Polar Biol (2003) 26: 672–679
DOI 10.1007/s00300-003-0537-5

ORIGINAL PAPER

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Krill (*Euphausia superba*) recruitment indices from the western Antarctic Peninsula: are they representative of larger regions?

Received: 2 April 2003 / Accepted: 4 July 2003 / Published online: 5 September 2003

Abstract This study presents data on krill demography west of the Antarctic Peninsula covering many years since 1982. The recruitment indices are compared with those for other mesoscale study regions collected over the last 25 years. We use these data to investigate whether results from such mesoscale surveys are representative of large-scale stocks or regional populations. Generally, the proportional recruitment indices for 1- (R_1) and 2-year-old (R_2) krill differ substantially between years for a given area. However, indices were in conformity with the results from other regional scientific surveys. Recruitment indices showed a significant correlation for age-class 1 krill between scientific surveys from the northern Bellingshausen Sea, the Elephant Island area and South Georgia. The correlation becomes weaker for R_2 recruitment indices. There was no correlation between krill recruitment indices from Atlantic and Indian Ocean survey sites. Problems of single-year outliers from Elephant Island are discussed, as well as the problem of "undersized" length classes of the age-1 group that occur in the samples of some years.

Introduction

The proportional recruitment index was defined by de la Mare (1994a), where R_1 is the ratio of numbers in age-class 1 to the number in that age class and above. Additionally, the R_2 index was established as the proportion of 2-year-olds. Siegel and Loeb (1995) calculated the proportional recruitment from standardized mesoscale research surveys around Elephant Island. More recent data and results from the same area were added by Siegel et al. (1998, 2002). Data from commercial-sized trawls were analysed by Kawaguchi et al. (1997). Due to the larger mesh size of the commercial net, there is a strong effect of net selectivity. Therefore, the last study could only estimate the 2-year-old component of the stock in the South Shetland Islands, including the Elephant Island fishing ground. There are two major uses for the krill recruitment index. The first is the use as one of the essential parameters for the Generalized Yield Model (GYM) (Constable and de la Mare 1996), to estimate the potential krill yield in the CCAMLR Convention Area. Second, it can be utilized as a key demographic parameter that gives insight into between-year variation in the krill stocks.

One of the biggest concerns with the recruitment index is whether it can be considered representative of an entire population which is likely to be much larger than the survey area. To date, most of the sampling comes from time series of relatively small survey areas within the Scotia Sea. Very few large-scale survey data have been collected. Therefore, values from different regions are frequently compared to look for similarities and differences. In the summer of 1994, Siegel and Harm (1996) found that the length-frequency composition of the krill stock and the recruitment index were very similar in the central and eastern Bellingshausen Sea and the Elephant Island area. Watkins (1999) estimated krill recruitment indices from South Georgia for year-classes between 1988 and 1997, and concluded that krill concentrations around South Georgia are connected to the Peninsula stock. However, Siegel et al. (2003) showed results of a large-scale survey across the Scotia Sea, and found that completely different recruitment values may occur in various parts of the Scotia Sea. This result was attributed to differences in the origin of the krill concentrations, and that the populations had experienced different life histories in their respective upstream areas (Antarctic Peninsula vs Weddell Sea). Similarly, Siegel (2000) observed that recruitment in the Atlantic sector

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does not seem to match recruitment in the same years in the Indian Ocean (de la Mare 1994a; Nicol et al. 2000).

The circulation pattern, constructed from historical data sources, for the region west of the Antarctic Peninsula shows that the large-scale geostrophic flow may have a simple structure, with a northeastward flow over the deep areas past the northern continental slope of the South Shetland Islands into the Scotia Sea, due to the ACC (Antarctic Circumpolar Current). A weaker but more complex southwestward flow is characteristic of waters nearer to the coast, with meanders and gyres on the shelf (Makarov et al. 1988; Stein 1988; Hofmann et al. 1996; Smith et al. 1999). Drifter-buoy experiments confirmed the potential teleconnection between the western side of the Antarctic Peninsula, the South Shetland Islands and South Georgia (Ichii and Naganobu 1996). However, over the shelf waters between Anvers and Adelaide Islands, Smith et al. (1999) found that hydrographic data support the presence of a large cyclonic gyre encompassing two sub-gyres.

The present contribution, therefore, compares data from the upstream area of the Elephant Island survey grid. The krill demographic data are from the austral summer season, and were collected during German surveys in the 1980s and during the annual cruise of the Palmer Long-Term Ecological Research (LTER) programme since 1993 (Quetin and Ross 2003). The intention is to compare the recruitment indices derived from these two mesoscale surveys and analyse whether results from mesoscale surveys are representative of a wider region, i.e. the general concordance of interannual direction of variation, as well as same-year amplitude of variation.

Materials and methods

The Palmer LTER sampling grid covers areas falling inside CCAMLR subareas 88.3 and 48.1, the so-called northern approaches of the Bellingshausen Sea (Fig. 1). Stations have been sampled annually since 1993 during January at regular spatial

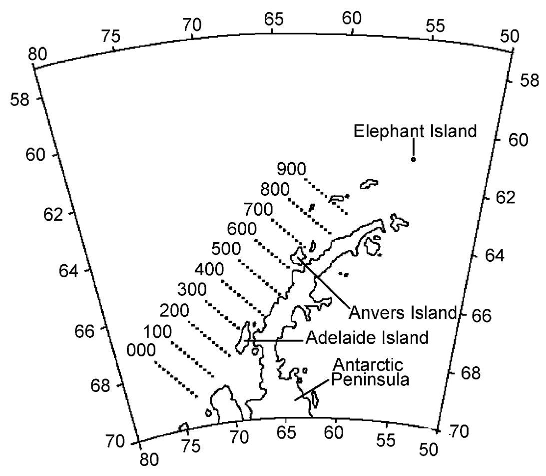

Fig. 1 Palmer LTER regional station grid. Transects are 100 km apart alongshore. Stations on transects are spaced 20 km apart from the coast to 200 km offshore

intervals. Despite the fact that not all stations displayed in Fig. 1 are always sampled, the station coverage considered the relative proportion of inner shelf, outer shelf and slope within a survey region to allow appropriate comparisons (see Discussion).

Additionally, three German cruises from the second half of the 1980s sampled stations along 5–6 inshore-offshore-transects west of 63°W (similar to transects 200–800 in Fig. 1). Those data were also used in the current analysis. During the LTER surveys, oblique net tows were carried out for non-targeted krill samples, deploying a 2-m-square Metro net (0.7-mm mesh and 0.5-mm mesh in cod end). Standard tows were oblique from the surface to 120 m. This fishing depth is slightly shallower than that of the German surveys, where the RMT 8 (4-mm mesh and 1-mm mesh in cod end) was towed down to 200 m. This difference is certainly of importance when comparing absolute numerical krill densities, but it does not affect the proportional recruitment indices. Both net types were rigged with flowmeters to measure volume filtered, and a time-depth-recorder to record the maximum depth of the tow. All krill catch data were standardized to density values (N 1,000 m^{-3}). The density values and length measurements were used to calculate length-density distributions, and the actual proportions of the 1- and 2-year-old krill were calculated from the length-density distributions. The total length measurement was tip of rostrum to end of the uropods for the Palmer LTER samples (standard 1 body length according to Mauchline 1980), and was anterior margin of the eye to tip of the telson (total length AT, Discovery method) for the German survey data. For the 1-year-old, 20 to 30 mm length class, the difference between the two methods is approximately 0.7–1.0 mm (Siegel 1982). However, this slight difference only affects the results on the mean length of the first or second age group, and does not influence the calculation of the proportion of the different components of the distribution mixture.

Recruitment of *Euphausia superba* was first defined as the proportion of recruits known as the R_1 ratio, the ratio of numbers in age-class 1 to the numbers in age-class 1 and all age classes above (de la Mare 1994a). This procedure can also be applied for age-class 2. Since krill distribution is extremely patchy, neither stock density estimates nor density for each length class of standardized length-frequency distributions show a Gaussian distribution. The underlying statistics of these distributions were analysed and a new approach was developed by de la Mare (1994b) to create density-at-length (instead of length frequency) data from scientific surveys as a basis for recruitment estimates. He also modified the Macdonald and Pitcher least-square approach of fitting the data to the maximum likelihood method. As a result, the quantitative proportions, as well as the mean length of the distribution mixture components, can be calculated including a statistical test for the goodness of fit to the data. The software CMIX by de la Mare (1994b) is available from the CCAMLR secretariat in Hobart.

There are additional requirements for the krill data, because of the krill stock and its underlying geographical non-random distribution pattern of different age groups across the distribution range. In the Elephant Island area, as well as in the northern Bellingshausen Sea (Palmer LTER survey area), younger krill are concentrated above the shelf whereas the adult spawning stock is found along the continental shelf break and in oceanic waters (Siegel 1987; Ross et al. 1996). The implications are clear. The ability to detect trends or quantify interannual and interregional differences in krill recruitment, abundance and productivity depends on the time of data collection and the relative proportion of inner shelf, outer shelf and slope within a survey region (Siegel and Loeb 1995; Siegel et al. 1997; Lascara et al. 1999; Quetin and Ross 2003). Surveys were designed accordingly to cover both shelf and deep-water regions, because the proportion of the shelf has an effect on the recruitment index.

Results

The analysis of krill length-density distributions from most years showed that the mean size of the first

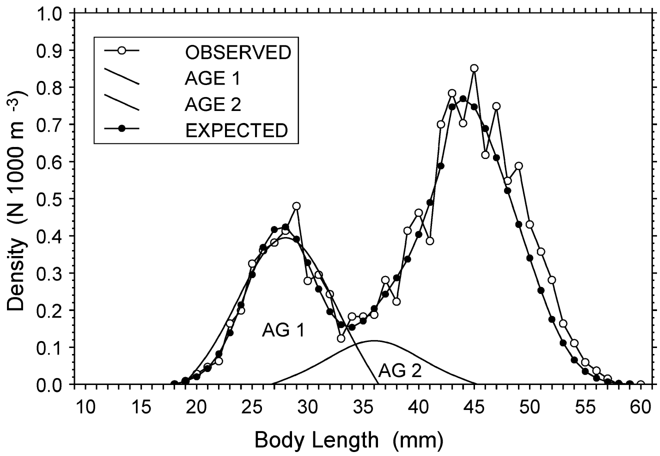

Fig. 2 Overall observed krill length-density distribution from January 1995 with the expected composite distribution according to the results of the distribution mixture analysis. Note the expected unimodal juvenile age-1-year-old (and subadult age-2-year) size component

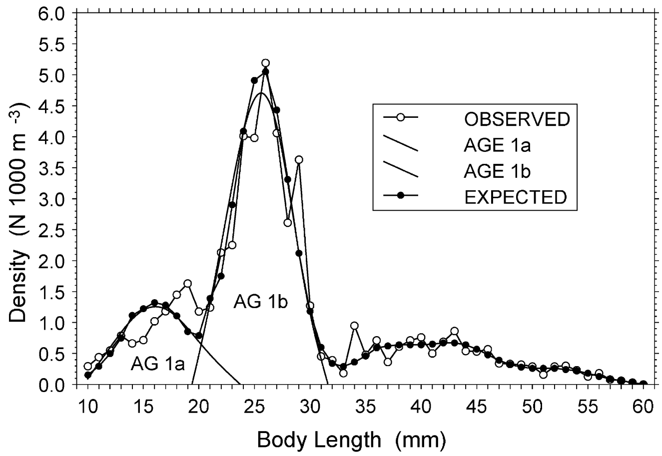

Fig. 3 Overall observed krill length-density distribution from January 2002 with the expected composite distribution according to the results of the distribution mixture analysis. Note the bimodal juvenile age-1-year-old size component

component of the distribution mixture was generally 25–28 mm (Fig. 2). This component represented a unimodal distribution of the juvenile developmental stage, similar to length-at-age data provided by Siegel (1988) from the Antarctic Peninsula, Pakhomov (1995) and Hosie et al. (1988) for the Indian Ocean, and Watkins (1999) for South Georgia. Since the 0 age group is still in the early larval phase and of a mean size of less than 2 mm during the ongoing spawning season between December and February, the component with an average length of 25–28 mm in January has been commonly accepted as age-group 1. The mean size of age-group 2 varied around 35–37 mm total length.

However, in some years of the present data set, we found evidence of a bimodal juvenile size component. The larger length classes were again in the range of mean lengths as mentioned above, but an additional, smaller component occurred simultaneously in the samples with mean lengths between 15 and 18 mm (in one case 21 mm). This phenomenon occurred especially in 1996, 1997 and 2002 (Fig. 3) . A similar observation was made from the 1987/1988 German survey data from the Elephant Island area close to the tip of the Antarctic Peninsula. Such small-mean-size groups were recorded by Siegel (1988) from the southeastern Weddell Sea and by Nast (1982), Siegel et al. (1990) and Melnikov and Spiridonov (1996) from the northwestern Weddell Sea, always in close proximity to perennial sea ice. These smaller juvenile length classes were assumed to be of different origin than the "normal" size classes, and obviously had a different life history. Furthermore, in data from the year following the occurrence of the small age-1 component, we never observed a bimodal length distribution of the subadult 2-year-olds. Therefore, these undersized length classes were omitted from the first run of analyses, and the larger-size component was assumed to represent the R_1 recruitment index. In a second run, the small-size component was included. The R_{SL} values

Table 1 Proportional recruitment indices of 1 (R_1) and 2-year-old (R_2) krill and their standard errors in the northern Bellingshausen Sea during 1985–2002 derived from German and Palmer LTER net-sampling surveys. R_{SL} represents recruitment values for the combined small and large size fraction of age group 1 (see e.g. Fig. 3)

Cruise Year	R_{SL}	R_1	SE	R_2	SE
1985		0.000	0	0.008	0.0601
1988	0.182	0.175	0.0728	0.018	0.0173
1990		0.000	0	0.323	0.3613
1993		0.005	0.0083	0.630	0.0900
1994		0.088	0.0252	0.049	0.0211
1995	0.281	0.267	0.0509	0.177	0.1350
1996	0.852	0.639	0.0781	0.495	0.0813
1997	0.436	0.147	0.0620	0.899	0.0511
1998		0.095	0.0149	0.640	0.0283
1999		0.000	0	0.095	0.0830
2000	0.080	0.062	0.0156	0.045	0.0212
2001		0.076	0.0263	0.145	0.0289
2002	0.886	0.748	0.0653	0.356	0.1522

listed in Table 1 represent the recruitment values when the small and large components of age-group 1 were combined.

All recruitment indices from the present study of the length-density distributions are summarized in Table 1 and are listed according to the year of the cruise. Furthermore, in Tables 2 and 3, these recruitment values are assigned to the year in which these krill were spawned, together with all published results so far on R_1 and R_2.

Both indices R_1 and R_2 vary substantially between years. Recruitment failure was observed for year-classes 1982/1983, 1983/1984, 1988/1989, 1991/1992 and 1997/1998, contributing less than 1% to the numerical total stock size. Extremely successful year classes were spawned in 1994/1995 and 2000/2001, when the recruiting age-class 1 made up more than 60% of the total krill stock, and in 1995/1996 when absolute densities of age-class 1 were similar to the 1994/1995 year

Table 2 Proportional recruitment at age 1 (R_1) of *Euphausia superba* in different areas. R_{SL} values from the present study in the northern Bellingshausen Sea (see also Table 1) are given in *parentheses*

Year-class	Indian Ocean (de la Mare 1994b)	Central Bellingshausen Sea (Siegel and Harm 1996)	Northern Bellingshausen Sea (present study)	Elephant Island (Siegel et al. 2002)	South Georgia (Watkins 1999)	Eastern Scotia Sea (Siegel et al. 2003)
1975/1976						
1976/1977				0.048		
1977/1978						
1978/1979						
1979/1980	0.167			0.559		
1980/1981	0.001			0.757		
1981/1982				0.470		
1982/1983	0.016			0.030		
1983/1984	0.528		0.000	0.0001		
1984/1985				0.175		
1985/1986	0.025					
1986/1987			0.175 (0.182)	0.156		
1987/1988				0.651		
1988/1989			0.000	0.057	0.013	
1989/1990	0.314			0.099	0.007	
1990/1991				0.375		
1991/1992	0.064		0.005	0.000	0.038	
1992/1993		0.076	0.088	0.068	0.075	
1993/1994			0.267 (0.281)	0.046		
1994/1995	0.303[a]		0.639 (0.852)	0.622	0.682	
1995/1996			0.147 (0.436)	0.198	0.179	
1996/1997			0.095	0.120	0.164	
1997/1998			0.000	0.000		
1998/1999			0.062 (0.080)	0.000		0.600
1999/2000			0.076 (0.056)	0.573		
2000/2001			0.748 (0.886)			

[a]Nicol et al. (2000).

Table 3 Proportional recruitment at age 2 (R_2) of *Euphausia superba* in different areas. Indices given by Kawaguchi et al. (1997) are derived from commercial trawl samples

Year-class	Indian Ocean (de la Mare 1994b)	Northern Bellingshausen Sea (present study)	Elephant Isl. (Siegel et al. 2002)	Elephant Isl. (Kawaguchi et al. 1997)	Livingston Isl. (Kawaguchi et al. 1997)	South Georgia (Watkins 1999)
1975/1976			0.144			
1976/1977						
1977/1978						
1978/1979	0.096		0.069	0.451	0.336	
1979/1980	0.561			0.086	0.000	
1980/1981					0.462	
1981/1982	0.557		0.663	0.427	0.585	
1982/1983	0.431	0.008	0.001	0.142	0.156	
1983/1984			0.214	0.072	0.147	
1984/1985	0.231			0.165	0.191	
1985/1986		0.018	0.633	0.334	0.316	
1986/1987			0.291	0.360	0.194	
1987/1988		0.323	0.275	0.000	0.000	0.49
1988/1989	0.556		0.063	0.000	0.000	0.95
1989/1990			0.345	0.083		
1990/1991	0.02	0.630	0.587	0.129	0.574	0.30
1991/1992		0.049	0.012	0.169	0.719	0.62
1992/1993		0.177	0.029	0.000	0.000	
1993/1994	0.476[a]	0.495	0.125	0.000	0.058	0.75
1994/1995		0.899	0.837			0.66
1995/1996		0.640	0.384			0.66
1996/1997		0.095	0.000			
1997/1998		0.045	0.000			
1998/1999		0.145	0.357			
1999/2000		0.356				

[a]Nicol et al. (2000).

class (Quetin and Ross 2003). Generally, the recruitment index of 2-year-old krill (R_2) was higher than the R_1 values, but the standard error of the R_2 estimates was also much higher. This observation has already been made and discussed in Siegel et al. (1997) in reference to the Elephant Island survey area.

Recruitment estimates from the present study were compared with those published from other areas. All R_1 data came from research surveys using scientific nets. A non-parametric correlation analysis was carried out between recruitment values from the northern Bellingshausen Sea, Elephant Island, South Georgia and the Indian Ocean. Results of the analyses (Table 4) show significant positive correlations for R_1 recruitment between the northern Bellingshausen Sea, Elephant Island and South Georgia. Krill recruitment in the Indian Ocean was not correlated to any of these areas in the Atlantic sector. The same observations held for the R_{SL} recruitment values.

Results for the 2-year-old krill (R_2) were slightly different. We still found no correlation in recruitment between the Atlantic and Indian Ocean survey sites, but the former correlation between South Georgia and the Antarctic Peninsula mesoscale surveys no longer existed. The only significant correlation remaining was between Bellingshausen Sea and Elephant Island. Interestingly, the recruitment data from the commercial trawls were not correlated to any other region except between themselves for the adjacent areas of Elephant and Livingston Islands. As mentioned above, 2-year-olds are usually 35–37 mm on average. Commercial trawls show a high degree of net selectivity, with an L_{50} value of 33 mm and an underestimation of length classes up to 40 mm. Quantitative analyses of relative frequencies of these size groups from commercial trawls are therefore doubtful (Klages and Nast 1981) and this difference probably explains the deviation from the results of the scientific nets with smaller mesh sizes.

The relationships between the recruitment indices from various regions can be described with linear regressions. The regression lines for R_1 values are given in Fig. 4. The slope (b) of the regression line Elephant Island versus Bellingshausen is slightly below 1, indicating that the Elephant Island R_1 index is generally lower than the Bellingshausen estimate. The slope of the regression line South Georgia versus Bellingshausen is close to 1, but this should not be overemphasized, since the number of observations is relatively low. Adding the small-size component with the use of the R_{SL} index in the regression analysis does not improve the slope of the regression line; instead, the deviation between the the other regions and Bellingshausen R_{SL} becomes greater (R_{1EL} vs $R_{SL\ Bell}$: $a=0.003$, $b=0.6487$ and R_{1SG} vs $R_{SL\ Bell}$: $a=0.0181$, $b=0.7018$ with $a=$ intercept and $b=$slope). This indicates that the small-size fraction of the 1-year-olds is confined to the Bellingshausen survey site.

In earlier studies, the observed R_2 index for a given year class was generally higher than the relevant R_1 estimate. We therefore plotted the R_2 against the R_1 values from the Bellingshausen surveys. The slope of the regression line is clearly above 1, indicating that the R_2 values are well above the R_1 estimates. When we include the small-size component again, and plot R_{SL} against

Table 4 Statistical table of the non-parametric correlation analyses for krill recruitment indices (R_1 and R_2) from different areas. R_2 indices derived from commercial trawls are indicated by (*com*)

Areas	Valid *N*	Kendall Tau	*Z*	*P*-level
R_1				
Bellingshausen vs Indian Ocean	4	−0.547	−1.116	0.2642
Bellingshausen vs Elephant Isl.	12	0.444	2.011	0.0442
Bellingshausen vs Elephant Isl.[a]	12	0.539	2.442	0.0145
Bellingshausen vs South Georgia	6	1.000	2.818	0.0048
Elephant Isl. vs Indian Ocean	7	−0.238	−0.751	0.4526
Elephant Isl. vs South Georgia	7	0.619	1.952	0.0508
South Georgia vs Indian Ocean	3	−0.333	−0.522	0.6015
R_{SL}				
Bellingshausen vs Elephant Isl.	12	0.571	2.586	0.0097
Bellingshausen vs South Georgia	7	1.000	2.818	0.0048
R_2				
Bellingshausen vs Indian Ocean	3	−0.333	−0.522	0.6015
Bellingshausen vs Elephant Isl.	12	0.473	2.142	0.0321
Bellingshausen vs Elephant Isl. (*com*)	7	−0.411	−1.298	0.1944
Bellingshausen vs Livingston (*com*)	7	0.000	0.000	1.0000
Bellingshausen vs South Georgia	6	0.138	0.389	0.6970
Elephant Isl. vs Indian Ocean	6	0.666	0.187	0.8510
Elephant Isl. vs Elephant Isl. (*com*)	13	0.266	1.270	0.2040
Elephant Isl. vs Livingston (*com*)	12	0.264	1.193	0.2328
Elephant Isl. vs South Georgia	7	−0.293	−0.923	0.3558
Elephant Isl. (*com*) vs Indian Ocean	8	−0.255	−0.882	0.3778
Elephant Isl. (*com*) vs Livingston (*com*)	14	0.659	3.282	0.0010
Elephant Isl. (*com*) vs South Georgia	5	−0.359	−0.878	0.3797
Livingston (*com*) vs Indian Ocean	8	0.546	−1.889	0.0588
Livingston (*com*) vs South Georgia	5	−0.316	−0.775	0.4385
South Georgia vs Indian Ocean	3	1.000	1.566	0.1172

[a]Correlation analysis was calculated with different values for the Elephant Island data set (see Table 2).

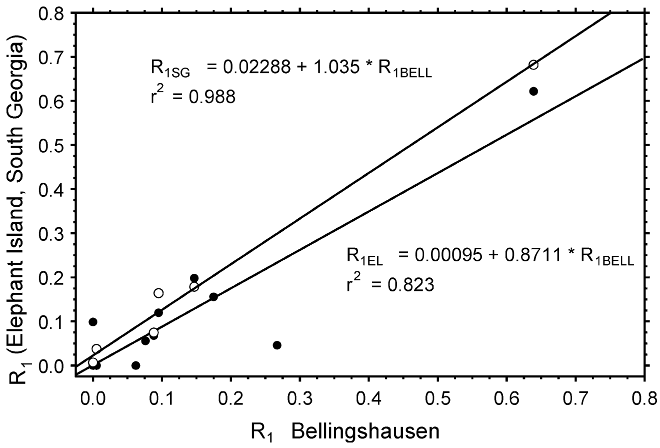

Fig. 4 Recruitment index of 1-year-old krill from Elephant Island (R_{1EL} *filled circles*) and South Georgia (R_{1SG} *unfilled circles*), respectively, plotted against recruitment of 1-year-olds from the northern Bellingshausen Sea

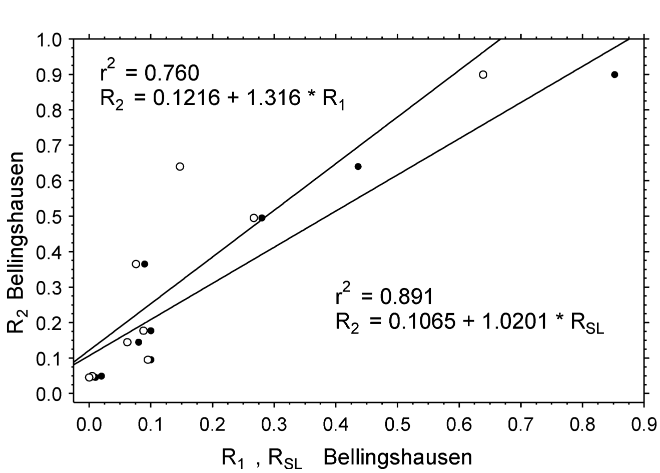

Fig. 5 Recruitment index of 2-year-old krill (R_2) plotted against large (R_1) (*unfilled circles*) and small and large-sized (R_{SL}) 1-year-old krill recruits from the Bellingshausen Sea

R_2, then the slope of the regression line is very close to 1 and the correlation coefficient increases substantially (Fig. 5). In this case, the proportion of 1-year-olds would be almost identical to 2-year-olds in the Bellingshausen population.

Discussion and conclusions

During austral summer, the first mode of krill length-frequency distributions usually represents a unimodal distribution of the juvenile developmental stage (Hosie et al. 1988; Siegel 1988; Pakhomov 1995; Wang et al. 1995). However, in some areas and years a much smaller mean length or even a bimodal distribution pattern was observed for this age component (Nast 1982; Siegel 1988; Siegel et al. 1990; Melnikov and Spiridonov 1996). Prior to this study, all such data were recorded from areas in close vicinity to or even within perennial sea ice.

In the present data set, bimodal length frequencies for age-class 1 do not occur in all years, but mainly in those years with a high abundance of juvenile recruits. Possibly, in such years, conditions are favourable enough to allow successful spawning and larval development even in the permanent pack-ice region. The composite length-frequency distribution given by Siegel et al. (1990) for the northwestern Weddell Sea showed a clear bimodal juvenile size distribution. In early spring, generally larger krill were found in the marginal ice zone, and smaller krill were in the more southerly closed pack-ice zone. From these data and the spatial distribution pattern, Siegel et al. (1990) concluded that the two different juvenile size groups had a different geographical origin (Peninsula vs Weddell Sea). Nast (1982) observed 18-mm-modal-size juvenile krill in the marginal ice-zone of the northern Weddell Sea during the FIBEX cruise in January/February 1981. Melnikov and Spiridonov (1996) sampled krill in the western Weddell Sea during austral summer 1994 and found, almost exclusively, the small component of the age-class 1 krill in this permanent pack-ice region with a mean total length of 12–14 mm. These krill were undoubtedly advected within the western branch of the Weddell Gyre.

Similar size classes were sometimes found on the shelf of the tip of the Antarctic Peninsula (e.g. in 1987/1988) and are now recorded from the LTER study region, which in some years is in close proximity to the perennial sea ice of the Bellingshausen Sea. However, this bimodality in the length data of the juvenile 1-year-old krill does not seem to be carried on into the second age class, because we never observed a bimodal length-frequency distribution pattern for the generally 2-year-old subadults in the year following their occurrence as undersized juveniles.

This phenomenon of undersized juvenile krill may be locally restricted and the small-size groups disappear from the study area with the retreating pack ice, or survival of these krill with retarded growth is poor and few manage to survive the next winter into their 2nd year of life. In these instances, undersize juvenile krill will not contribute substantially to later subadult stock, and even more importantly, to the spawning stock. Based on these scenarios, undersized juvenile krill should be eliminated from the recruitment index. Alternatively, the two modes of juvenile krill are the results of pulses in spawning, and after 2 years of growth they merge into one mode. Under this scenario, the smaller mode of juveniles contributes to the spawning stock and elimination of the smaller mode of age-class 1 krill underestimates R_1.

From the published results and the analysis presented here, it is obvious that the proportional recruitment indices for 1 (R_1) and 2-year-old (R_2) krill differ substantially between years and regions. Furthermore, it is obvious that, in most cases, the R_2 values are larger than R_1. Finally, the R_2 estimates vary far more—even between adjacent areas—than the R_1 values do (normally not more than 5%).

Interestingly, R_1 correlations between areas are more far-reaching than for R_2 indices. This may be a result of the less accurate estimates of R_2, which may negatively affect any correlation coefficient. However, older age classes also have a slightly different distribution pattern than younger juveniles (see discussion by Siegel et al. 1997), which may also partly explain why the correlation between the Antarctic Peninsula and South Georgia vanishes for the 2-year-olds. Additionally, South Georgia is—at least from time to time in some years—under the influence of krill advected from the Weddell Sea (Siegel et al. 2003). The longer the time and further away recruits are from their place of birth, the greater the chance that the stock composition downstream is modified by mixing with krill that experienced a different life history, e.g. higher mortality rate or growth rates. This seems to be true specifically for the Scotia Sea and may be a possible scenario for the Bellingshausen Sea, too.

However, when the small-size component of the 1-year-old krill of the Bellingshausen Sea was introduced into the regression analysis, it became clear that this "undersized" component seems to be restricted to the Bellingshausen Sea. The inclusion of the small krill did not improve the regression results between the Bellingshausen site and Elephant Island and South Georgia, respectively. However, the discrepancy between R_1 and R_2 almost vanished in the Bellingshausen Sea when we included the small-size component in the estimate of R_1, which we called here R_{SL}. This observation favours the idea that we should treat the small-size component as a genuine part of the 1-year-old recruits in the Bellingshausen Sea.

One might assume that these size classes do not play a part in the general northeasterly drift along the Antarctic Peninsula, which usually carries the larger juveniles to the South Shetland Islands and to South Georgia. The smaller-size component could remain in more nearshore waters or in proximity to pack ice, which may act as a retention area. Here they grow into their 2nd year of life. As 2-year-olds, they could then move further offshore, come under the influence of the northeasterly drift and appear around Elephant Island in summer as R_2 recruits. This would at least explain the higher correlation coefficient and the congruence between R_{SL} of the Bellingshausen Sea and R_2 from the Bellingshausen Sea and Elephant Island, respectively. This described possibility is still hypothetical, and the time series is still too short to decide on one of the various options. Variability in recruitment indices is very high, and as is apparent from Figs. 4 and 5, we need more data from years with high recruitment indices in particular, to get a more precise view of the recruitment relationships between the various regions or between the various age groups in one region.

One side effect of the correlation analysis was the identification of a single R_1 value from Elephant Island that clearly fell outside the estimates of adjacent areas. Usually the difference between the estimates of the Atlantic-sector sites did not differ by more than 5% in a given year. In January 2001, R_1 from the Elephant survey was 0.573, which is considerably greater than the $R_1 = 0.076$ estimate from the Bellingshausen Sea. This high value in the Elephant Island region was estimated from a survey grid extended south to the coast of the Antarctic Peninsula. The argument to extend the grid during the 2001 Polarstern cruise had been the incomplete coverage of the possible juvenile distribution range and the potential underestimation of the recruitment index R_1 during earlier surveys with a southern extension of transects to only 61°45′S. If only the standard station grid is considered (see Tables 2 and 4), the recalculated R_1 equals 0.056 for the 1999/2000 year class. Although the correlation (Bellingshausen to Elephant) was significant using the high recruitment index of the larger survey grid, the Elephant Island recruitment was in much closer conformity to the Bellingshausen value when replacing the data with the lower value from the original station grid. During the 2001 survey, the relative large mean size of the first component of the distribution mixture (27 mm) led to the conclusion that these krill were obviously of Peninsula and not of Weddell Sea origin. However, the current Bellingshausen R_1 result and the highly significant correlation between the Bellingshausen Sea and Elephant Island suggest that the majority of the juveniles in the extended grid during the 2001 Polarstern cruise were possibly krill from the Weddell Sea. The result of the Bellingshausen R_2 estimate does not clarify the issue, because the R_2 value from the Bellingshausen Sea is intermediate between the extremes of a high R_1 from the extended and the low R_1 from the standard Elephant Island survey.

New information gained from the 2001 Polarstern cruise to Elephant Island, which was not available during the analysis of the 2001 krill data, showed a very high density of *E. crystallorophias* above the shelf of the northern tip of the Peninsula. The high abundance of ice-krill in the area supports the idea of a stronger influence of the Weddell Sea on the shelf of the Peninsula and a different origin for the juvenile krill found here compared to the juveniles found further north in the Bransfield Strait and around Elephant Island. However, a final conclusion cannot be drawn from the information presently available and further analyses from consecutive years are required to properly estimate the R_2 recruitment and the proportion of recruits of Weddell and Bellingshausen origin.

In general, the present analysis strongly supports the hypothesis that indices derived from mesoscale surveys can describe the krill annual recruitment process for much larger regions (e.g. Bellingshausen Sea—Elephant Island—South Georgia). If, however, this large area contains more than one krill stock, then the mesoscale surveys provide a reasonable estimate only for a single stock. The boundaries between potential stocks (e.g. Weddell-Scotia boundary), as well as between larger regions (Atlantic-Indian Ocean sector), and their interannual variability in boundary locations are as yet unclear and to be determined. Further research is needed to reveal the role and the influence of the "undersized" age-1 group fraction on the spawning stock. The question to be answered is whether this is simply a local phenomenon of the perennial pack-ice zone or is it a question of survivorship and/or growth at the extreme end of the krill niche. This will provide us with the answer as to whether the small-size mode of a cohort has an impact on the development of the future stock size.

Acknowledgements This work would not have been possible without the many people spending weeks at sea year after year, collecting and measuring samples. We thank all our colleagues for their great assistance during the past years of the survey time-series. We also thank Drs. S. Kawaguchi (AAD), F. Litvinov (AtlantNIRO) and one anonymous referee for their constructive comments to improve the manuscript. Some material for this study is based upon work supported by the National Science Foundation, Office of Polar Programs, under Award nos. OPP-9011927 and OPP-9632763, the Regents of the University of California, the University of California at Santa Barbara, and the Marine Science Institute, UCSB. This is Palmer LTER contribution no. 241.

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