b) to determine krill density from the 4 survey transects closest to the mooring from the surveys immediately before and after the mooring deployments, and considered mooring-derived krill densities in this context. Before the mooring deployment (RRS *James Clark Ross* cruise JR107), the mean krill density was 73.2 g m^{-2} (SD 21.7), and after the cruise (JR116) the mean was 24.1 g m^{-2} (SD 8.6). Cruise values are not statistically different from the densities derived from the mooring data at the start and end of the deployment (2-sample t test between 4 ship transects from the predeployment survey and first 6 days' mooring observations, $P = .18$; 2-sample t test between 4 ship transects from the postdeployment survey and last 14 days' mooring observations, $P = .58$).

Discussion

The step changes in krill density apparent in the mooring-derived time series after Nov. 30 (from mean 29.7 g m^{-2} to mean 5.8 g m^{-2}) and Dec. 6 (from mean 5.8 g m^{-2} to mean 33.6 g m^{-2}) are, to our knowledge, the first instances that abrupt changes in krill density have been detected directly at sea. Changes such as these had been hinted at by abrupt changes in predator foraging behavior but, because of previous sampling limitations, had not been observed directly. The analyses reported here thus demonstrate clearly that the moorings meet the defined need—that is, to gather data able to resolve short-term fluctuations in krill density. The high-to-low change in krill density apparent in the early part of the krill-density time series would be sufficient to change our opinion, in terms of interpretation of conventional ship-based observations, that the 2004/05 summer season was one of adequate krill availability for predators to the opinion that it was a season of poor krill availability. This illustrates well why it has so far proved impossible to link krill abundance and predator breeding performance (Reid et al., 2005): if changes such as these are typical of most breeding seasons, then single ship-based snapshots of krill availability may not provide a krill abundance estimate that is a good reflection of the predator's view of krill availability. We hope that ongoing analyses of longer time-series of mooring data—using the methods described here—will provide insight on the time scale of variability over multiple seasons. In the meantime, we must continue to attribute with caution changes in predator behavior to changes in krill availability as indicated by existing ship-based time series of krill density. Ultimately, of course, it will be important to understand both temporal and spatial variability, and the causes thereof, if we are to progress to the point where we can predict changes in krill abundance at South Georgia and establish ecosystem-based management procedures that are responsive to such changes. Ship-based and mooring-based data will therefore be essential to obtain spatially and temporally extensive views on the South Georgia ecosystem.

The moorings provide new insight on the physical processes associated with the short-term changes in krill density at South Georgia. The changes in krill density reported here after Nov. 30 and Dec. 6 coincided with abrupt changes in water temperature (from ~1.3° C to 1.1° C and back to 1.3° C, as detected by the mooring CTD) and velocity (from ~7 cm s^{-1} to 12 cm s^{-1} and back, as detected by the ADCP). It is not the purpose of this article to present an in-depth analysis of the oceanographic causes of such changes, but they could be indicative of the passage of a front or eddy over the mooring.

Inspection of the progressive vector plot from ADCP velocity data (Fig. 1) shows that flow direction is not constant. Ward et al. (2002) reported the presence of 2 fronts on a transect running 160 km northeast from South Georgia. They suggested that the fronts, which they considered to be two sides of a meander in the SACCF, exhibited higher velocities than surrounding water, and that the SACCF water was cooler. It is possible that the mooring has detected a temporal manifestation of the changes observed spatially by Ward et al. (2002). Again, analysis of our longer mooring krill-density time series, and full consideration of the oceanographic data collected simultaneously, may provide a clear view of the oceanographic changes that presage changes in krill abundance at South Georgia, and provide completely new insight on the hitherto unobserved winter period.

Comments and recommendations

South Georgia is a particularly hostile environment for mooring deployment. Icebergs frequently pass by and can remain for periods of many months if they become grounded. The moorings described here were designed to survive iceberg collisions, and did so on numerous occasions. The CTDs recorded several instances when the moorings were knocked downwards by the passage of a berg, only to float back to the original depth once the berg had drifted by. The robust nature of the moorings makes it likely that they would survive deployment in most other oceanic or lake locations. As long as an acoustic signature of the target species is known, it should prove possible to use the method we describe here to assess temporal variations in abundance of most passively drifting pelagic species.

The acoustic instruments on the moorings gathered data that provide plausible estimates of krill density that are consistent with ship-based estimates in adjacent time periods. Krill density at South Georgia, however, can sometimes be very high (> 150 g m^{-2}), and on these occasions very high-density swarms are detected during ship-based surveys. Although the ADCP and WCP were not saturated during the deployment reported here, had swarms of very high density been present, they may well have been. Hamner and Hamner (2000) suggest numerical densities of up to 64,000 krill per m^3 are possible, and these would provoke S_v values of around –20 dB. Although ADCPs can provide quantitative estimates of backscatter density in some circumstances (Lee et al., 2004), this is not the principal purpose of the instrument and they do not always deliver values directly equivalent to those obtained by scientific echosounders (Brierley et al., 1998a). This, and the fact that they cannot easily be calibrated in situ (athough we understand absolute calibration is now possible; Eberhard Fahrbach, Alfred Wegener Institut, personal communication, 2005), makes these instruments less than ideal for quantitative backscatter measurement. The ADCP is essential, however, for obtaining the current velocity measurements that are an integral component of the method reported here. Given unlimited finances, we would choose to equip the moorings with purpose-designed scientific echosounders that have documented calibration stability and high dynamic range (such as the EK60 used on the ship; these instruments have been housed for remote deployment under battery power), and to have at least 2 echosounder frequencies on the mooring in addition to the ADCP. Frequencies would be chosen so that uncertainty in krill orientation had less of an influence on target strength (see Fig. 3) and thus density calculation. For use in other environments, on different target species, operating frequency could be chosen to best meet the compromise between resolution, range, and species discrimination.

Although the moorings survived iceberg strikes, the offshore mooring fared less well on one occasion in an encounter with fishing gear. Longliners operate along the shelf break, deploying baited hooks for Patagonian toothfish. On May 12, 2003, a transmission from the Argos beacon on the off-shelf mooring alerted us to the fact that the mooring was on the surface. The mooring was eventually recovered for us by a fishing vessel operating in the area, and it seems likely that it was dragged to the surface after becoming entangled in a longline. In future we may opt to place the off-shelf mooring further away from the shelf break, out of the zone targeted by fishing vessels.

To conclude, although acoustic data collected from moorings present some unusual challenges for analysis, they provide a window of observation onto pelagic systems not open from conventional research vessels. At South Georgia, they have provided data giving a completely new insight on the function of the coupled biological-physical marine system. We believe that incorporation of mooring data into regional ecosystem analyses will lead to much-improved understanding of ecosystem function there; moorings will likely deliver equally new insight on ecosystem function elsewhere, and we encourage our colleagues to consider this approach.

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