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SIGNIFICANT INTRA-ANNUAL VARIABILITY IN KRILL DISTRIBUTION AND ABUNDANCE AT SOUTH GEORGIA REVEALED BY MULTIPLE ACOUSTIC SURVEYS DURING 2000/01

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Abstract

Three separate acoustic surveys of Antarctic krill (*Euphausia superba*) were conducted around South Georgia in the 2000/01 season: in October 2000 (early-season); during late December/early January 2000/01 (mid-season), and in March 2001 (late-season). The surveys were the first in a newly planned five-year series of observations designed to complement and extend an existing time series regularly maintained by the British Antarctic Survey since 1996 (and on a more ad hoc basis since the early 1980s). We hoped that conducting several surveys in one season would provide information on short-term variability that could be used to set data from more restricted once-per-season 'snap-shot' cruises in a broader context. The early- and late-season surveys were associated with logistic support voyages to South Georgia and were restricted to four transects within a box to the northwest of South Georgia. The dedicated mid-season survey covered that box in more detail (twice as many transects) and, in addition, examined boxes to the north, northeast and southwest of the island. Together these surveys provided temporally and spatially extensive coverage around South Georgia. Krill density in the western box in the early-season survey was very low (3.5 g m^{-2}) but rose significantly ($P = 0.020$) by mid-season (to 34.7 g m^{-2}). In a pattern that is consistent with observations from previous years, krill density in the western box in the mid-season survey was less than that in the eastern box (80.4 g m^{-2}). Analysis of transect data obtained in the western box in the mid-season survey revealed no significant difference in the mean krill density derived from only those four transects surveyed early- and late-season, or from the full eight transects. Our first occupation of a survey box off the central north coast of South Georgia in mid-season revealed a krill density of 47.2 g m^{-2} that was intermediate between the eastern and western areas. The size structure of the krill in the central region also reflected a mix of those to the east (generally small) and west (generally large). Krill density to the southwest of South Georgia was 32.1 g m^{-2} in mid-season. By March, krill density in the western survey area had fallen significantly ($P = 0.037$) from the mid-season high to 7.8 g m^{-2}. Our multiple surveys at South Georgia have revealed major intra-annual changes in krill density at the island and have shown that the timing of the acoustic survey can affect significantly the estimate of krill density. The multiple estimates of krill density will allow reproductive performance indices for top level predators to be compared to prey availability at more appropriate time-scales than previous single 'snap-shot' acoustic survey data have allowed. This is a crucial step in the elucidation of response functions of dependent species to changes in krill abundance, and could be a useful contribution to ecosystem management.

Résumé

Trois campagnes d'évaluation acoustique distinctes du krill antarctique (*Euphausia superba*) ont été menées autour de la Géorgie du Sud pendant la saison 2000/01 : en octobre 2000 (au début de la saison), fin décembre 2000/début janvier 2001 (mi-saison) et en mars 2001 (vers la fin de la saison). Ces campagnes étaient les premières d'une série d'observations prévue sur cinq ans pour compléter et prolonger la série chronologique existante maintenue régulièrement par le British Antarctic Survey depuis 1996 (et de manière plus ponctuelle depuis le début des années 80). Nous espérions qu'en menant plusieurs campagnes en une même saison, on obtiendrait des informations sur la variabilité à court terme qui serviraient à élargir le contexte des données provenant de campagnes «instantanées», limitées à une par saison. Les campagnes du début et de la fin de la saison faisaient partie des campagnes de soutien logistiques en Géorgie du Sud et étaient restreintes à quatre transects à l'intérieur d'une case, au nord-ouest de la Géorgie du Sud. La campagne de mi-saison, entièrement consacrée à ce projet, couvrait cette case de manière plus détaillée (avec deux fois plus de transects) et examinait également des cases au nord, au nord-est et au sud-ouest de l'île. Ensemble, ces campagnes d'évaluation ont assuré une couverture spatio-temporelle étendue autour de la Géorgie du Sud. La densité du krill dans la case occidentale qui était très faible (3,5 g m^{-2}) lors de la première campagne de la saison avait nettement augmenté (P = 0,020) au milieu de la saison (34,7 g m^{-2}). Suivant une tendance qui coïncide avec les observations notées les années précédentes, la densité de krill pendant la campagne de mi-saison était moins importante dans la case ouest que dans la case est (80,4 g m^{-2}). L'analyse des données des transects obtenues dans la case occidentale pendant la campagne d'évaluation de mi-saison ne révélait aucune différence importante dans la densité moyenne du krill dérivée uniquement des quatre transects évalués au début et à la fin de la saison ou des huit transects. La première fois que nous avons atteint une case de la campagne d'évaluation au large de la côte nord centrale de la Géorgie du Sud au milieu de la saison, nous avons constaté une densité de krill de 47,2 g m^{-2}, soit entre celles des secteurs est et ouest. La structure des tailles du krill dans la région centrale reflétait également une combinaison de celles de l'est (plutôt petites) et de l'ouest (plutôt grandes). La densité du krill au sud-ouest de la Géorgie du Sud était de 32,1 g m^{-2} en milieu de saison. En mars, la densité du krill dans la zone occidentale de l'évaluation était fortement tombée (P = 0,037) par rapport à celle de pointe au milieu de la saison, de 7,8 g m^{-2}. Nos campagnes d'évaluation multiples en Géorgie du Sud ont révélé d'une part d'importants changements de densité de krill et d'autre part, que l'époque de la campagne d'évaluation risque d'affecter sérieusement l'estimation de la densité de krill. Les estimations multiples de la densité de krill permettront une comparaison des indices du succès de la reproduction des prédateurs supérieurs avec la disponibilité des proies à des échelles temporelles plus appropriées que celles des données des campagnes d'évaluation acoustique «instantanées». Pour les espèces dépendantes, cette étape cruciale dans l'élucidation des fonctions de réponse aux changements affectant l'abondance du krill pourrait s'avérer utile pour la gestion de l'écosystème.

Резюме

В сезоне 2000/01 г. в районе Южной Георгии были проведены 3 акустические съемки антарктического криля (*Euphausia superba*): в октябре 2000 г. (начало сезона), в конце декабря/начале января 2000/01 г. (середина сезона), и в марте 2001 г. (конец сезона). Это были первые съемки в недавно намеченной 5-летней серии наблюдений, которая дополнит и продолжит существующий временной ряд, регулярно обновляемый Британской антарктической съемкой с 1996 г. (и, более спорадически, с начала 1980-х годов). Мы надеялись, что выполнение нескольких съемок в течение одного сезона даст информацию о краткосрочной изменчивости, которая предоставит более широкий контекст для рассмотрения данных, полученных в результате более ограниченных, проводящихся раз в сезон и фиксирующих «мгновенное состояние» съемок. Съемки в начале и конце сезона проводились во время рейсов по материально-техническому обеспечению Южной Георгии и ограничивались 4 разрезами в клетке к северо-западу от Южной Георгии. Специально проведенная съемка в середине сезона лучше охватила эту клетку (в 2 раза больше разрезов); кроме этого, были обследованы клетки к северу, северо-востоку и юго-западу от острова. Вместе эти съемки обеспечили хороший временной и пространственный охват района Южной Георгии. По результатам съемки, проведенной в начале сезона, плотность криля в западной клетке была очень низкой (3.5 г $м^{-2}$), однако она существенно возросла (P = 0.020) к середине сезона (до 34.7 г $м^{-2}$). Аналогично наблюдениям прошлых лет, съемка в середине сезона выявила более низкую плотность криля в западной клетке по сравнению с восточной клеткой (80.4 г $м^{-2}$). Анализ полученных в западной клетке в середине сезона данных по разрезам не выявил значительных различий между значениями средней плотности криля, полученными в результате проведения только 4 разрезов в начале и конце сезона, или всех 8 разрезов. Первые наблюдения (в середине сезона) в клетке у центра северного побережья Южной Георгии выявили плотность криля в 47.2 г $м^{-2}$ – промежуточное значение между восточными и западными районами. Размерная структура криля в центральном районе также представляла собой смесь размеров к востоку (в основном мелкий криль) и западу (в основном крупный криль). В середине сезона плотность криля к юго-западу от Южной Георгии составила 32.1 г $м^{-2}$. К марту плотность криля в западном районе съемки резко сократилась (P = 0.037) по сравнению с высоким значением в середине сезона (до 7.8 г м$^{-2}$). Наша серия съемок у Южной Георгии выявила существенные внутригодовые изменения в плотности криля в этом районе и показала, что время проведения акустических съемок может сильно повлиять на оценку плотности криля. Множественные оценки плотности криля позволят провести сравнение индексов репродуктивного успеха хищников с наличием добычи, используя более подходящие временные масштабы, чем позволяли данные единичных акустических съемок. Это – важный шаг на пути к пониманию реакции зависимых видов на изменения в численности криля, что может содействовать управлению экосистемой.

Resumen

Se realizaron tres prospecciones acústicas separadas de kril antártico (*Euphausia superba*) alrededor de Georgia del Sur en la temporada 2000/01: en octubre de 2000 (a principios de la temporada), a fines de diciembre y comienzos de enero de 2000/01 (mediados de la temporada) y en marzo de 2001 (a fines de la temporada). Estas prospecciones constituyen la primera serie de una serie de observaciones de cinco años de duración planeadas recientemente para complementar y ampliar la serie cronológica existente mantenida regularmente por el British Antarctic Survey desde 1996 (que desde el comienzo de la década de los 80 había sido mantenida irregularmente en la medida que se obtenían los datos). Se esperaba que varias prospecciones en una temporada proporcionarían información sobre la variabilidad a corto plazo que podría ser utilizada para interpretar los datos 'instantáneos', provenientes de campañas realizadas una sola vez por temporada, en un contexto más amplio. La primera y última prospección de la temporada coincidieron con campañas de apoyo logístico a Georgia del Sur, y se limitaron a cuatro transectos en una cuadrícula al noroeste de Georgia del Sur. La prospección realizada a mediados de la temporada realizó un muestreo más extenso de la cuadrícula (el doble de transectos) y además examinó las cuadrículas hacia el norte, noreste y suroeste de la isla. En conjunto, las prospecciones cubrieron una amplia zona en una escala temporal extensa alrededor de Georgia del Sur. La densidad de kril en la cuadrícula del oeste durante la prospección realizada a comienzos de la temporada fue muy baja (3,5 g m^{-2}), pero al llegar a mediados de la estación se observó un aumento significativo (a 34,7 g m^{-2}, (P = 0,020). La densidad de kril observada en la cuadrícula del oeste durante la prospección realizada a mediados de la temporada fue menor que en la cuadrícula del este (80,4 g m^{-2}) y esta observación es congruente con las observaciones de años anteriores. El análisis de los datos obtenidos de los transectos de la cuadrícula del oeste durante la prospección a mediados de la temporada reveló que no había diferencias significativas entre el promedio de las densidades de kril derivado de los cuatro transectos estudiados a comienzos y a fines de la temporada y el promedio del total de los ocho transectos. La densidad de kril estimada en la primera prospección de una cuadrícula frente a la costa central al norte de Georgia del Sur a mediados de la temporada corresponde a un valor intermedio (47,2 g m^{-2}) entre las áreas este y oeste. La estructura de tallas de las poblaciones de kril en la región central fue también una mezcla entre las poblaciones del este (por lo general de talla pequeña) y del oeste (por lo general de talla grande). La densidad de kril hacia el suroeste de Georgia del Sur fue de 32,1 g m^{-2} a mediados de la temporada. Ya en marzo la densidad de kril en la zona oeste había disminuido de manera significativa (a 7,8 g m^{-2}, P = 0,037) con relación al alto valor observado a mediados de la temporada. Las prospecciones múltiples que hemos realizado en Georgia del Sur han demostrado que en el transcurso del año se observa una gran variabilidad en la densidad de kril alrededor de la isla y que la fecha escogida para llevar a cabo las prospecciones acústicas puede afectar significativamente las estimaciones de la densidad de kril. Las estimaciones múltiples de la densidad de kril permitirán la comparación de los índices del rendimiento reproductivo de los depredadores situados en el extremo superior de la cadena trófica, con la disponibilidad de la presa en escalas temporales más apropiadas que las estimaciones proporcionadas por datos 'instantáneos' obtenidos de una sola prospección acústica. Esta comparación es esencial para modelar la respuesta de las especies dependientes a los cambios de la abundancia del kril, y podría ayudar en la ordenación del ecosistema.

Keywords: acoustic survey, variability, Antarctic krill, abundance, South Georgia, CCAMLR

INTRODUCTION

The British Antarctic Survey (BAS) has conducted annual acoustic surveys off the northern coast of South Georgia along a standard series of transects regularly since 1996 (see Brierley et al., 1997). Surveys have also been carried out at the island prior to this, but on a more ad hoc basis (see Brierley et al., 1999 for a summary of all surveys). In order to maintain the time series of acoustic estimates of krill density (and other associated biological and oceanographic datasets), a new series of surveys was planned for the five years 2000/01 to 2004/05.

Surveys in previous years have generally been restricted to a single, month-long period in the austral summer, providing a single 'snapshot' estimate of krill density. Concern has been voiced, however, that such assessments reveal nothing of intra-annual variability in krill density (McClatchie et al., 1994) and, as a consequence, apparent interannual variability (e.g. Brierley et al., 1999) may simply reflect aliasing of shorter-term fluctuations. Furthermore, an objective of the acoustic surveys has been to provide data on krill abundance to link with the performance of various predator species, some of which breed ashore at Bird Island but forage for krill, sometimes quite widely, in the waters off South Georgia. The period of increased demand for krill from land-based predators is longer than the duration of previous ship surveys: the breeding season for fur seals and macaroni penguins typically covers the period from November to March. Given this mismatch in the temporal scales of sampling, it has proved difficult to elucidate the detailed nature of functional responses between predator performance and krill abundance. Data on the condition of mackerel icefish suggest some rapid changes in krill abundance (see Everson and Kock, 2001). A change in the krill survey strategy for the new five-year series addresses these temporal shortcomings by including surveys at the very beginning and end of the field season (October and March) in addition to the main effort in December–January. A second change extends the geographic area of coverage, particularly into the central north coast of South Georgia, in an effort to try to expose mechanisms of krill flux along the island's north coast (cf. Watkins et al., 1999; Brandon et al., 1999, 2000). No extra ship time was available to accommodate these survey extensions and so sampling intensity had to be reduced in the early- and late-season surveys. This paper outlines the new sampling design and reports the results of surveys conducted in the first year (2000/01) of the new series, commenting additionally on the consequences of reduced sampling effort in the early and late surveys for comparison with the mid-season survey.

MATERIALS AND METHODS

All acoustic surveys were conducted by the RRS *James Clark Ross* using a Simrad EK500 scientific echosounder operating hull-mounted 38, 120 and 200 kHz transducers. The echosounder was calibrated using standard targets at Stromness Bay, South Georgia, on 24 December 2000.

The surveys were conducted in three phases: first in October 2000 in association with a logistic voyage to supply BAS bases at Bird Island and King Edward Point, second during a dedicated research cruise in December 2000–January 2001, and third during March 2001 in association with the final logistic call at South Georgia before the onset of winter.

SURVEY DESIGN

The survey design, adapted from that used by or for BAS between 1996 and 2000 (Brierley et al., 1997), had the dual objectives of providing data to continue our existing time series and extending within-year coverage both spatially and temporally. No more ship time was available than in previous years and so survey effort had to be reduced. Analysis of krill density data by transect from previous surveys revealed that a minimum of four transects would have to be surveyed in a 100 km survey area in order to attain stability in sampling variance (see Brierley et al., 1999), and that acceptable survey precision could be obtained from only four transects per survey box. Geostatistical analysis of krill density distribution within the east and west survey boxes suggested that semivariance reached a plateau at a range of less than 10 km. Since our original transects were spaced more than 10 km apart, relationships between data points from neighbouring transects in our original survey design would not have contributed to the important range-dependent component of the variogram. We concluded that transect spacing for the new survey could be extended without suffering loss of between-transect spatial information as compared to the original design. In order to facilitate continued time series comparisons of some individual transect means, we chose to retain every other of the 10 transects from the original pre-2000 design (see Brierley et al., 1997 for details of that original design).

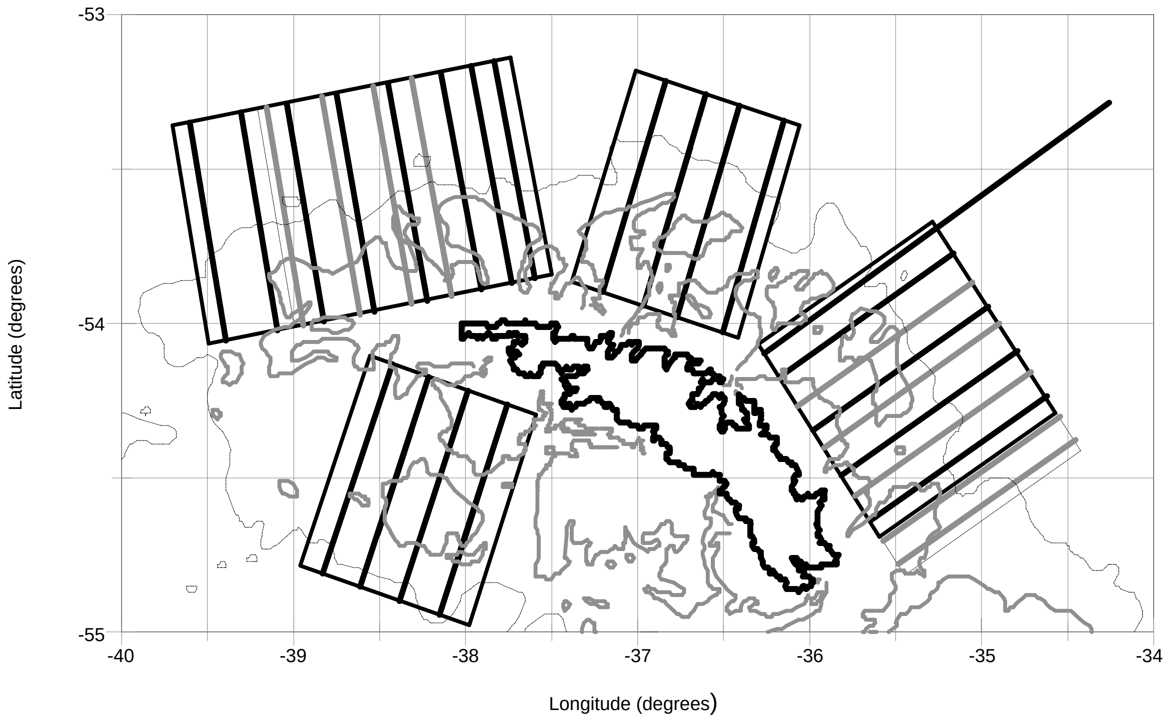

Figure 1: South Georgia and the 200 m (grey) and 1 000 m (black) depth contours, showing the bounds of the 2000–2005 survey areas (black boxes) and transects (black). The bounds of the 1996–2000 boxes (thin lines) and transects that are not surveyed under the new survey strategy (grey) are also shown.

Having decided on survey intensity, we then redefined our survey areas. The western box was extended westwards by 33.33 km to include a region where fur seals are now known to forage (e.g. Boyd et al., 1998). The on/off shelf dimension was left unaltered, and all transects were nominally 80 km long. Two new transects were laid down using the same two-stage randomisation process that had been used to place the original transects (Brierley et al., 1997). The new western survey box became 133.33 km wide with eight transects, a mean transect effort of one per 16.66 km survey box width. The eastern survey box was altered in two ways. First, the original western-most transect was doubled in length from 80 to 160 km, running further offshore down the centre of a canyon. Stations were placed at 10 km intervals along this long transect, with the intention of conducting full-depth CTDs that would provide data to reveal the location of the Southern Antarctic Circumpolar Current Front (SACCF). This front is believed to be an important component of the mechanism transporting krill to South Georgia (see Hofmann et al., 1998; Thorpe et al., in press), and annual variations in the position of the front could contribute towards annual variation in krill abundance. Second, the eastern boundary of the eastern box was moved westwards by 16.66 km (reducing the box width from 100 km to 83.33 km) such that the five transects we were to run would also be at a mean density of one per 16.66 km. A new central box containing four transect pairs (width = 4 x 16.66 = 66.66 km) was defined to run perpendicular to the shelf break, with its southern boundary midway between the western and eastern boxes. A southern survey box was defined to the south of Bird Island, again to facilitate investigation of an area where fur seals were believed to forage, by transposing the central box 105 km south and 100 km west (in geometric space). The southern box also contained four transects, the locations of which were set by the two-stage randomisation process. The locations of the new and pre-2000 survey boxes and transects are shown in Figure 1.

The early- and late-season surveys were designed to take just 48 hours on site, capitalising on voyages to the island that were primarily for logistic purposes. These surveys sampled every other transect of the main-survey western box grid, progressing sequentially eastwards from transect 1 to 7, sampling two transects per day.

All transects were run in daylight hours because of the known impact of vertical migration and change in the angle of krill orientation on acoustic surveys (Everson, 1982; Demer and Hewitt, 1995).

With the exception of the long transect in the eastern box, which, with associated stations, took more than 48 hours out and back, the intention was to survey two transects per day starting in the western box and moving from west to east against the prevailing ocean currents.

Acoustic Sampling

Pings were transmitted every 2.5 s along transects (nominal survey speed – 10 knots) and echoes were logged ping by ping to Echolog_EK. Data were calibration corrected in Echoview. Krill were identified on the basis of dB difference (S_V 120 kHz to S_V 38 kHz between 2 and 12 dB) (Watkins and Brierley, in press) within integration bins 2 m deep by 100 s horizontal extent (approximately 0.5 km at a survey speed of 10 knots) using the virtual echogram cascade developed for analysis of acoustic data from the CCAMLR 2000 Krill Synoptic Survey of Area 48.

Krill Length-frequency Estimation

Krill were obtained using an RMT-8 during the mid-season survey; krill target strength (TS) for each survey area was calculated in dB kg^{-1} (see Brierley and Watkins, 1996) on the basis of the mean length of 100 krill from each net fished within each area. TS was calculated in terms of dB kg^{-1} because of the relative insensitivity of this expression to errors in krill length estimation (Hewitt and Demer, 1993). The intention had been to sample krill using a surface net during the early- and late-season surveys. Bad weather, however, prevented any net sampling during the early-season survey, and TS was derived from the length of krill in the diet of Antarctic fur seals at Bird Island (Reid and Arnould, 1996; Reid and Brierley, 2001). Predator data were also used to determine TS for the late-season survey.

Data Analysis

To determine mean along-transect krill densities, 120 kHz S_V values, identified as originating from krill targets, were scaled by TS. Transect-specific mean krill densities were averaged within survey areas to determine weighted mean krill densities (and weighted variances) after Jolly and Hampton (1990).

In order to identify any significant between-survey differences in mean krill density, *t*-tests were carried out between groups of individual transect means from the western survey area from the early-, mid- and late-season surveys. In addition, *t*-tests were used to compare the mean krill density in the mid-season western survey box derived from all eight transects with the mean for the same area at the same time derived from only those four transects that were covered in the early- and late-season surveys.

RESULTS

Both the early- and mid-season surveys were beset by periods of very bad weather. The early-season survey had to be completed over a period of three days rather than the planned two, and during the mid-season survey the boxes were tackled in the following order: east, west, central, south as opposed to the planned west, central, east, south. With the exception of one transect in the southern box (the planned eastern most), however, all transects were completed. The late-season survey was completed to schedule in the planned sequence.

The EK500 was calibrated at Stromness Bay on 24 December 2000 (during the mid-season survey) using standard spheres. Calibration data are given in Table 1.

Mean krill lengths from net and predator samples and the associated TS values are given in Table 2.

Transect lengths achieved and mean krill densities for each transect are given in Table 3.

Weighted mean krill densities (and their variances) are given for each survey in Table 4.

For the mid-season survey, the mean krill density in the western survey box determined from all eight transects was not significantly different from the mean determined from just those four transects surveyed in the early- and late-season surveys (*t*-test, $P = 0.58$). A significant difference was, however, detected between the western box early- (3.5 g m^{-2}) and mid-season (34.7 g m^{-2}) surveys ($P = 0.020$). By the time of the late-season survey krill density had fallen significantly ($P = 0.037$) from the mid-season level to just 7.8 g m^{-2}.

In addition to the significant temporal differences in krill density within the western survey area, substantial differences in krill density were apparent regionally around South Georgia. Of particular note is the difference in density between east and west South Georgia, the east being substantially higher.

Table 1: Calibration results.

Frequency (kHz)	Gain	Survey Value (dB)	Calibrated Value (dB)
38	S_v	25.49	25.59
38	TS	25.6	25.33
120	S_v	20.26	20.32
120	TS	20.26	20.32
200	S_v	22.78	22.71
200	TS	23.07	22.74

Table 2: Krill lengths and target strengths. Suffix 'preds' denotes data from predators, 'nets' denotes data from scientific nets. 'TSc preds' denotes TS determined from predators with a correction applied for net selectivity (Reid and Brierley, 2001).

Box, Survey	Mean Krill Length (mm)	TS, dB kg^{-1} (% Difference using TSc preds cf. nets)
West, early	47.5 preds	-38.57 TSc preds
West, mid	45.7 nets, 49.4 preds	-38.59 nets, -38.52 TSc preds (-1.6%)
Central, mid	35.8 nets	-38.89 nets
East, mid	32.3 nets	-39.02 nets
South, mid	41.3 nets	-38.71 nets
West, late	46.7 preds	-38.61 TSc preds

Table 3: Transect lengths and associated krill densities for all 2000/01 survey transects.

Survey	Box	Transect	Date	Length (km)	Mean Krill Density (g m^{-2})
Early	West	W11	28 Dec 2000	80.54	2.53
	West	W21	29 Dec 2000	81.49	0.70
	West	W31	30 Dec 2000	76.26	10.52
	West	W41	30 Dec 2000	81.50	0.61
Mid	West	W11	2 Jan 2001	80.8	43.81
	West	W12	2 Jan 2001	80.41	31.85
	West	W21	3 Jan 2001	80.70	100.69
	West	W22	3 Jan 2001	81.26	27.81
	West	W31	4 Jan 2001	74.04	37.61
	West	W32	4 Jan 2001	79.43	7.33
	West	W41	5 Jan 2001	80.60	23.13
	West	W42	5 Jan 2001	81.39	5.66
	Central	C11	6 Jan 2001	80.41	72.83
	Central	C12	6 Jan 2001	80.36	54.52
	Central	C21	7 Jan 2001	80.11	48.36
	Central	C22	7 Jan 2001	80.46	13.10
	East	E1	26 Dec 2000	80.00	82.63
	East	E21	30 Dec 2000	83.28	206.98
	East	E22	30 Dec 2000	74.61	7.32
	East	E31	31 Dec 2000	80.49	32.22
	East	E32	31 Dec 2000	82.46	63.59
	South	S12	8 Jan 2001	80.78	71.95
	South	S21	9 Jan 2001	80.35	19.66
	South	S22	9 Jan 2001	80.66	4.70
Late	West	W11	18 Mar 2001	80.91	1.60
	West	W21	18 Mar 2001	80.47	6.56
	West	W31	19 Mar 2001	79.78	10.43
	West	W41	19 Mar 2001	80.73	12.48

Table 4: Mean krill density, variance and CV for each box in each survey.

Survey	Box	Dimensions (km)	No. Transects	Mean Density (g m^{-2})	Variance	CV (%)
Early	West	133.33 x 80	4	3.5	5.2	65.6
Mid	West	133.33 x 80	8	34.7	113.5	30.7
Mid	West	133.33 x 80	4	51.6	299.2	33.5
Mid	Central	66.66 x 80	4	47.2	156.6	26.5
Mid	East	88.33 x 80	5	80.4	1228.0	43.6
Mid	South	66.66 x 80	3	32.1	416.8	63.6
Late	West	133.33 x 80	4	7.8	27.9	68.1

DISCUSSION

The fact that no significant difference was apparent between the mean krill densities determined for the mid-season survey using the full eight transects or just the four surveyed at each end of the season provides reassurance that meaningful data can be obtained from reduced survey effort. Brierley et al. (1999) have shown previously that just four transects are required to obtain mean krill densities representative of those obtained from 10 or more survey transects in the South Georgia region, and this study further supports that observation. Clearly, survey precision is reduced with reduced survey effort and, from a mapping point of view, the fact that transect spacing was approximately halved for the early- and late-season surveys compared to the mid-season survey means that we know less about the distribution of krill within the survey area at these times. However, in this instance mapping was not the priority and the surveys have achieved their objectives of gathering robust krill density data for describing intra-annual abundance variability. These surveys together will also provide valuable data for the season-wide interpretation of predator performance in response to changing prey availability.

The mean krill density in the western survey box determined from the early-season survey was exceptionally low. The upper 95% confidence limit of the mean krill density for this survey was only 8.0 g m^{-2}. Brierley et al. (1999) suggested that if this upper 95% confidence limit fell below about 15 g m^{-2} in any year, that year could be considered one of 'unusually low' krill abundance, in which predator performance might be expected to be significantly reduced. The 15 g m^{-2} threshold was set on the basis of krill density data from single annual acoustic surveys and illustrates the problem of attempting to relate instantaneous measures of krill density from acoustic surveys with predator performance indices that effectively integrate measures of krill availability over an entire breeding season: data from our mid-season survey in 2000/01 show that mean krill density was 34.7 g m^{-2}, with the upper 95% confidence limit above 55 g m^{-2}. Clearly the mid-season survey does not suggest unusually low krill abundance, whereas the early-season survey does. This pattern of an early-season low krill density followed by a later-season high was also observed on the only other recent occasion when two acoustic surveys were conducted at South Georgia in the same season. In October 1997 an acoustic survey to the west of the island revealed a mean krill density of just 5 g m^{-2}; a repeat survey in January 1998 found over 21 g m^{-2} (see Brierley et al., 1999). At the Antarctic Peninsula there is a recognised seasonal change in distribution – and hence regionally in biomass – as adult krill migrate on/off shore in summer/winter (Lascara et al., 1999). Although we have no evidence to support the presence of this mechanism at South Georgia, this or another type of migration process could have a significant temporal effect on the South Georgia marine ecosystem and warrants further study. Reid et al. (1999) have suggested that immigration is the major factor contributing to variation in krill abundance at South Georgia; if this immigration is pulsed, perhaps with small, young krill arriving at the island at a reasonably consistent time each year, then knowledge of the timing of this pulse would be vital for ecosystem management (e.g. Everson, 1992), for example regulating the timing of fishing effort in order to minimise the impact on dependant predators. Furthermore, for the first time we are able to present a third krill density estimate for the same season at South Georgia. Our late-season estimate for the western survey area is significantly less than the estimate for the same area mid-season. This perhaps provides evidence for a depletion of krill by predators throughout the peak of the summer breeding season; by the time of our late-season survey it is possible that the majority of the krill that migrated to the island between the early- and mid-season surveys have been eaten. Whatever the mechanism, however, it is important that intra-annual change in krill abundance at South Georgia be recognised. Time series of krill abundance may suggest more variability than actually exists because of temporal aliasing. Survey timing is an important contributory factor for the calculation of the proportion (γ) of the acoustic estimate of krill abundance that can be caught each year (de la Mare, 1996); if results from acoustic surveys at South Georgia are to be used to determine the amounts of krill that can be caught there, then a consistent approach to survey timing must be adopted.

During the mid-season survey, the pattern of a higher krill density in the east than in the west follows previous observations: from the seven previous surveys where estimates of krill density are available from east and west of the island, five have been higher in the east; the two seasons where density was higher in the west were seasons of generally low overall krill abundance. The relative size distributions of krill observed mid-season in the western and eastern survey areas are also similar to previous surveys (Watkins et al., 1999), with smaller animals in the east and larger in the west. The additional new observation here in the central region revealed an intermediate density and intermediate krill length. This is consistent with the developing hypothesis that krill arrive at South Georgia predominantly by a route that introduces them first to the eastern end of the island, and that they are transported westwards along the northern coast, growing as they do so and suffering mortality, either from increased predator pressure or other means, the further west they go, explaining the reduced density. It has been hypothesised that the influx of krill to South Georgia is mediated by the Southern Antarctic Circumpolar Current Front (SACCF) (see, for example, Thorpe et al., in press). Further exploration of this hypothesis is beyond the scope of this paper, but suffice it to say that in the extended transect running 160 km offshore in the western survey box (positioned precisely with the objective of locating the SACCF) we observed elevated krill densities in association with the front.

In conclusion, the series of surveys described here have enabled us to gain further insight into temporal and spatial patterns of krill distribution around South Georgia. The early- and late-season voyages of opportunity have proved to be very informative, opening a previously unavailable window of observation on short-term variability in the South Georgia marine ecosystem. Short-term variability in krill abundance has been described elsewhere in the Antarctic (e.g. at Elephant Island, see McClatchie et al., 1994) but has, until these voyages, gone largely unobserved at South Georgia. Such voyages of opportunity, in conjunction with novel sampling approaches such as the use of predator diet data to provide krill target strength, allow valuable data to be collected with minimal effort (i.e. no netting required; TS can be determined from predators with minimal error (maximum 1.6% error here)). These data can contribute much to our understanding of ecosystem function at a number of trophic levels, and developing understanding of within-season changes should, for example, enable functional responses of predators to fluctuations in their prey availability to be elucidated. Given the isolated location of South Georgia and levels of shipping there, it seems improbable that any finer-scale temporal resolution than that reported here will be achieved from ship surveys at the island. We have, however, recently secured funding to develop and deploy moorings on- and off-shelf at the island. These moorings will be equipped with dual-frequency echosounders and acoustic Doppler current profilers enabling 'virtual' acoustic survey transects to be surveyed at very fine temporal resolution (possibly daily). The moorings are also to be equipped with conductivity temperature depth probes and may make it possible for us to associate short-term changes in krill abundance with short-term oceanographic changes, such as changes in the positions of fronts. Daily estimates of krill abundance will also enable high-frequency comparisons of predator performance and prey availability.

CONCLUSIONS

Multiple acoustic surveys at South Georgia have revealed major intra-annual changes in krill density at the island and have shown that the timing of acoustic surveys can significantly affect the estimate of krill density.

The resulting multiple estimates of krill density will allow indices of reproductive performance of top level predators to be compared to prey availability at more appropriate time-scales than previous single 'snap-shot' acoustic survey data have allowed. This is a crucial step in the elucidation of response functions of dependent species to changes in krill abundance, and could be a useful contribution to ecosystem management.

Future comparisons of krill density with prevailing oceanographic conditions, such as the position of the SACCF, may reveal mechanisms responsible for variation in krill abundance at South Georgia.

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