INTRA-ANNUAL VARIABILITY IN THE DENSITY OF ANTARCTIC KRILL (*EUPHAUSIA SUPERBA*) AT SOUTH GEORGIA, 2002–2005: WITHIN-YEAR VARIATION PROVIDES A NEW FRAMEWORK FOR INTERPRETING PREVIOUS 'ANNUAL' ESTIMATES OF KRILL DENSITY

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Abstract

Upward-looking acoustic Doppler current profilers (300 kHz) and echo sounders (125 kHz) were deployed on moorings on- and off-shelf to the northwest of South Georgia between 14 October 2002 and 29 December 2005 to measure density of Antarctic krill and environmental parameters continuously. A distinct seasonal pattern in krill density, recurring consistently over all three years, was detected. Krill densities in winter were predominantly low (mean = 18.7 g m^{-2}, SD = 24.3), but had risen substantially by summer in each year (mean = 89.5 g m^{-2}, SD = 64.2). A sinusoidal regression model (period = 52 weeks) with time as the independent variable explained 64% of the observed week-to-week variation. Estimates of krill density from moored instruments were not statistically different ($P > 0.05$) from estimates derived from standard ship-based krill surveys in adjacent time periods, suggesting that the point estimates from moored instruments were representative of krill density in a wider spatial context (ship surveys cover c. 100 x 100 km). Data from moored instruments were used to explore whether high-frequency temporal variation (i.e. within-year) could have led to the perceived between-year variation in krill density arising from previous summer surveys in the South Georgia western core box region between 1990 and 2005. Comparison of these 'snap-shot' ship survey estimates with the observed pattern of within-year variability showed that some of the apparent 'year-to-year' variation could simply be attributed to sampling on different dates of the year (e.g. November cf. February). However, there were some survey estimates that were significantly different ($P < 0.01$) from the regression-predicted within-year variation. Years that stand out for markedly low krill density (i.e. densities below the range expected due to intra-annual variation) were 1993/94, 1998/99 and 1999/2000. Moored instruments provide valuable data that could be important for ecosystem-based management at South Georgia because, for example, they will enable predator–prey functional responses to be explored there for the first time at appropriate temporal scales, and will enable hypotheses relating variation in krill abundance to physical oceanographic variability to be tested.

Résumé

Des profileurs de courant acoustique à effet Doppler (300 kHz) orientés vers le haut et des échosondeurs (125 kHz) ont été mis en mouillage sur le plateau et au large de ce dernier, au nord-ouest de la Géorgie du Sud entre le 14 octobre 2002 et le 29 décembre 2005 pour mesurer en continu la densité de krill antarctique, ainsi que des paramètres environnementaux. Une tendance saisonnière nette de la densité de krill s'est dégagée, se manifestant régulièrement au cours des trois années. Les densités de krill, qui étaient le plus souvent faibles en hiver (moyenne = 18,7 g m^{-2}, SD = 24,3), sont remontées considérablement chaque année avant l'été (moyenne = 89,5 g m^{-2}, SD = 64,2). Un modèle de régression sinusoïdale (période = 52 semaines) dont la variable indépendante est le temps explique 64% de la variation observée d'une semaine à l'autre. Sur le plan statistique, les estimations de la densité de krill tirées des instruments en mouillage ne diffèrent pas ($P > 0{,}05$) de celles dérivées des campagnes d'évaluation types du krill menées par des navires en des périodes adjacentes, ceci laissant penser que les estimations ponctuelles provenant des instruments en mouillage sont représentatives de la densité de krill dans un contexte spatial plus large (surface de campagne d'environ 100 x 100 km par navire). Les données provenant des instruments en mouillage sont utilisées pour déterminer si une variation temporelle à fréquence élevée (c.-à-d., au cours d'une année) serait à l'origine de la variation interannuelle de la densité de krill apparente lors d'anciennes campagnes d'évaluation menées en été dans le rectangle principal ouest de la région de la Géorgie du Sud entre 1990 et 2005. La comparaison entre ces estimations instantanées provenant de campagnes d'évaluation effectuées à partir de navires et la tendance observée d'une variabilité en une même année montre que la variation apparente «d'année en année» pourrait en fait s'expliquer, en partie, par le fait que l'échantillonnage aurait eu lieu à des périodes différentes de l'année (novembre cf. février, par ex.). Certaines estimations de campagne d'évaluation diffèrent toutefois grandement ($P < 0{,}01$) de la variation intra-annuelle prévue par la régression. Les années qui se démarquent par une densité de krill particulièrement faible (c.-à-d., une densité inférieure à l'intervalle prévu en raison d'une variation intra-annuelle) sont 1993/94, 1998/99 et 1999/2000. Les instruments en mouillage fournissent des données utiles qui pourraient s'avérer importantes pour une gestion écosystémique en Géorgie du Sud. En effet, ils pourraient, par exemple, permettre d'étudier pour la première fois les réponses fonctionnelles des prédateurs et des proies aux échelles temporelles qui conviennent et de tester les hypothèses reliant la variation de l'abondance de krill à la variabilité physique de l'océan.

Резюме

В период с 14 октября 2002 г. по 29 декабря 2005 г. на шельфе и вне его, к северо-западу от Южной Георгии, с целью постоянного измерения плотности антарктического криля и параметров окружающей среды были прикреплены к дну направленные вверх допплеровские акустические профилографы течений (300 кГц) и эхолоты (125 кГц). Они обнаружили четкую сезонную картину распределения криля, систематически повторяющуюся на протяжении всех трех лет. Плотность криля зимой была преимущественно низкой (среднее = 18.7 г $м^{-2}$, SD = 24.3), но каждый год значительно возрастала к лету (среднее = 89.5 г $м^{-2}$, SD = 64.2). Синусоидальная модель регрессии (период = 52 недели), где время является независимой переменной, объясняла 64% наблюдавшихся понедельных изменений. Оценки плотности криля с помощью прикрепленной к дну аппаратуры статистически не отличались ($P > 0.05$) от оценок, полученных в результате стандартных судовых съемок криля в сопредельные периоды времени, что свидетельствует о типичности точечных оценок, полученных с использованием прикрепленных к дну приборов, для плотности криля в более широком пространственном контексте (судовые съемки охватывают площадь 100 х 100 км). Данные прикрепленных к дну приборов использовались для изучения того, могли ли высокочастотные временные изменения (т.е., происходящие в рамках одного года) привести к замеченным колебаниям плотности криля между годами, о которых свидетельствуют предыдущие летние съемки в районе западной основной клетки Южной Георгии в период 1990–2005 гг. Сравнение этих полученных судами «моментальных» съемочных оценок с наблюдавшейся картиной внутригодовых изменений показывает, что некоторые явные межгодовые колебания могут просто объясняться тем, что отбор образцов проводился в разное время года (напр., в ноябре и феврале). Однако имелся ряд съемочных оценок, которые сильно отличались ($P < 0.01$) от внутригодовых колебаний, прогнозируемых по методу регрессии. Особенно выделяются необычайно низкими оценками плотности криля (т.е. плотности ниже диапазона, ожидаемого в соответствии с межгодовыми колебаниями) 1993/94, 1998/99 и 1999/2000 гг. Прикрепленные к дну приборы предоставляют ценные данные, которые могут быть важны для экосистемного управления в районе Южной Георгии, т.к. они, к примеру, позволят впервые изучить функциональный отклик «хищники–добыча» в соответствующих временных масштабах, а также позволят проверить гипотезы, связывающие колебания численности криля с физической океанографической изменчивостью.

Resumen

A fin de medir continuamente la densidad de kril antártico y los parámetros ambientales, se utilizaron perfiladores de corriente ultrasónicos Doppler (300 kHz) y ecosondas (125 kHz) colocados cara arriba en instalaciones fijadas sobre la plataforma y en alta mar en la zona noroeste de Georgia del Sur, entre el 14 de octubre de 2002 y el 29 de diciembre de 2005. Se pudo detectar una pauta estacional clara en la densidad de kril que se repitió sistemáticamente en los tres años de estudio. Las densidades del recurso en invierno fueron predominantemente bajas (promedio = 18.7 g m^{-2}, SD = 24.3), pero aumentaron progresivamente cada año con la llegada del verano (promedio = 89.5 g m^{-2}, SD = 64.2).

Un modelo de regresión sinusoidal, con un período de 52 semanas y con tiempo como variable independiente dio cuenta del 64% de la variación observada de una semana a otra. Asimismo, se encontró que la diferencia entre las estimaciones de la densidad de kril a partir de los instrumentos fijos y las derivadas de las prospecciones estándar de kril efectuadas por barcos aproximadamente en los mismos períodos no era estadísticamente significativa ($P > 0.05$), lo que sugiere que las estimaciones de punto obtenidas de los instrumentos fijos eran representativas de la densidad de kril en una escala espacial más amplia (las prospecciones realizadas por barcos cubren un área aproximada de 100 x 100 km). Se utilizaron los datos obtenidos de los instrumentos fijos para determinar si la variación temporal de alta frecuencia (es decir, la variación intra-anual) podría haber dado lugar a la aparente variación inter-anual de la densidad de kril observada en las prospecciones anteriores realizadas durante el verano en la región rectangular principal al oeste de Georgia del Sur entre 1990 y 2005. La comparación entre las estimaciones 'instantáneas' de las prospecciones de barcos con la pauta observada de la variabilidad intra-anual demostró que parte de la aparente variación 'inter-anual' simplemente puede deberse a que el muestreo se realizó en distintas épocas del año (por ejemplo, en noviembre comparado con febrero). Sin embargo, algunas de las estimaciones de las prospecciones fueron significativamente diferentes ($P < 0.01$) de la variación intra-anual estimada con el modelo de regresión. Los años en los cuales la densidad de kril fue extremadamente baja (esto es, menor que el valor mínimo del margen esperado de la variación intra-anual) fueron 1993/94, 1998/99 y 1999/2000. Los instrumentos fijos proporcionan datos valiosos que podrían ser importantes para la ordenación basada en el ecosistema de Georgia del Sur porque, por ejemplo, permitirán estudiar las respuestas funcionales de los depredadores y sus presas por primera vez en escalas temporales apropiadas, y también permitirán probar las hipótesis relacionadas con la variación de la abundancia de kril en función de la variabilidad de los parámetros físicos del océano.

Keywords: Antarctic krill, moorings, intra-annual variability, South Georgia, CCAMLR

Introduction

Interannual variation is a characteristic feature of the Southern Ocean ecosystem (Hardy and Gunther, 1935; Everson, 1984; Murphy et al., 1998). Acoustic surveys conducted during brief periods (typically two weeks) over the past two decades at South Georgia have revealed significant variation in the density of Antarctic krill (*Euphausia superba*) (Brierley et al., 1999), and it has been argued that this is indicative of year-to-year variation in krill density at the island. However, there are some instances when multiple surveys have been conducted several weeks apart in the same year, and have detected significant differences in krill densities (e.g. 2 g m^{-2} wet mass in October 1997 versus 21 g m^{-2} in January 1998; Brierley et al., 1999). This raises the possibility that apparent interannual variability is actually a temporal alias of shorter-term (intra-annual) variability. Most at-sea data available to date on the South Georgia pelagic marine environment are restricted (for logistic reasons) to single month-long periods in the austral summer. As a consequence, it has not yet been possible to address in detail, by direct observation, variation in krill density on sub-annual time scales, or to address directly the potential mechanisms driving any such change. Data from predators breeding ashore at South Georgia have suggested that krill availability can vary significantly throughout the summer breeding season (November–February), but lack of corroborating at-sea data have prevented direct verification of this (Mori and Boyd, 2004). Evidence from elsewhere around Antarctica also suggests that local krill abundances can fluctuate substantially within seasons (McClatchie et al., 1994; Siegel, 1988).

The possible existence of significant within-year or seasonal variations in krill density have potentially worrying implications for analyses of ecosystem processes at South Georgia that are based on short-term cruise observations, because the timing of the cruise could significantly affect the estimate of krill density for a given 'year'. Understanding the magnitude, timing and causes of intra-annual variability is thus an essential prerequisite for ecosystem management (Everson, 1992) and for understanding change on an interannual scale. Moored instrument arrays ('moorings') can provide simultaneous biological and oceanographic data at the temporal resolution required to resolve short-term variation in krill abundance and the potential causal mechanism thereof (Cochrane et al., 1994; Brierley et al., 2006). Mooring data have now been collected almost continuously between October 2002 and December 2005, and enable the scale of within-year variation in krill density at South Georgia to be explored. This paper details such within-year variation, and examines previously published interannual estimates of krill density (arising from typically month-long cruises in

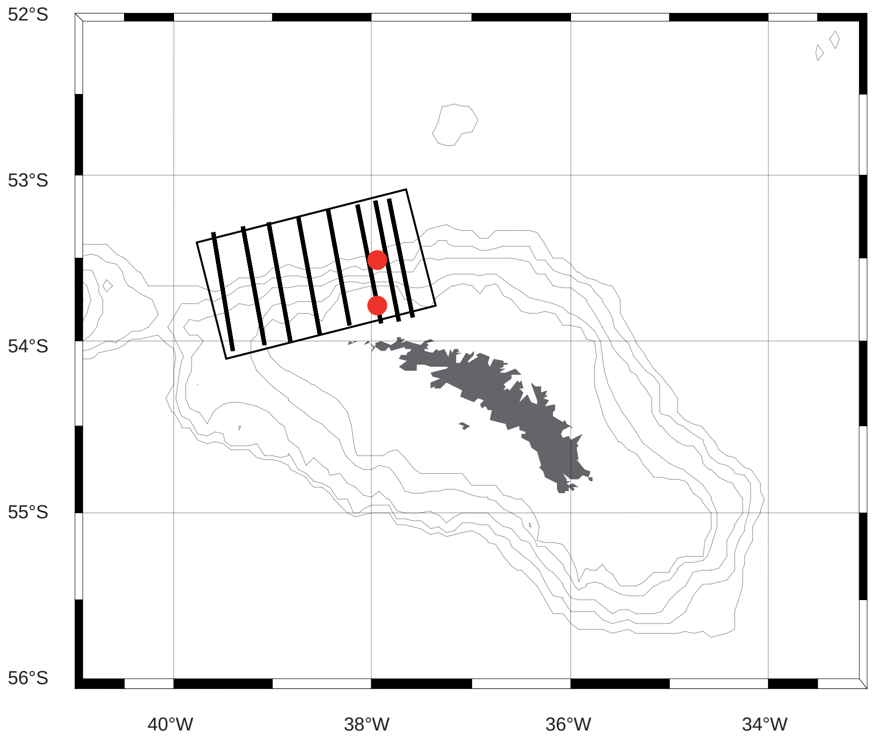

Figure 1: Map of South Georgia showing the positions of the moorings and the surrounding bathymetry (300, 500, 1 000, 1 500 and 2 000 m depth contours). The bounds of the British Antarctic Survey western core box region and the eight standard survey transects are also shown.

summer) in the light of repeated observations of within-year changes to address the question, 'Can apparent year-to-year variation in krill density be explained as a simple function of the dates of previous ship-based surveys?'.

Materials and methods

Mooring design and acoustic sampling

The methods used for the mooring component of this investigation are detailed in Brierley et al. (2006), and so only a summary is given here. Two moorings were deployed at on-shelf and off-shelf locations to the northwest of South Georgia (Figure 1). The moorings were first deployed in October 2002 and have remained more or less continually in place, apart from brief periods (to enable data download, battery replacement and servicing) to the present. Both moorings were equipped with an ASL Environmental 125 kHz Water Column Profiler (WCP), an RDI Workhorse acoustic Doppler current profiler (ADCP) operating at 300 kHz, and a Seabird SBE37 conductivity/temperature/depth logger (CTD). The arrays were positioned in approximately 1 300 m and 300 m of water on standard acoustic survey transects (Figure 1), and each mooring was engineered so that the instrument package floated at approximately 200 m below the sea surface with the acoustic devices orientated to sample vertically upwards. The ADCPs were configured to collect data in 8 m depth bins and to ping 7 times within a 4 min ensemble interval. The WCPs were configured to collect data in 0.5 m bins, with a sampling rate of 1 ping every 2 min. Each WCP was calibrated with reference to echo intensities recorded from a standard target during a calibration exercise conducted in Stromness Bay, South Georgia.

Mooring data analysis

Mean volume backscatter (S_v dB re 1 m^{-1}) was determined from the WCPs and ADCPs using forms of the SONAR equations presented by Brierley et al. (2006) and Deines (1999) respectively. Both acoustic data streams were processed using SonarData Echoview software. The echograms were first scrutinised for regions of bad data (e.g. near-surface dead zones, 'blank after transmit' and periods of interference). TVG-amplified background noise was then removed following the method of Watkins and Brierley (1996), and the WCP data were resampled (averaged in the linear domain) onto 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.

Echoes arising from krill were identified on the basis of the theoretical difference in echo intensity at the operating frequencies of the ADCP and the WCP (S_v 300–S_v 125 kHz; Brierley et al., 2006). However, both WCPs failed on a number of occasions throughout the time series (Table 1), and an alternative approach was devised to infer krill-related backscatter from single-frequency ADCP data as follows. Firstly, a regression analysis was conducted to investigate the relationship between ADCP backscatter (30-minute Nautical Area Scattering Coefficient (NASC) values) filtered using the dual-frequency technique (i.e. data containing identified krill echoes only) and unfiltered ADCP backscatter (i.e. echoes from all targets). The analysis showed that filtered backscatter arising from krill could be inferred using the equation:

$$\text{ADCP NASC}_{\text{filtered}} = 0.86 \text{ ADCP NASC}_{\text{unfiltered}} - 95.97 \; (r^2 \; 0.92, P < 0.0001)$$

(i.e. approximately 86% of targets detected were attributable to krill). Secondly, ADCP-derived S_v data were integrated to give unfiltered NASC values at 30-minute intervals. No thresholds were applied to the data prior to echo integration. Finally, all unfiltered NASC values were scaled using the equation above, and values below a threshold of 111 m^2 n $miles^{-2}$ (equivalent to a mean S_v of –78 dB over the mean sampled water column, ~192 m) were removed from the regression-corrected data, so that negative values were not included in the krill density calculation.

Target strength (TS) and krill length-frequency estimation

The Demer and Conti (2005) stochastic distorted-wave Born approximation (SDWBA) model was used to determine 125 and 300 kHz ventral aspect TS (dB kg^{-1}) for populations of krill having the length-frequency distributions apparent during each mooring deployment period (Table 2). Representative krill length-frequency distributions for each time period were determined from length-frequency data obtained from diet samples of Antarctic fur seals and macaroni penguins that breed ashore at Bird Island and forage in the vicinity of the moorings (Reid and Brierley, 2001). 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 target strength (TS).

'Virtual' survey transects

ADCP velocity measurements were used to scale time-based acoustic observations of krill over the moorings to area-based abundance estimates following Brierley et al. (2006). The north and east velocity components for bin 14 (100–108 m depth) were used to construct progressive vector plots (PVPs), which provide a Lagrangian display of Eulerian measurements, and can be considered analogous to the cruise track of a research vessel. Each point along the PVPs was transformed to equivalent latitude and longitude coordinates relative to the position of the moorings (using the Geographic Calculator v. 3.09, a Universal Transverse Mercator projection and zone 24°S/42°W to 36°W), and these data were loaded into Echoview as if they were a survey ship's GPS track data. The latitude and longitude data were then linked by time to the acoustic backscatter data to give a virtual position for each observation.

Calculation of krill density from mooring data

Echo integration of echoes identified on the basis of their frequency difference as arising from krill enabled 125 kHz NASC values attributable to krill to be determined at 30-minute intervals throughout the deployment period. WCP and regression-corrected ADCP values were scaled to krill density (g m^{-2}) using the appropriate TS for each instrument, generating time-series of krill density at 30-minute intervals for both the on-shelf and off-shelf mooring. For each daily period (military sunrise + 1 hr to sunset – 1 hr), 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)] following Jolly and Hampton (1990). Longer-term means for multiple-day periods were calculated as the mean of days within the period, weighted by the sampling distance for each day: this is equivalent to the Jolly and Hampton (1990) method for calculating strata mean densities from data from several transects. Data from the two arrays were combined during periods in which both on-shelf and off-shelf data were obtained. During such instances, longer-term means were calculated as the mean of the combined number of days within each period, weighted by the combined sampling distance for each day.

Table 1: Deployment details of the moored instrument arrays. The amount of data collected by each moored instrument and the depth range sampled effectively by the acoustic devices are also shown. ✓ – complete data stream obtained from instrument; × – no data obtained; ✓* – data obtained between 20/11/2005 and 20/12/2005.

Deployment	Deployment dates	Approx. water depth (m)	On-shelf mooring depth (m)	Depth range sampled (m)	On-shelf WCP data	On-shelf ADCP data	On-shelf CTD data	Approx. water depth (m)	Off-shelf mooring depth (m)	Depth range sampled (m)	Off-shelf WCP data	Off-shelf ADCP data	Off-shelf CTD data
1	14/10/02–12/02/03	300	196	30–182	×	✓	✓	1300	203	20–189	×	✓	✓
2	19/02–28/04/03	300	198	32–184	×	✓	✓	no deployment due to icebergs on site					
3	29/04–12/11/03	309	190	32–176	×	✓	✓	1336	208	na	×	×	×
4	12/11/03–13/01/04	310	200	34–186	×	✓	✓	1334	227	21–213	×	✓	✓
5	14/01–24/03/04	300	198	32–184	×	✓	✓	1300	226	20–212	×	✓	✓
6	26/03–20/11/04	320	199	33–185	×	✓	✓	not deployed off-shelf to avoid fishing fleet					
7	20/11/04–10/01/05	319	197	na	×	×	✓	1300	226	20–210	✓*	✓	✓
8	11/01–03/04/05	320	201	35–187	✓	✓	✓	1300	223	17–209	✓	✓	✓
9	04/04–29/12/05	300	180	30–166	×	✓	✓	not deployed off-shelf to avoid fishing fleet					

Table 2: Krill lengths and ventral aspect target strength at 300 kHz (ADCP) and 125 kHz (WCP). Values were calculated from predator-derived length-frequency data obtained during each mooring deployment period.

Mooring deployment	Dates of predator diet sampling	Mean krill length (mm) (=*n*)	Mean TS 300 kHz (dB kg^{-1})	Mean TS 125 kHz (dB kg^{-1})
1	09/10/02–19/02/03	50.5 (1511)	–43.59	–44.82
2	19/02–30/04/03	48.4 (754)	–43.57	–44.72
3	30/04–12/11/03	45.7 (911)	–42.98	–44.95
4	12/11/03–14/01/04	54.8 (655)	–43.74	–45.04
5	14/01–24/03/04	54.0 (733)	–43.63	–44.98
6	24/03–24/11/04	61.3 (781)	–43.01	–44.41
7	24/11–20/12/04	52.6 (478)	–43.83	–44.92
8	12/01–30/04/05	54.5 (779)	–43.84	–45.12
9	30/04–12/11/05	46.5 (823)	–42.98	–44.96

Table 3: Cruise dates, krill length and dorsal aspect target strength at 120 kHz (shipboard EK60). Values were calculated from predator-derived length-frequency data obtained at times coinciding with the ship surveys, except during JR107 where length-frequency data were obtained using a rectangular midwater trawl (RMT8) net.

Cruise	Cruise dates	Dates of predator diet sampling	Mean krill length (mm)	(= n)	Mean TS 120 kHz (dB kg^{-1})
JR79	15/10–19/10/02	09/10–23/10/02	46.3	(150)	–42.98
JR82	13/02–16/02/03	05/02–19/02/03	50.3	(281)	–43.37
JR107	21/11–25/11/04	RMT8 net on 20/11/04	44.2	(157)	–42.76
JR116	06/01–10/01/05	06/01–10/01/05	57.1	(144)	–44.92
JR121	30/03–02/04/05	16/03–30/03/05	51.8	(220)	–43.58

Calculation of krill density from ship data

Standard acoustic surveys were conducted in the western core box (Figure 1) (Brierley et al., 1997) from RRS *James Clark Ross* during the mooring sampling regime (Table 3) such that mooring-based estimates of krill density could be considered in the context of possible variability over a wider spatial scale. Data were collected from eight standard transects (80 km long and c. 10 km apart) using a calibrated EK60 scientific echo sounder operating 38, 120 and 200 kHz transducers. Krill were identified on the basis of the theoretical difference in echo intensity at 38 kHz and 120 kHz (S_V 120–S_V 38 kHz between 2 and 16 dB, as per the recommendations of Demer and Conti, 2003), and echo integration was used to generate 120 kHz NASC values for krill at along-track intervals equivalent to the mean flow distance past the mooring in a half-hour interval (typically 137 m) over the depth ranges sampled by the moored devices at the corresponding time periods (Table 1). Data were also partitioned for regions on-shelf (landward of the 210 m depth contour) and off-shelf (seaward of the 300 m depth contour) such that shipboard estimates of krill density could be determined for a like-for-like comparison with the on-shelf and off-shelf moorings. Dorsal-aspect krill target strengths were calculated using predator-derived length-frequency data obtained during each cruise period (Table 3). 120 kHz TS values were calculated from the TS-to-krill length relationship given by Demer and Conti (2005) that is a polynomial approximation of the SDWBA model output. Weighted transect and box krill mean densities (and variances) were calculated using the method of Jolly and Hampton (1990).

Investigation of temporal aliasing

Acoustic estimates of krill density in the western core box between 1990 and 2005 (Brierley and Goss, 1999; Brierley et al., 1999; Sushin et al., 2000; Reid et al., 2005) were compared to the mooring-derived pattern of within-year variation to assess how much of the apparent year-to-year variation could be attributed to the survey date. However, these previously published estimates had been calculated using the krill TS model of Greene et al. (1991) and were thus not directly equivalent to the krill density estimates from this investigation (determined using the SDWBA modelled TS). Firstly, therefore, existing krill density estimates were rescaled as follows to account for the TS differences. The SDWBA model of Demer and Conti (2005) was used to calculate new 120 kHz TS appropriate for the mean krill lengths observed during each of the previous surveys. The dB difference between TS derived from the model of Greene et al. (1991) and TS from the model of Demer and Conti (2005) was determined, and an appropriate scaling factor was calculated to apply to each survey density estimate (scaling factor = $10^{(\text{dB difference}/10)}$). Finally, all previously published krill density estimates were multiplied by the respective scaling factor: where possible rescaling was performed at the level of individual line-transect densities to enable calculation of the appropriate mean weighted variances for the entire surveys following Jolly and Hampton (1990).

Results

An almost continuous time series of ADCP data was obtained at the on-shelf location between 14 October 2002 and 29 December 2005 (Table 1). However, the off-shelf time series was interrupted on a number of occasions. The off-shelf mooring was not deployed during February 2003 due to the presence of large icebergs at the site, and no data were obtained between 29 April and 12 November 2003 following the mooring being dragged prematurely to the surface by fishing gear. The mooring was not deployed at the off-shelf location during the subsequent over-winter periods (26 March–20 November 2004 and 4 March–29 December 2005) to avoid potential instrument loss by fishing. Furthermore, the reliability of the WCPs was disappointing: both the on-shelf and off-shelf instruments were subject to a number of mechanical and technical faults during each deployment and, despite extensive efforts to improve their performance (including tank tests), data were only obtained from the two deployment periods 11 January–3 April 2005 and 20 November–20 December 2005.

A distinct pattern of seasonal variation in krill density was evident from the ADCP time series, and this pattern recurred over all three seasons (Figure 2). Power spectrum analysis showed maximal power at approximately 52 weeks (i.e. annual). In each year, prominent changes in krill density occurred after March and November, dividing the time series into three distinct summer (December–April 2002/03, 2003/04 and 2004/05) and winter periods (May–November 2003, 2004 and 2005). Peaks in density generally occurred in summer (mean = 89.5 g m^{-2}, SD = 64.2), with predominantly low krill density apparent throughout the winter (mean = 18.7 g m^{-2}, SD = 24.3). Shipboard estimates of krill density were not statistically different from those from moored ADCP and WCP data during adjacent time periods (for each cruise, 2-sample *t*-tests between 8 ship transects and the first 8 days' mooring observations during corresponding time periods, $P > 0.05$).

Average seasonal variation in krill density from the 3-year period is shown in Figure 3. These mean time-series data were explored using regression analysis. An exponential sinusoidal function with annual cyclicity (i.e. period = 52 weeks) fit the weekly mean data significantly ($P < 0.0001$). Based on the 3-year ADCP time-series, the density of krill for a given week of the year is given by:

$$\text{Krill density (g m}^{-2}) = \exp(3.079 + 1.545\cos[0.1208(x - 5.35)]) \quad (r^2 = 0.64, P < 0.0001)$$

where x is the week of the year from 1 to 52 (1–7 January = week 1).

Many (14 from 17) of the published ship-based estimates of krill density in the western core box region between 1990 and 2005 did not differ significantly from the values predicted for the week of survey (for each cruise, Student's *t*-tests between the multiple ship-transect densities and the corresponding regression-predicted value, $P > 0.05$). However, some survey estimates were significantly different ($P < 0.01$) from the densities expected under the average pattern of within-year variation detected by the moorings. The mid-summer density estimates obtained during 1993/94 (JR06: 17.1 g m^{-2}, CV 15.5%), 1998/99 (ATLD: 29.1 g m^{-2}, CV 26.0%) and 1999/2000 (JR38: 40.3 g m^{-2}, CV 12.3%) were significantly lower than the expected values for the times of year at which the surveys were conducted (Figure 3).

Discussion

The time series of monthly variation in krill density at South Georgia presented here provides insight into the timing and magnitude of variation in krill abundance that has hitherto been hidden from conventional ship-based approaches. Mooring-derived estimates of krill density were not statistically different from the point values obtained from standard ship methods in overlapping or close time periods (±2 weeks), indicating that the moorings provided a representative view of change in krill density at the spatial scale of at least the western core box (80 × 100 km). This was reassuring considering that krill distributions are characteristically patchy around South Georgia (Trathan et al., 2003). Problems with using an ADCP as a substitute for a calibrated echo sounder, and issues with identifying echoes from target organisms in single-frequency acoustic data without concurrent net samples have been well documented (Cochrane et al., 1994; Brierley et al., 1998). The shipboard data were collected using a calibrated scientific echo sounder operating at several frequencies, thus enabling robust estimates of krill density to be calculated via standard protocols which, to a large extent, validated the mooring-derived values that in many instances were calculated without the ability to directly identify krill echoes. The relatively low pelagic species diversity at South Georgia and the swarming behaviour of krill mean that this species in this habitat lends itself well to study conducted using moorings.

The pattern of seasonal variation observed here was consistent with that reported previously at the Antarctic Peninsula (Lascara et al., 1999) and from limited data from South Georgia (Heywood et al., 1985; Brierley et al., 2002), i.e. high in summer and low in winter. The seasonal trend was also consistent with that evident in fisheries data (Taki et al., 2005). Furthermore, the time series suggests that occasional peaks of high krill density may occur against the predominately low winter signal (e.g. July–August in 2005) (Figure 2), and these peaks corresponded well with marked shifts in the location of the krill fishery from the northeast to the northwest during these times (Trathan et al., 1998;

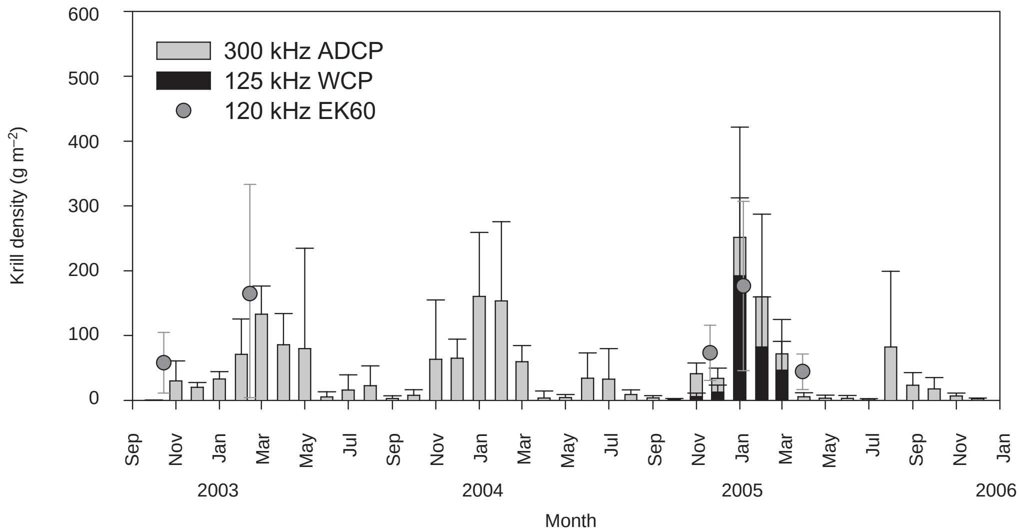

Figure 2: Monthly estimates of krill density from the on-shelf and off-shelf moorings from 2002 to 2005. Estimates of krill density in the western core box obtained from standard acoustic surveys are also shown. The error bars are the 95% confidence intervals.

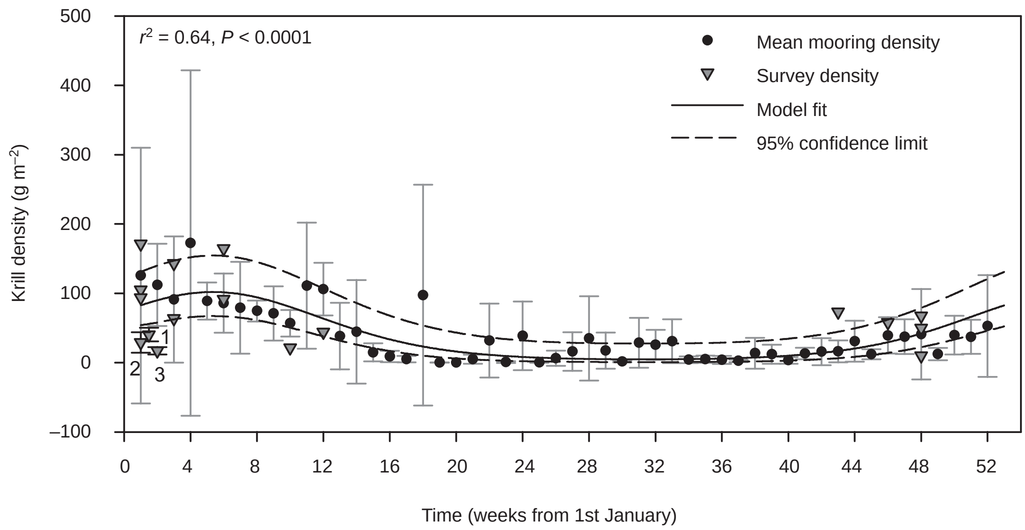

Figure 3: Observed variability in krill density at South Georgia by week from 2002 to 2005. The error bars are the ±95% confidence intervals of the observations. Cruise numbers of the outliers are denoted as follows: 1 = JR38 (1999/2000), 2 = ATLD (1998/99) and 3 = JR06 (1993/94).

Taki et al., 2005). Thus the results support the notion that shifts in the krill fishery may relate to local availability of krill (Kawaguchi et al., 2006).

The moorings detected high within-year variation in krill density, and a sinusoidal regression model, with time as the independent variable, explained 64% of the weekly variation. Although the precision of the predictive capacity of the mooring-derived model was quite low (relatively large confidence limits at some times of year) (Table 4), the analyses provided the first quantitative framework to resolve the possible effects of temporal aliasing associated with 'annual' surveys in the western core box region. Comparison of previous acoustic survey estimates with the observed pattern of within-year variation showed that some of the apparent year-to-year variability detected between 1990 and 2005 could be attributed solely to the fact that ship-based sampling had occurred at different times of year. Thus, this variation was not so much interannual as a manifestation

Table 4: Predicted mean krill density (g m^{-2}) and ±95% confidence limits for each week of the year. See text for the equation used to calculate the predicted mean values.

Month	Week	Mean	+95% CI	–95% CI
Jan	1	82.7	130.9	52.3
	2	89.9	139.9	57.8
	3	95.8	147.0	62.4
	4	99.8	152.0	65.6
Feb	5	101.8	154.3	67.1
	6	101.4	153.9	66.8
	7	98.8	150.8	64.8
	8	94.2	145.1	61.2
Mar	9	87.9	137.3	56.3
	10	80.4	128.0	50.5
	11	72.1	117.7	44.2
	12	63.5	106.9	37.8
Apr	13	55.1	96.1	31.6
	14	47.2	85.8	26.0
	15	40.0	76.3	20.9
	16	33.5	67.6	16.6
	17	28.0	60.0	13.0
May	18	23.2	53.5	10.1
	19	19.3	47.9	7.7
	20	16.0	43.3	5.9
	21	13.4	39.4	4.5
Jun	22	11.2	36.3	3.5
	23	9.6	33.9	2.7
	24	8.2	32.0	2.1
	25	7.2	30.5	1.7
Jul	26	6.3	29.4	1.4
	27	5.7	28.7	1.1
	28	5.3	28.1	1.0
	29	4.9	27.8	0.9
	30	4.7	27.6	0.8
Aug	31	4.6	27.5	0.8
	32	4.7	27.5	0.8
	33	4.8	27.6	0.8
	34	5.0	27.9	0.9
Sep	35	5.4	28.3	1.0
	36	5.9	28.9	1.2
	37	6.5	29.7	1.4
	38	7.4	30.9	1.8
	39	8.6	32.5	2.3
Oct	40	10.0	34.5	2.9
	41	11.8	37.2	3.8
	42	14.1	40.4	4.9
	43	16.9	44.5	6.4
Nov	44	20.3	49.4	8.4
	45	24.5	55.3	10.9
	46	29.5	62.1	14.0
	47	35.3	70.0	17.8
Dec	48	42.0	78.9	22.3
	49	49.4	88.7	27.5
	50	57.5	99.2	33.4
	51	66.0	110.0	39.6
	52	74.5	120.7	46.0

of expected intra-annual change. The model was also in line with estimates from other broad-scale krill surveys that covered part of the northwestern region of South Georgia. These included acoustic surveys conducted in November 1982 (11.7 g m^{-2}, CV = 9.5%; Murphy et al., 1991) and February 1986 (29.71 g m^{-2}, CV = 47.2%; Goss and Grant, 1999). Some of the previously reported variation detected by the 'annual' shipboard surveys was however not simply a temporal alias of short-term, intra-annual variability, but was unusual within the expected framework. There were three instances when the annual survey estimates were substantially lower than those expected given the new knowledge of seasonal variation, and these densities indicated 'poor' krill years. The 1994 (JR06) value, for example, was one of the lowest acoustic estimates reported for *E. superba* at South Georgia. Thus the notion that large between-year fluctuations in krill density occur within the South Georgia pelagic ecosystem was borne out by comparisons with the mooring observations. As the time series of mooring data extends, knowledge of the scale of intra-annual variation will increase, providing an increasingly robust view of the scale of within-year and between-year variation in krill density at South Georgia.

The causes of interannual variability in krill density at South Georgia may well be complex, and involve a number of biological and physical interactions operating at various scales throughout the Scotia Sea (Murphy et al., 1998) and possibly beyond. Analysis of physical data from the moorings alongside the biological data should provide increased understanding of intra- and interannual change within the South Georgia pelagic ecosystem, and help to elucidate causal mechanisms. Potential mechanisms include intra-annual variation in ocean circulation, seasonal variation in krill migratory behaviour, and variation in krill population processes, such as growth and predation. Initial analyses suggested that the mooring-derived krill density data were not consistent with a pattern of seasonal growth, production and mortality of a resident krill population, but were consistent with the notion of large influxes of krill in early summer, and of a predator-driven reduction between mid- and late summer. Seasonal changes in aspects of krill behaviour, such as diel vertical migration and swarming, might also have been important factors. For example, studies have shown a distinct winter deepening in the vertical distribution of krill across the Scotia Sea, with swarms occurring as deep as 300 m during the day (Gutt and Siegel, 1994; Taki et al., 2005). It is therefore possible that the apparent reduced krill densities in winter might also have been a function of individuals residing below the moorings during the daytime hours in which the acoustic observations were made (cf. Enderlein et al., submitted). Such behavioural mechanisms warrant further investigation (Nicol, 2006).

The mooring time series casts some light on the scale of deviation from the norm that would have to occur before an 'annual' ship survey could detect a 'low' or 'high' krill year. In general terms, this was around ±35 g m^{-2} in summer and ±20 g m^{-2} in winter from the regression model prediction (exact values are shown in Table 4). For example, the expected krill density for week 2 (8–15 January) would be 89.9 g m^{-2} based on the model of intra-annual variability (Table 4). A ship survey would have to detect a krill density value with an upper 95% confidence limit that was less than 57.8 g m^{-2} during this time, in order for observers to be able to assert that the year in question was one of atypically low krill abundance from the perspective of an acoustic survey. This contrasts markedly with the previous notion that any 'annual' krill density estimate with an upper 95% confidence limit of less than 15 g m^{-2} is indicative of a 'low' krill year (Brierley et al., 1999). The results suggested that a krill density estimate could be considerably higher than 15 g m^{-2} but could, depending on the time of year it was measured, still reflect a period of abnormally low krill density. Furthermore, it is unrealistic to expect 'annual' ship-based surveys to detect, with much sensitivity, subtle variations in krill density from the now expected within-year pattern. This may explain why efforts to link functional responses (e.g. breeding success) of upper-trophic-level species to fluctuations in prey abundance have so far been largely unsuccessful (however, see Reid et al., 2005). It is likely that mooring data will overcome this limitation, leading in the future to a better understanding of ecosystem functions at South Georgia, and will assist in the setting of catch limits in an ecosystem context. Indeed, a network of moorings throughout the Scotia Sea might ultimately lead to a greatly improved knowledge of krill throughout the region, and may aid substantially in the management of the resource in this region and beyond.

Conclusions

- A regular annual cycle of variation in krill density was detected at South Georgia between 14 October 2002 and 29 December 2005, with krill densities being high during summer (89.5 g m^{-2}, SD 64.2) and low in winter (18.7 g m^{-2}, SD 24.3).

- A sinusoidal regression model with time as the independent variable explained 64% of the observed week-to-week variation in krill density.

- Within this intra-annual framework, 'annual' ship surveys can only be expected to detect 'high' or 'low' krill density events at South Georgia if they deviate from the mean expectation by more than approximately 35 g m^{-2} in summer and 20 g m^{-2} in winter. From the model predictions, therefore, scientists should not expect functional response analyses to be very revealing within these ranges of krill density.

- The use of moored instruments will provide new insight into the functional responses of upper-trophic-level species to fluctuations in prey abundance at South Georgia, and analyses are ongoing.

- Linking concurrent biological and physical observations from the moorings will enable the hypothesis that variation in krill density at South Georgia is mediated by prevailing oceanic processes, such as changes in the position of the Sub-Antarctic Circumpolar Current Front, to be tested.

Acknowledgements

We thank the masters, officers and crew of RRS *James Clark Ross* for their efforts with the deployment and recovery of the moorings. We also thank M. Brandon and S. Jenkins for providing oceanographic data for use in our SONAR equations, logistic personnel at BAS for their efforts in recovering a mooring that was dragged prematurely from the seabed by a fishing vessel, and P. Rothery for advice on statistical methodology.

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Liste des tableaux

Liste des figures

Список таблиц

Список рисунков

Lista de las tablas

Lista de las figuras