Distribution, Abundance and Demography of Krill

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Abstract The results presented here are based on analysis of postlarval and larval krill collected by 101 net samples in the South Shetland Island and Bransfield Strait region during January 2009.

- Postlarval krill exhibited a relatively uniform distribution of modest concentrations across the survey region.
- Relatively small proportions of one-year-old krill, in conjunction with generally low krill concentrations in the Bransfield Strait, suggest reduced recruitment from 2007/08 compared to 2006/07, 2005/06 and 2004/05 year classes.
- An actively reproductive krill population with large proportions of advanced female maturity stages and presence of early calyptopis stage larvae indicate peak spawning activity during the survey period.

Introduction

Here we provide information on the distribution, abundance and demographic structure of Antarctic krill (Euphausia superba) in the vicinity of the South Shetland Islands (Livingston, King George, and Elephant Islands) and the Bransfield Strait (Joinville Island). Abundance statistics (frequency of occurrence, mean, standard deviation and median) reveal information about krill distribution patterns that are related to hydrography and krill demography. Essential krill demographic information includes length, sex ratio, maturity stage composition, reproductive condition as well as distribution, abundance and developmental composition of the larval stages. Information useful for determining the relationships between krill distribution patterns and ambient environmental conditions was derived from net samples taken at established CTD/ phytoplankton stations. Results from Leg I are compared to those from previous AMLR Surveys to assess inter-annual differences in krill demography and abundance over the 1992-2009 period.

Methods

Krill were obtained from a 1.8 m Isaacs-Kidd Midwater Trawl (IKMT) fitted with a 505 μ m mesh plankton net. Flow volumes were measured using a calibrated General Oceanics flow meter mounted on the frame in front of the net. All tows were fished obliquely to 170 m or to ca. 10 m above bottom in shallower waters. Real-time tow depths were derived from a depth recorder mounted on the trawl bridle. Tow speeds were ca. two knots with flow volumes averaging 5,005 (+/- 755) m³ based on a calibration factor of 0.0752, calculated from the net's fishing dimensions. Sample data are considered with respect to the four distinct areas in the survey region. All samples were processed on board. For diel considerations, twilight samples are defined as those collected one hour before to one hour after local sunrise and sunset.

Demographic analyses of krill postlarvae were made using fresh or freshly frozen specimens. Postlarval krill were removed and counted prior to other sample processing. All krill from samples of <100 individuals were analyzed. For larger samples, at least 100 individuals were measured, sexed, and staged. Measurements were made of total length (mm), and krill maturity stages were based on the classification scheme of Makarov and Denys (1981). Length-at-age estimates were based on Siegel (1987) and Siegel and Loeb (1994). Data on the larval stages were obtained from zooplankton sample analysis described by Loeb et al. (Chapter 5). Recruitment indices (R), indicating the relative reproductive success and survival of each year class, were based on the proportion of one-year-old krill (by length) relative to total krill (all year classes) sampled in the Elephant Island Area each year, calculated according to the methods presented by Siegel et al (2002).

Statistical Analyses

Data from the total survey region and four areas were analyzed inter- and intra-annually. Analyses include a variety of parametric and nonparametric techniques: Index of Dispersion (ID) to demonstrate the evenness or patchiness of krill distribution; Analysis of Variance (ANOVA) with Post-Hoc comparison of means (Tukey Honest Significant Difference) to establish abundance differences at the 95% probability level; Kolmogorov-Smirnov D_{MAX} values to indicate similar length-frequency distributions; Kendall's Tau (T) correlation coefficients to

Table 4.1. Krill abundance (No. per 1,000 m³) and distribution attributes in the South Shetland Islands during January 2009 relative to January-February 2001-2008. N is number of samples within each area. The Joinville Island Area was not sampled in 2001. Largest concentrations typically reflect juveniles, hence recruitment success from the previous year's spawn (R1). Index of Dispersion (ID) is a measure of distribution; smaller numbers indicate evenness and larger numbers patchiness. Inter-annual variation in distribution patterns reflects demographic and hydrographic differences.

Krill Abundance AMLR Survey Leg I											
Year	2001	2002	2003	2004	2005	2006	2007	2008	2009		
West Area N=	30	25	25	24	25	25	23	22	23		
Mean	8.3	27	24.6	7.3	5.4	6.4	27.7	31.7	5.6		
SD	12	90.8	55.2	13.7	8.4	8.1	43.5	60	6.8		
Median	1.5	0.3	5.1	1.4	1.5	5.1	11.3	5.5	2.2		
ID	17.3	305.7	124	25.6	13	10.3	68.4	113.3	8.2		
Elephant Island Area	60	44	38	46	48	48	48	34	47		
Mean	13.3	25.1	204.5	38.5	17.5	15.3	42.7	119.9	23.2		
SD	23.6	60	891.6	109.7	21.2	30.7	62.1	400.1	74.1		
Median	3.8	4.8	19.9	2	9.9	7.1	21.4	14.3	3.3		
ID	41.8	143.5	3887.5	312.4	25.7	61.4	90.3	1335.5	236.5		
Joinville Island Area	n.a.	9	3	5	6	6	7	10	11		
Mean		50.4	323	0.2	17.8	61.1	237.2	165.9	1.3		
SD		98.7	428.7	0.3	36.2	119.3	457.3	251.6	2.2		
Median		6.6	38.6	0	1.2	10.2	2	1.5	0.2		
ID		193.2	569.1	0.3	73.8	232.8	881.5	381.7	3.6		
South Area	11	17	17	16	20	20	20	20	20		
Mean	74.7	104	56.2	41.9	8.8	16.9	102.1	25.7	52.4		
SD	115.6	251.2	123.3	72.1	23.8	38.9	205.6	83.7	129.4		
Median	14.5	0.5	0.7	0.8	0.6	5	14	1	0.9		
ID	178.7	606.4	270.9	124.1	64.7	89.8	413.9	271.9	319.8		
R1		0.403	0.478	0.001	0.014	0.2	0.23	0.373			



Figure 4.1. Distribution and concentration of postlarval krill, January 2009. Locations of sampling stations within the West, Elephant Island, Joinville Island and South Areas are included.

identify the joint variation of environmental parameters over time; Percent Similarity Indices (PSI) to indicate similarity in proportions of maturity stages; and Cluster Analysis to define distribution patterns of different krill length/ maturity stages. Cluster analysis applied here is based on the proportional length-frequency distributions in each net sample containing at least 17 krill and uses Euclidean distance and Ward's linkage method, with significant groupings (clusters) distinguished by a distance of 0.30 to 0.70. Statistical analyses were performed using Statistica (StatSoft) and NCSS software.

Results

Postlarval Krill

A total of ca. 11,000 postlarval krill were collected during the survey. Krill were present in 85 of the total 101 samples with an overall mean abundance of 23 (+/- 79) per 1,000 m³ and a median catch of 2.3 per 1,000 m³. These values, and index of dispersion of 273, indicate a





Figure 4.2. Overall krill length-frequency distribution and maturity stage composition, January 2009. Arrows denote approximate ages associated with the different length modes (Siegel, 1987).



Figure 4.3. Krill length-frequency distributions in four survey areas, January 2009

relatively uniform distribution of modest krill concentrations across the region.

Two of the five largest concentrations (471-2,338 individuals, 106-562 per 1,000 m³) were in the northeast Elephant Island Area, while the three others were in the south and central Bransfield Strait, within the South Area (Figure 4.1).

Night catches were greatest, with a mean of 56 (+/-146) per 1,000 m³, followed by twilight and day with respective mean concentrations of 38 (+/-113) and 11 (+/- 34) per 1,000 m³. These differences were not significant, however, due to catch variability within each diel period (ANOVA, P>0.05). As with all Leg I surveys, the number of day samples (69) vs. night and twilight samples (16 each) suggests that the overall mean is a conservative estimate.

Despite a relatively even overall krill distribution, the four areas exhibited regional catch differences. Krill were least frequent (75% of samples) but had greatest mean abundance in the South Area (52 per 1,000 m³), reflecting a patchy distribution there relative to the other areas (Figure 4.1). This is also indicated by the low median (0.9 per 1,000 m³) and relatively high ID (320) values (Table 4.1). In contrast, moderate concentrations were distributed more evenly across the Elephant Island Area, where krill were present in 92% of samples with mean and median values of 23 and 3.3 per 1,000 m³, respectively. Only small catches were made in the Joinville Island Area, where nine of the 11 samples netted a total of only 74 individuals (1.3 and 0.2 per 1,000 m³ mean and median, respectively). Catch frequency was relatively low in the West Area, where 700 individuals were caught in 18 of 23 samples (78%) with respective mean and median concentrations of 5.6 and 2.2 per 1,000 m³.

Krill lengths ranged from 12-58 mm and demonstrated a polymodal distribution with similar proportions of one-, two- and three-year and older individuals, representatives of the 2007/08, 2006/07 and 2005/06 and older year classes (Figure 4.2). Overall, individuals < 35 mm (generally one-year old), 36-44 mm (two-year old) and > 45 mm (three-year old and older) each represented 33% of the catch. Of note is the bimodal length distribution of one-year old krill, one group comprised of small individuals with lengths centered around a 21 mm mode and a second, more abundant group of individuals with an apparent 34 mm mode, most likely augmented by the contribution of small two-year old individuals. This bimodal length distribution is interesting in that it suggests the input of krill from two different sources (i.e., spatially and/or temporally separated reproductive efforts) during the 2007/08 spawning season.

Overall, juveniles comprised 14%, immature stages 28% and mature stages 58% of the krill sampled (Table



Figure 4.4. Krill maturity stage composition in four survey areas, January 2009

4.2). Mature males outnumbered mature females by 50% and most (80%) mature females were in advanced stages with developing ovaries, gravid or spent, indicating peak seasonal spawning activity.

2009

Different krill length/maturity stages were represented in each area: large, mature individuals were primarily offshore of smaller immature and juvenile stages. Latitudinal gradients also reflect different mixtures of the various length/maturity categories (Figures 4.3 and 4.4), likely due to hydrographic processes such as advective transport, fronts and gyres occurring across the region.

While a wide range of krill lengths was represented across the region, catches in the West and Elephant Island Areas were overwhelmingly dominated by individuals >35 mm (Figure 4.3). The length-frequency distribution in the West Area had 50 mm modal and 48 mm median lengths, while that in the Elephant Island Area was bimodal at 44 mm and 48 mm with a 45 mm median. Mature males outnumbered females by 80% and the majority of animals were in mating condition. Advanced reproductive stages constituted 72% and 88% of mature females in the West and Elephant Island Areas, respectively. The increased proportion of advanced female stages in the Elephant Island Area compared to the West Area (Figure 4.4) reflects the advancing season and/or an earlier onset of reproductive activity in the Elephant Island Area.

Demographic information for Joinville Island Area krill is limited by the small sample size, but, like the South Area, 93% of individuals were <45 mm, representatives of the 2007/08 and 2006/07 year classes. One-year old length krill (<35 mm) comprised 69% and 32% of the South and Joinville Island Areas, respectively. The dichotomous one-year old size groups were represented in both areas, although the larger (30-35 mm) group was not as well represented in the Joinville Island Area. Juvenile and immature krill comprised 86% of the South Area krill catch, and 74% in the Joinville Island Area. Elevated patchiness in the South Area was due to infrequent, relatively dense concentrations of these young krill. The few mature krill collected in the South and Joinville Island Areas were, for the most part, not reproductively active. Mature females were primarily unmated (F3a) or spent (F3e), suggesting that spawning had already taken place in the Bransfield Strait.

Cluster analysis performed on length-frequency data from 42 samples resulted in three distinct krill groupings with spatially coherent distribution patterns (Figures



Figure 4.5. Length-frequency distribution and maturity stage composition of krill clusters, January 2009.



Figure 4.6. Distribution of krill length/maturity clusters in relation to hydrographic features, January 2009. Temperature at 350 m shows major hydrographic features in the region: 2oC isotherm denotes core waters of the ACC; 1.8oC the ACC southern front; 0oC the ACC southern boundary. The region between the southern boundary and southern front is characterized by mixing of ACC-derived and coastal waters.

4.5, 4.6). The smallest of these, Cluster 1, was represented at four stations in the southwest Bransfield Strait and one station over the northwest shelf of Elephant Island. Virtually all of the krill (99%) were <44 mm and 69% were in the one-year-old length class (<35 mm).

Cluster 2, the most frequent group, occurred at 22 stations primarily over and adjacent to the South Shetland Island shelves; an exception was one station in the southeast Bransfield Strait (Figure 4.6). The majority of individuals (66%) were 35-45 mm representatives of the two-year old (2006/07) year class. Smaller krill made up only 7% of the total (Figure 4.5). Mature males and females were similarly represented (each ca. 38% of total) and 80% of the females were in advanced reproductive stages, mostly with developing ovaries and gravid.

Cluster 3 occurred at 15 stations, largely offshore of the island shelves (Figure 4.6). Most (88%) individuals were >45 mm (i.e., three-years old and older) with a 50 mm median and modal length. Virtually all (98%) were mature and, like Cluster 2, most of the females (85%) were in advanced reproductive stages (Figure 4.5). Males outnumbered females by 50%, suggesting that a substantial number of large spawning females may have been located

Larval Krill Stage Composition														
Stage (%)	A96	A97	A98	A99	A00	A01	A02	A03	A04	A05	A06	A07	A08	A09
Calyptopis	100	93	68	100	n.a.	100	70	100	95	99	100	100	99.8	99.5
Furcilia		7	32		n.a.		30		5	1			0.2	0.5
No. 1,000 m ⁻³														
Mean	2.7	15.4	1	103.1	n.a.	100.3	12.8	2.4	4.5	11.9	646.6	9.2	33	8.6
STD	7.5	27.1	4.5	587.4	n.a.	445.2	31.4	7.5	9.4	43	2381.8	32.3	64.4	29.6
Median	0	0.8	0	2.6	n.a.	8.1	0	0	0.1	0.3	2.7	0.1	6.2	0
February-March														
Stage (%)	D96	D97	D98	D99	D00	D01	D02	D03	D04	D05	D06	D07	D08	D09
Calyptopis	86	100	99	97	97	98	85	89	44	85	n.a.	n.a.	100	n.a.
Furcilia	14		1	3	3	2	15	11	56	15	n.a.	n.a.		n.a.
No. 1,000 m ⁻³														
Mean	13.9	25	1.6	49.8	1374.5	439.2	39.5	2.5	75.2	117.8	n.a.	n.a.	94.8	n.a.
STD	40.2	81.4	14.1	119.3	4682.1	2320.4	142.1	6.7	340.9	540.7	n.a.	n.a.	391	n.a.
Median	3	0	0	9	22	6.2	0	0	13.1	0	n.a.	n.a.	4.9	n.a.
R	0.198	0.12	0	0	0.573	0.403	0.478	0.001	0.014	0.2	0.23	0.373		

4.2. Overall larval krill stage composition (%) and abundance (numbers per 1,000 m³) during Leg I of the AMLR Survey. n.a. indicates no survey was conducted. R is the proportional recruitment index associated with larval abundance for each year class.



Figure 4.7. Distribution and abundance of larval krill in relation to implied flow (dynamic height at 500 m relative to the surface) across the survey region, January 2009. Box indicates the Elephant Island Area. Dynamic height indicates generally northeast flow through central Bransfield Strait and Drake Passage, a large eddy east of the Shackleton Fracture Zone, clockwise gyral circulation in southeast Bransfield Strait and over the island shelf regions.

farther offshore during the survey period. *Larval Krill*

Krill larvae were present in 38 of 101 samples, with an overall mean concentration of 8.6 (+/-29.6) per 1,000 m³ (Table 4.3, Figure 4.7). They were most frequent in the Joinville Island Area, present in nine of the 11 samples (82%). The largest catch (226 per 1,000 m³) was also in the Joinville Island Area, resulting in relatively large mean and median abundance values of 32 (+/- 62) and 7.8 per 1,000 m³, respectively. Concentrations here were significantly greater than in the other areas (ANOVA, P<0.03). Two other relatively large catches (103 and 123 per 1,000 m³) occurred north of Elephant Island. While larvae were present in 40% of samples in both the Elephant Island and South Areas, their mean abundance was almost an order of magnitude greater in the Elephant Island Area (10.4 vs. 1.2 per 1,000 m³). Small numbers of larvae were present in only two of 23 West Area samples, yielding a mean of 0.4 per 1,000 m³. Krill larvae exhibited diel catch differences with night and twilight mean concentrations nearly twice what they were during day (12-13 vs. 6.7 per 1,000 m³), possibly due to vertical migration into surface layers. As with the postlarvae these differences were not significant due to catch variability.

Calyptopis stages made up 99.5% of larvae sampled. Overall, 82% were Calyptopis stage 1 (C1), the first feeding stage to reach surface waters from hatching at depth. Older C2 and C3 stages comprised 16% and 1.6% of total larvae. South Area samples differed from the other areas in that, despite low concentrations, they contained the greatest variety of larval stages. Here C1-3 stages represented 39%, 16% and 35%, respectively, and more advanced Furcilia F1-2 stages contributed 7% and 3%, respectively, of the total.

Using the data from the Elephant Island Area, we determined the length-density contribution of krill to

calculate the proportional recruitment of krill for 2009. Length-density was determined using the CMIX program (de la Mare, 1994). A small proportion of krill less than 25 mm were present in the Elephant Island Area; these were pooled into the 25 mm length class before sunning the CMIX program.

CMIX analysis determined that the most abundant krill lengths were 29.5, 42 and 49 mm, representing 2%, 56% and 42% of the krill in the Elephant Island Area, respectively. Krill in the 29.5 mm length class were considered to be from the 2008 cohort. Therefore, proportional recruitment of krill hatched during the previous breeding season was extremely low during the 2009 AMLR Survey.

Discussion

Postlarval Krill

Mean krill abundance in the Elephant Island Area during January 2009 (23.2 \pm 74.1 per 1,000 m³) was below the 18-year mean (39.7 \pm 220.3 per 1,000 m³), similar to that observed in 1992 and 2002, but was moderately high compared to abundance in 1995 and 1999-2001 (Figure 4.8). The median krill abundance was about half the long-term value (3.3 vs. 5.9 per 1,000 m³). However, with the exception of 1996, all of these values were significantly less than the 2003 and 2008 means (ANOVA, P<0.05), reflecting comparatively small contributions of one-year old individuals and low recruitment success from the previous years spawn.

Krill length-frequency distribution in the Elephant Island Area was most similar to January 1994 and 1999 (D_{MAX} =12.2-12.8), periods characterized by low recruitment from the previous two to three years (Figure 4.9). This is unusual given the extremely good recruitment success observed in 2008 (the 2006/07 year class) and suggests the advective loss of a substantial portion of these individuals to downstream regions (Atkinson et al., 2008). The paucity of individuals >53 mm is also notable in light of the relatively good recruitment success of the 2004/05 and 2005/06 year classes, now three- and four-year-old animals.

As indicated in Table 4.1, there is a great deal of interannual variability in krill distribution patterns that could affect assessment of recruitment success due to variable representation of one-year-old krill in the Elephant Island Area. In this respect, the relative abundance pattern of krill across the four areas during January 2009 was quite similar to that dur-



Figure 4.8. Inter-annual variation in mean abundance of postlarval krill in the Elephant Island Area during Leg I of the 1992-2009 AMLR Survey. Leg II is used for 2000, when there was no Leg I.

ing January 2004, with highest concentrations in the South and Elephant Island Areas and extremely low concentrations in the Joinville Island Area. The paucity of small krill, particularly in the Joinville Island Area, despite the relatively intense sampling effort there this year, lends support to the idea that there was relatively low recruitment from the 2007/08 spawning season. Poor recruitment success was anticipated based on the low proportions of advanced female maturity stages observed during January 2008 (Loeb et al., 2008).

The unusual bimodal length distribution of oneyear-old krill this year suggested input from two different sources during the 2007/08 spawning season. This could be explained by the observation of an early initiation of reproduction in the Bransfield Strait and a delayed spawning period in the Elephant Island Area that extended into early March (Loeb et al., 2008).

Within the Elephant Island Area the overall krill maturity stage composition was similar to that during January 1995 and 2006 (PSI=87 and 97), reflecting the overwhelming dominance of mature forms. The proportions of individual maturity stages were most similar to those in 1995, when gravid and spent females contributed 27-33% of all krill sampled. Over the 1992-2009 period recruitment success was significantly correlated with proportions of advanced female stages during January (N=15, T = +0.41, P=0.03), suggesting the potential for good recruitment of the 2008/09 year class.



Figure 4.9. Krill length-frequency distribution in the Elephant Island Area during Leg I, 1989-2009, showing the progression of successful year classes as they age. Leg II used for 2000, when there was no Leg I. The horizontal lines indicate possible under sampling of either small or large length categories due to their variable between-year distribution patterns relative to the Elephant Island Area.



Figure 4.10. Interannual variation in mean abundance of larval krill in the Elephant Island Area during January surveys 1995-2009. February data used for 2000, when there was no January survey.

Larval Krill

As with most years, mean larval krill abundance in the Elephant Island Area in 2009 was significantly lower than the extreme highs monitored in January 2006, when there was an extremely early onset of seasonal reproductive activity, and in February 2000 (ANOVA, P<0.05) suggesting that the January value is more an indication of timing, rather than output, of reproductive effort (Figure 4.10).

The overall distribution pattern, abundance and stage composition of larval krill was quite similar to what was observed during January 2007, a year characterized by strong recruitment. Larval krill abundance and stage composition in the AMLR Survey areas are highly variable from year to year. However, back-to-back surveys typically demonstrate seasonal increases in larval abundance and stage development. Notable exceptions were 1998 and 2003, when few larvae were encountered during either survey. Over the 2000-2009 period, greatest larval krill concentrations typically were in the Joinville Island and Elephant Island Areas. As observed during 2009, this is likely due to prevailing northeast advection and concentration in frontal zones and eddies in these areas. Exceptions to this were both 2001 surveys and the 2002 February-March survey, when greatest concentrations occurred in the West Area, possibly in association with the nearshore location of the ACC.

Recruitment success does not appear related to either larval stage composition or location of maximum abundance each year, but is significantly correlated with the total mean larval abundance observed during February-March surveys (N=10, T=+0.54, P=0.03). These results are consistent with the relationship between recruitment success and proportions of advanced female maturity stages in January and indicate the importance of optimally timed seasonal reproductive output. The timing of this year's spawning peak is favorable as it allows the larvae sufficient time to feed, grow and develop to advanced overwintering stages (Siegel and Loeb, 1995).

Protocol Deviations

There were no changes to standard sampling and analytical techniques used during AMLR field work.

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Disposition of Data

Data are available from Christian Reiss, NOAA Fisheries, Antarctic Ecosystem Research Division, 3333 Torrey Pines Court, Room 412, La Jolla, CA 92037. Ph: 858-546-7127, FAX: 858-546-5608

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UNITED STATES AMLR ANTARCTIC MARINE PROGRAM

AMLR 2008/2009 FIELD SEASON REPORT

Objectives, Accomplishments and Tentative Conclusions

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