



ELSEVIER

Deep-Sea Research II 51 (2004) 1411–1419

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Variation in the biomass density and demography of Antarctic krill in the vicinity of the South Shetland Islands during the 1999/2000 austral summer

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Accepted 18 June 2004

Available online 17 September 2004

Abstract

Vessels from Japan, Peru, and the USA conducted four sequential surveys designed to estimate the biomass density and demography of Antarctic krill in the vicinity of the South Shetland Islands between late December 1999 and early March 2000. The surveys were conducted during the same austral summer as the CCAMLR 2000 Survey in the Scotia Sea (Watkins et al., Deep-Sea Research, II, this issue [doi: 10.1016/j.dsr2.2004.06.010]), and the data were analyzed in a similar manner. Biomass densities were not significantly different between the surveys and averaged 49 g m⁻². Maps of krill biomass indicate three areas of consistently high density: one near the eastern end of Elephant Island, one mid-way between Elephant Island and King George Island, and one near Cape Shirreff on the north side of Livingston Island. The areas of highest krill density appeared to move closer to the shelf break as the season progressed. This apparent movement was accompanied by a change in the demographic structure of the population, with smaller krill absent and a larger proportion of sexually mature animals present in late summer.

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1. Introduction

During the summer months, swarms of Antarctic krill (*Euphausia superba*) are transported past the South Shetland Islands, moving with the Antarctic Circumpolar Current as it concentrates and accelerates through Drake Passage transporting massive quantities of water (130 Sv, Deacon, 1984) from the South Pacific to the South Atlantic (Fig. 1). Krill predators breeding on the South Shetland Islands, such as chinstrap penguins, Adelie penguins, gentoo penguins, and Antarctic fur seals, consume approximately 0.83 million tonnes of krill during the reproductive season (November to March; Croll and Tershy, 1998). The krill fishery in the area took approximately 50,000 tonnes each year between 1990 and 2000 (CCAMLR, 2000a, b), which was less than 10% of the estimated consumption by land-breeding krill predators. While the historical catches are small relative to predator demand, Agnew (1992) estimated that 90% of this catch was within 80 km of the breeding colonies. Consumption of krill by pelagic predators, such as baleen whales, crabeater seals, fish, and other seabirds, is more difficult to estimate but may be of the order of 1 million

tonnes per annum in the vicinity of the South Shetland Islands (following the logic of Everson and de la Mare, 1996, see also Reilly et al., 2004). In January 2000, the standing stock of krill along the north side of the South Shetland Islands was estimated at 1.8 million tonnes, with an average density 38 g m^{-2} (Hewitt et al., 2004). Average krill densities in the area, as measured by acoustic surveys between 1992 and 2002, ranged from 1 to 60 g m^{-2} resulting in standing stock estimates of 0.1–2.5 million tonnes (Hewitt et al., 2003).

While the annual consumption of krill in the vicinity of the South Shetland Islands is of the same order as the standing stock, the ratio is quite different around South Georgia 1000 km downstream. There, krill consumption is of the order of ten times the standing stock (Boyd, 2002; Everson and de la Mare, 1996; Hewitt et al., 2004; Trathan et al., 1995), and reproductive failures in krill predator populations are associated with occasional low levels of krill availability (Boyd and Murray, 2001; Brierley et al., 1999; Croxall et al., 1999).

Siegel (1988) proposed a model of spatial succession for krill age groups in the vicinity of the South Shetland Islands. This took the form of

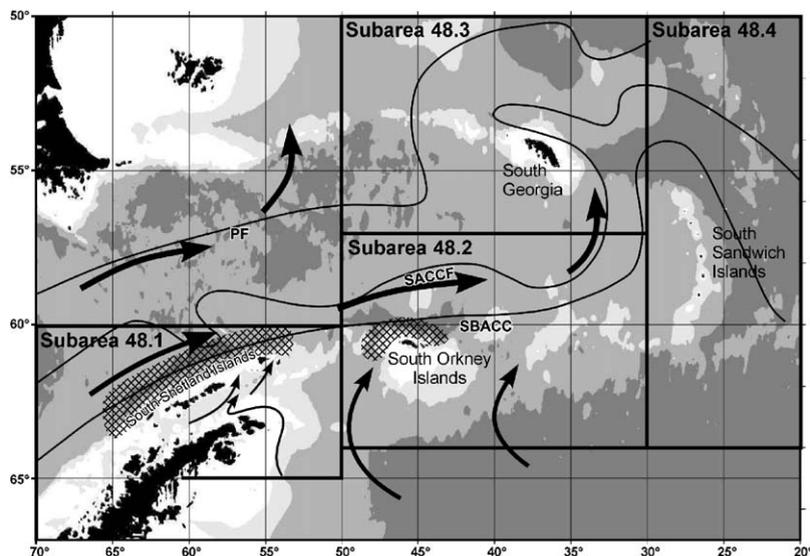


Fig. 1. Krill spawning areas (cross-hatched), and major currents and frontal zones within the Scotia Sea. PF indicates the Polar Front; SACCF the Southern Antarctic Circumpolar Current Front; and SBACC the Southern Boundary of the Antarctic Circumpolar Current (from Hewitt and Linen Low, 2000; sources: Hofmann et al., 1998; Marr, 1962, Orsi et al., 1995).

Table 1
Survey details

		Survey dates	No. transects	Area surveyed (km ²)	\bar{p} (g m ⁻²)	CV (%)	Biomass (103 tons)
Survey 1	<i>Kaiyo Maru</i> (Japan)	14–18 Dec 1999	7	30,704	50.45	20.3	1549
Survey 2	<i>Humboldt</i> (Peru)	24–28 Jan 2000	8	37,319	54.22	23.2	2023
Survey 3	<i>Kaiyo Maru</i> (Japan)	29 Jan to 2 Feb 2000	8	37,319	46.50	20.4	1735
Survey 4	<i>Yuzhmorgeologiya</i> (USA)	22–26 Feb 2000 (WA)	7	34,149	44.25	14.0	1511
	<i>Yuzhmorgeologiya</i> (USA) ^a	26 Feb to 5 Mar 2000 (EIA)	9	41,673	39.77	19.1	1657
	<i>Yuzhmorgeologiya</i> (USA) ^a	5–6 March 2000 (SA)	3	8,102	23.46	46.1	190

WA: West Area; EIA: Elephant Island Area; SA: South Area.

^aData from Survey 4 (Elephant Island Area) and Survey 4 (South Area) are included for completeness but not discussed in the text.

an order of magnitude increase in krill abundance as the austral spring progressed into summer and autumn, and then a dramatic decline as krill apparently left the area before winter. This seasonal change in abundance is characterized by an increase in the numbers of juvenile krill near the South Shetland Islands and in Bransfield Strait between the South Shetland Islands and the Antarctic Peninsula, and by an influx of sexually maturing adults further offshore. As the summer progresses post-breeding adults move shoreward and juveniles move further southward or out of the area. Lascara et al. (1999) described similar temporal and spatial krill distribution patterns from sampling conducted along the western side of the Antarctic Peninsula southwest of the South Shetland Islands.

In addition to seasonal changes in krill abundance, large interannual variations in krill density and recruitment have been described from net samples obtained in the vicinity of the South Shetland Islands (Loeb et al., 1997; Siegel and Loeb, 1995; Siegel et al., 1998). During any particular year the age structure of the population appears to be dominated by one or two age classes. These strong year classes are auto-correlated in time such that several poor years of reproduction are followed by one or two good years, with a repeating cycle of four to five years. Krill abundance, viewed as the sum of all age classes in the population, is also cyclical, declining with successive years of poor reproductive success and

increasing dramatically with the recruitment of strong year classes. Three relatively strong year classes, produced from spawning in 1986/87, 1990/91 and 1994/95 appear to have sustained the population during the late 1980s and 1990s. Although krill are seasonal visitors to the South Shetland Islands, the data presented by Siegel, Loeb and colleagues suggest that the relative contribution of year classes, and their effect on population size, can be tracked over several years by sampling in the area during spring and summer.

The surveys reported here were conducted in the vicinity of the South Shetland Islands by scientists aboard ships from Japan, Peru and the USA during the austral summer of 1999/2000 (Table 1). The surveys were designed to complement the CCAMLR 2000 Survey of krill across the Scotia Sea (Watkins et al., 2004). Two surveys were conducted by the Japanese R/V *Kaiyo Maru*: one in mid-December (Survey 1) and another in late January to early February (Survey 3); the Peruvian R/V *Humboldt* conducted a survey in late January (Survey 2); and the US chartered R/V *Yuzhmorgeologiya* conducted a survey in late February to early March (Survey 4). A survey conducted by the Korean R/V *Onnuri* in mid-January encountered technical problems and these data are not presented here.

Historically, the krill fishery has operated near South Georgia in winter (Constable et al., 2003) and then moved south and west with the retreat of sea ice to operate around the South Orkney

Islands and South Shetlands Islands in the late spring and summer. In recent years a reduction in the development of winter sea ice (Smith et al., 1998; Stammerjohn and Smith, 1996), coincident with a warming trend in the Antarctic Peninsula region (Vaughan and Doake, 1996), has allowed the winter fishery access to the more predictable concentrations of krill near the South Shetland Islands. As the probability of interactions between the krill fishery and krill predators increases in this region, the need for proactive management has become more urgent. However, any management option will require quantitative knowledge of the seasonal and ontogenetic movements of krill through the region.

2. Materials and methods

The survey vessels were all equipped with Simrad EK500 echo sounders and hull-mounted transducers operating at 38 and 120 kHz. Standard sphere calibrations were conducted before and after each survey. Ping intervals were 2 s and pulse durations were 1 ms for all frequencies. Samples of volume backscattering strength (S_V) were obtained every 0.71 m from the transducer faces to 500 m depth for Surveys 1, 3, and 4, and every 0.5 m from the transducer faces to 250 m depth for Survey 2.

The analytical protocol used to estimate the dispersion of krill biomass across the survey areas followed that of the CCAMLR 2000 Survey (Hewitt et al., 2004) and included the following procedures:

- echograms were constructed from S_V samples and filtered to include just transect periods between stations;
- echoes from surface turbulence and the bottom were removed;
- echograms were resampled into 5 m (vertical) by 50 ping (horizontal) bins;
- time-varied echograms of noise only were created and subtracted from the resampled echograms;
- the noise-free resampled 38 kHz echogram was subtracted from the noise-free resampled 120 kHz echogram;
- portions of the 120 kHz noise-free resampled echogram were masked to exclude regions where the difference between the mean S_V at 120 kHz and at 38 kHz was less than 2 dB or greater than 16 dB;
- the masked noise-free resampled 120 kHz echogram was integrated from the bottom of the surface exclusion layer to the vertical extent of acoustic sampling at 120 kHz (500 m for Surveys 1, 3 and 4, and 250 m for Survey 2, or 5 m above the bottom if shallower) and averaged over 1852 m horizontal distance (1 nm);
- integrated volume backscattering area was converted to areal biomass density by applying a factor equal to the quotient of the weight of an individual krill and its backscattering cross-sectional area summed over the length frequency distribution of sampled krill; and
- mean areal biomass density of krill and its variance were calculated following Jolly and Hampton (1990).

Krill were directly sampled using Isaacs-Kidd Mid-Water Trawl (IKMT), Rectangular Mid-Water Trawl (RMT-8), and Engel Mid-Water Trawl gears as summarized in Table 2. Post-larval krill were removed from the catches (large catches were sub-sampled for at least 100 animals) and processed at sea. Length measurements were made from the tip of the rostrum to the tip of the telson; maturity stages were determined following Makarov and Denys (1981).

Net samples were categorized into three time periods: early summer (mid-December; Survey 1, 9 tows), mid-summer (mid-January to early February; Surveys 2 and 3, 24 tows), and late summer (late February to early March; Survey 4, 29 tows).

Length–frequency distributions were analyzed using a cluster analysis to compare similarities between stations following Siegel et al. (2004). Siegel and Loeb (1995) report negligible differences between the RMT-8 and the IKMT in their efficiency to sample post-larval krill. Therefore, the length data obtained with these two nets (Surveys 1, 3, and 4) were used for the cluster analysis. Length–frequency data obtained with the Engel net were used as qualitative information to

Table 2
Details of net sampling

Sampling Period	Timing	Survey	Net	Cross-sectional area of mouth and mesh size	Sampling method
Early summer	Mid-Dec	Survey 1	RMT-8	8 m ² , 5 mm	Oblique tow 200 m to surface
Mid-Summer	Late Jan to Early Feb	Survey 2 Survey 3	Engel RMT-8	14 mm 8 m ² , 5 mm	Directed at acoustic targets Oblique tow 200 m to surface
Late Summer	Late Feb to Early March	Survey 4	IKMT	2.5 m ² , 0.5 mm	Oblique tow 170 m to surface

support the determination of cluster boundaries during the mid-summer period.

Maps of krill biomass were constructed by generating estimates of mean areal krill biomass density using the procedures outlined above, but averaging over 5 nm instead of 1 nm. These data were interpolated onto a square grid with dimensions one-half the average spacing between transects, and then contoured.

3. Results

Aggregated length-frequency distributions, weighted by catch rates, indicated that each of the clusters identified had a reasonably narrow length–frequency distribution (Fig. 2). In early summer, three distinct clusters were observed: a small-mode cluster (median length 34 mm), a medium-mode cluster (median length 40 mm) and a large-mode cluster (median length 50 mm). During mid-summer, two clusters were observed: a medium-mode cluster (median length 44 mm) and a large-mode cluster (median length 51 mm). Although three clusters were detected during late summer, their size composition was very similar (with median lengths of 49, 50 and 51 mm, respectively) and so the catches were combined to describe a single large-mode cluster for the survey area as a whole.

The positions of tows associated with each cluster are shown in Figs. 3A–D. During early summer (Survey 1), spatial segregation among the

clusters was apparent with the smaller krill inshore and the larger krill offshore. During mid-summer (Surveys 2 and 3) the boundary separating medium-sized and large-sized krill moved shoreward. During late summer (Survey 4) only large krill were observed.

The sexual maturity of the krill sampled also increased as the season progressed (Table 3). During early summer (Survey 1) 33% of the krill sampled were juveniles and sub-adults and 37% immature adults. The proportion of juveniles and sub-adults in the samples decreased as the season progressed, falling to 1% in mid-summer (Survey 3) and was negligible in late summer (Survey 4). The proportion of adults at an advanced stage of sexual maturity increased as the season progressed. Only 30% of the krill sampled during Survey 1 were classified as Stage 3, increasing to 83% and 99% in Surveys 3 and 4.

Biomass densities, coefficients of variation, and total biomass are listed in Table 1. Biomass densities were of the same order of magnitude (44–54 g m⁻²) for all four surveys. The coefficients of variation ranged from 14.0 to 23.2%, with the highest value associated with the highest biomass density (Survey 2). During Survey 2 a region of very high biomass density was observed to the east of Elephant Island (Fig. 3B). The survey transect in this area had to deviate substantially to the east in order for the research vessel to navigate around the island and the consequent over-sampling was corrected by the use of interval weighting factors. Even with this adjustment, however, the mean

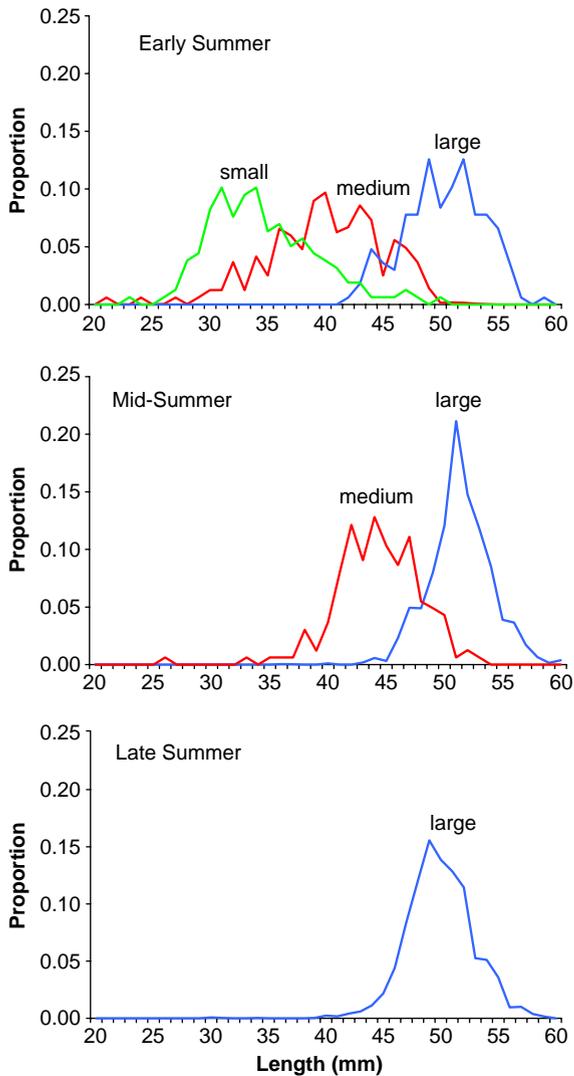


Fig. 2. Aggregated length-frequency distributions for krill from each sampling period. Green indicates a small-mode cluster; red a medium-mode cluster; and blue a large-mode cluster.

biomass density on this transect was double the overall survey mean, which contributed to the higher coefficient of variation.

Maps of krill biomass (Figs. 3A–D) indicate three areas of consistently high krill biomass density: one near the eastern end of Elephant Island, one mid-way between Elephant Island and King George Island, and one near Cape Shirreff on the north side of Livingston Island. The areas

of highest krill density appeared to move toward the shelf break as the season progressed. This apparent movement was accompanied by a change in the demographic structure of the population, with smaller krill absent and a larger proportion of sexually mature krill present in late summer.

4. Discussion

Biomass densities observed during four surveys conducted over an 11-week period during the austral summer of 1999/2000 were not significantly different and averaged 49 g m^{-2} . This value is mid-way between the lowest and highest values of krill biomass density observed during German and US acoustic surveys in the region of the South Shetland Islands since 1981 (Hewitt and Demer, 1994; Hewitt et al., 2003).

The low variation in krill biomass density over this period is remarkable given the dramatic change in the demographic composition of the surveyed population. The sampled krill represent five age classes: 1999 (as juveniles); 1998 and 1997 (relatively weak year classes); 1996 (a moderate year class); and 1995 (the last strong year class represented in the population) (Loeb et al., 2001). The demographic changes observed over the course of the surveys reported here could not have been caused by seasonal growth. Rather they were the result of shoreward movement by the adult population, which displaced the juveniles perhaps southward (as observed in 2001 by Siegel et al., 2002) and immigration from the southwest of large krill at advancing stages of sexual maturity. Despite these changes in the composition of the population, the mean biomass density did not change significantly. A 25-mm juvenile krill reflects approximately one quarter of the sound reflected by a 50-mm adult krill, implying that numerical densities of krill were 2–4 times higher during early and mid-summer than during late summer, particularly in the near-shore areas.

The consistency between the four surveys suggests low variability in krill biomass north of the South Shetland Islands throughout the summer of 1999/2000. However, the demographic composition of krill present in the survey area

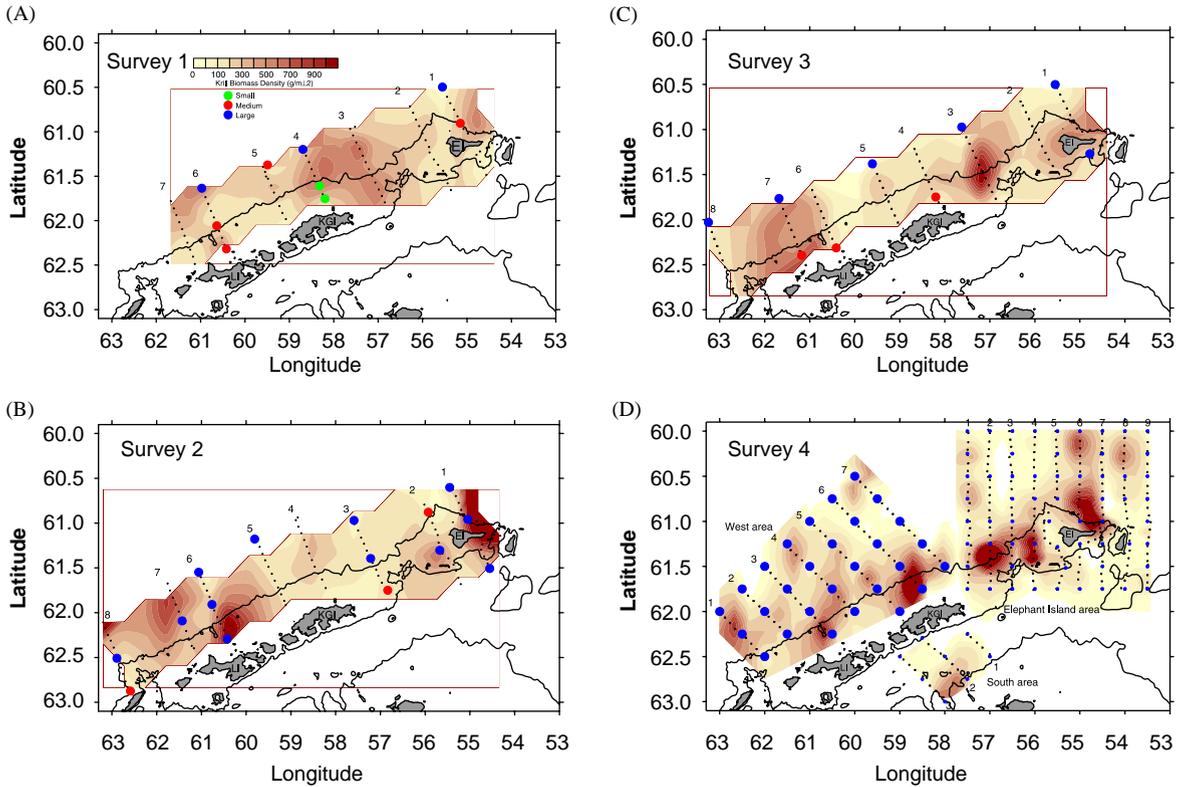


Fig. 3. (A–D) Krill biomass density in the vicinity of the South Shetland Islands. The islands are indicated by gray-shaded polygons; the shelf break is approximated by the 500 m isobath and indicated by a thin black line; the mid-positions of krill biomass density estimates averaged over 5 nm are indicated by small black dots; the positions of net sampling stations are indicated by large colored dots, with green denoting a member of a small-mode cluster, red a member of a medium-mode cluster, and blue a member of a large-mode cluster.

Table 3
Krill maturity stages

	Survey 1	Survey 3	Survey 4
Juvenile and sub-adult	0.3350	0.0141	0.0000
Adult male			
M 2A1	0.1853	0.0280	0.0004
M 2A2	0.0936	0.0841	0.0090
M 2A3	0.0074	0.0450	0.0021
M 3A	0.0081	0.0126	0.0598
M 3B	0.0335	0.3175	0.4159
Adult female			
F 2	0.0834	0.0000	0.0000
F 3A	0.2374	0.1409	0.0004
F 3B	0.0163	0.1851	0.0057
F 3C	0.0001	0.1223	0.1782
F 3D	0.0000	0.0504	0.2993
F 3E	0.0000	0.0000	0.0293

changed as the summer progressed from a mixture of juvenile, immature, and mature animals to a single mode of large, mature animals. These changes are consistent with the ontogenetic seasonal movements of krill in the vicinity of the South Shetland Islands described by Siegel (1988).

Transect-to-transect variation in mean krill biomass density was similar among the surveys, suggesting similar dispersion patterns at the scale of the transects. This may be interpreted as relatively constant prey availability to predators, although the numerical density and size composition of the prey changed as the season progressed. There is also the suggestion that prey may have moved closer to the shelf break as the season progressed.

These surveys cannot resolve where the juvenile krill went after moving through the survey area. Siegel et al. (2002) sampled high densities of juvenile krill in the southeastern section of the Bransfield Strait during January to February 2001. They acknowledged that these krill may have been transported from the Weddell Sea, but concluded that their observations were more likely to be the result of a southern shift in the position of krill from the Bellingshausen Sea moving with the Antarctic Circumpolar Current.

In addition, these surveys cannot unambiguously resolve the rate of movement of krill through the South Shetland Islands region. At least two models of krill transport are possible. The first assumes that large aggregations of krill move cohesively through the region. With this model it may be possible to identify and track the movement of the aggregations and thus quantify the flux of krill through the region and the amount of prey available to predators over a specific period of time, such as the breeding season. The second model assumes that much smaller aggregations of krill are transported into areas where their movement is stalled and they join other small aggregations to form persistent localized areas of high krill density. These areas may coincide with places where currents have been influenced by topographic features creating eddies, convergence zones, and other diversions of the water flow which may act to concentrate krill (Witek et al., 1988). Because there appear to be predictable regions of high density, the second model may be more likely. This implies that finer-scale observations, both in space and time, will be required to resolve this model of krill transport.

Acknowledgement

These surveys are the latest in a series of joint multi-ship surveys that also were conducted during the summers of 1994/95 and 1996/97. The results presented here were distilled from a workshop held in Seoul, Korea during June 2001. We appreciate the efforts of the scientists and crew on board the various research vessels and the support from national programs. We also thank the Korea

Ocean Research and Development Institute (KORDI) for hosting the workshop.

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