

Electrophoretic Investigation of Genetic Variation in Two Krill Species Euphausia superba and E. crystallorophias (Euphausiidae)

S. Kühl and R. Schneppenheim

Institut für Polarökologie, Christian-Albrechts-Universität Kiel, Olshausenstrasse 40 - 60, D-2300 Kiel, Federal Republic of Germany

Received 29 July 1985; accepted 11 December 1985

Summary. Specimens of Euphausia superba and of E. crystallorophias from different locations were analyzed electrophoretically for protein variation. The present study extends previous genetic studies on E. superba by analyzing samples from the East Wind Drift and repeat samples from the Bransfield Strait, Elephant Island and the Weddell Sea. E. crystallorophias was collected in the Weddell Sea and around the Antarctic Peninsula in order to provide information on the breeding structure of the species in this region. For all loki taking all sampling sites together for both species except GPI in E. crystallorophias no significant deviation of phenotype distributions from random mating expectations was observed. Furthermore, the allele distributions in all polymorphic loci for both species were found to be homogeneous. Estimates of genetic distance between samples within each species are low (0.0001 to 0.0003 in E. superba and 0.0001 to 0.0002 in E. crystallorophias), and are consistent with results expected for samples from a single interbreeding population. Estimate of genetic distance between these two species was 0.9729. These results suggest that for each species specimens from all locations investigated in the Bransfield Strait and Weddell Sea belong to a single genetically homogeneous population. A possible mechanism for maintaining such homogeneity and the implications for fishery management are discussed.

Introduction

Euphausiids are amongst the most abundant zooplankters in the Southern Ocean. The krill *Euphausia superba* assumes a key role in the Antarctic marine ecosystem and has a considerable potential for commercial exploitation. In localized areas around the Antarctic continent *Euphausia crystallorophias*, known as "ice krill", replaces *E. superba* with respect to abundance and its role in the marine food chain. *E. crystallorophias* is a neritic species, being confined to Antarctic shelf waters. It is most often found in the vicinity of shelf ice (Mauchline and Fisher 1969).

Information on the population structure of these euphausiids is of vital importance in the development of rational management plans for any future large scale fishery, as well as for a more general understanding of the Antarctic marine ecosystem. Recent studies of the breeding structure of E. superba have been carried out using electrophoretic analysis of enzymatic proteins to estimate genetic variation. Fevolden and Ayala (1981) and Anderson (1982) reported genetic differences between E. superba from the western side of the Antarctic Peninsula and those from the Weddell Drift (Fig. 1) indicating the presence of at least two discrete breeding populations. Schneppenheim and MacDonald (1984), however, did not find differences between samples collected from similar areas and from the Scotia Sea. Preliminary analysis of E. superba from the Prydz Bay region (MacDonald and Schneppenheim 1983) indicates no evidence of breeding isolation within this region or between the Indian Ocean and Atlantic sectors of Antarctic waters.

It is clear that further studies are required to determine the number and distribution of *E. superba* breeding populations. MacDonald and Schneppenheim (1983) have pointed out that the sampling must be carried out across the entire distribution of the species and should be repeated over time at some locations in order to develop an adequate appreciation of the spatio-temporal distributions of breeding population. The present study extends previous work on *E. superba* by analyzing samples from the East Wind Drift and by comparing these data with those obtained from repeat samples from the Bransfield Strait, Weddell Sea and Elephant Island (Fig. 1).

Only one genetic study of *E. crystallorophias* has been conducted to date (Fevolden and Ayala 1981) and as only one sample was analyzed no information on breeding structure in this species is available. Therefore, collections of *E. crystallorophias* have been made in the Weddell Sea and around the Antarctic Peninsula.

Materials and Methods

Samples of *E. superba* and *E. crystallorophias* were collected during three cruises:

a) Filchner-Schelfeis-Expedition 1980/81 on board MS Polarsirkel (Kohnen 1982) – station no. 279

b) Joint Biological Expedition 1982 on board *RRS John Biscoe* (Hempel and Heywood 1982) – stations no. 1137 and 1274

c) Antarktis-I-Expedition 1983 on board FS Polarstern (Drescher et al. 1983) – stations no. 130/2, 191 and 249

One sample of *E. superba* (DFB 83) was collected by courtesy of Dr. F. Buchholz during his stay at the Polish base Arctowsky in 1983.

E. superba sample no. 1274 includes material already analyzed electrophoretically as sample no. 9 by Schneppenheim and MacDonald (1984). However, the present study uses additional specimens from this station. *E. superba* sample no. 1132 is identical with Schneppenheim and MacDonald's sample no. 1 and was only analyzed additionally for the locus LDH_I by means of isoelectric focusing, a technique which was not previously applied.

A total of 1044 *E. superba* specimens from five locations and 612 *E. crystallorophias* specimens from four locations (Fig. 1) were electrophoretically analyzed. Collected specimens were processed and, with one exception, stored at -80 °C as described by Schneppenheim and MacDonald (1984). The sample collected at station no. 279 of the *Polarsirkel* cruise was initially stored at -30 °C to -40 °C during the expedition and then transferred to a -80 °C freezer in the laboratory. Preparation of samples, electrophoresis on cellulose acetate medium, histochemical staining procedures and the interpretation of electrophore mand MacDonald (1984). Electrophoretic conditions and staining mixtures for the three additional enzymes developed during the present study are given in Table 1.

A polymorphism at the *LHD*₁ locus of *E. superba* was detected using isoelectric focusing (IEF) on 12.5×25 cm agarose gels with a pH gradient from 5.0 to 8.0. The gel recipe, focusing conditions and the staining procedures are given in Schneppenheim et al. (1984).

Results

Electrophoresis and Isoelectric Focusing

In *E. superba* 16 enzymatic proteins were electrophoretically screened, from which a total of 15 loci could be reliably scored. Seven loci were monomorphic (*MDH; ME; IDH*₁; *IDH*₂; *PK*₁; *PK*₂; *ACON*₂) while eight loci were polymorphic at the $P \leq 0.99$ level for the most common allele (*LDH*₁; *LDH*₂; *AAT*₁; *ALAT*; *PGM*; *GDA*₂; *MPI*; *GPI*). A zymogram of *LDH*₁ and *LDH*₂ obtained by isoelectric focusing instead of cellulose acetate electrophoresis is shown in Fig. 2. *LDH*₁ heterozygotes showed the typical five-banded pattern of a tetrameric enzyme and *ALAT* heterozygotes displayed a threebanded dimeric pattern. Zymograms for the other polymorphic proteins and their proposed subunit structure have been represented by Schneppenheim and MacDonald (1984).

For *E. crystallorophias* six of 17 reliably scored loci were polymorphic at the $P \leq 0.99$ level for the most common allele (*MDH; PGD; AAT₂; PGM; MPI; GPI*). The remaining 11 loci were monomorphic (see Table 2).



Fig. 1. Sampling stations for *E. superba* (\blacktriangle) and for *E. crystallorophias* (\blacklozenge) in the Weddell Sea, Bransfield Strait and adjacent waters; *blank arrows* indicate direction of the East Wind Drift; *filled arrows* the direction of the West Wind Drift

Table 1. Electrophoretic buffers and staining mixtures for Euphausiid enzymes. Recipes for additional enzymes are given by Schneppenheim and MacDonald (1984)

Enzyme	Electr. buffer	Staining buffer	Substrate	Coenzyme	Staining reagent	Activator	Linking enzyme
HK Hexokinase (EC 2.7.1.1)	ТЕВ рН 8.5	1 ml 0.1 M tris/HCl pH 8.0	0.1 ml glucose (40 mg/ml) 0.1 ml ATP disodium salt (20 mg/ml)	0.1 ml NADP (20 mg/ml)	0.1 ml PMS (4 mg/ml) 0.1 ml MTT (8 mg/ml)	0.1 ml 1 M MgCl ₂	2 I.U. glucose-6- phosphat dehy- drogenase
CK Creatin kinase (EC 2.7.3.2)	a) TEB pH 8.5 b) TEM pH 7.8	1 ml 0.1 M tris/HCl pH 8.0	0.1 ml phosphocreatine disodium salt (20 mg/ml) 0.1 ml ADP sodium salt (20 ng/ml) 0.1 ml glucose (40 mg/ml)	0.1 ml NADP (20 mg/ml)	0.1 ml PMS (4 mg/ml) 0.1 ml MTT (8 mg/ml)	0.1 ml 1 M MgCl ₂	2 I.U. glucose-6- phosphat dehy- drogenase2 I.U. hexo- kinase
ACON Aconitase (EC 4.2.1.3)	TEM pH 7.8	1 ml 0.1 M tris/HCl pH 8.0	0.1 ml cis-aconitate (25 mg/ml)	0.1 ml NADP (20 mg/ml)	0.1 ml PMS (4 mg/ml) 0.1 ml MTT (8 mg/ml)	0.1 ml 1 M MgCl ₂	2 I.U. isocitrate dehydrogenase



Fig. 2. LDH phenotypes in E. superba detected by IEF in agarose gels (pH gradient 5-8)

Distribution of Phenotypes

No significant deviations from random mating expectations – according to the Hardy Weinberg principle (Hardy 1908) – were observed in any locus except *GPI* in *E. crystallorophias*. For *GPI* there are significant deviations from Hardy Weinberg equilibrium in sample 1207 ($\chi^2 = 4.75$, 0.05 > P > 0.02, significant at the P = 0.05 level) and 279 ($\chi^2 = 7.00$, 0.01 > P > 0.001, significant at the P = 0.05 level). In both cases these deviations are due to an excess of heterozygotes. *GPI* is an easy locus to score electrophoretically, and it is unlikely that the deviant phenotype distributions are a result of experimental error in typing the gel.

A possible explanation for the observed deviations is that at least some of the heterozygous GPI phenotypes are selectively advantageous to the survival of individuals that possess them. The lack of deviation in samples 1180 and 191 may merely indicate that the stocks from which these samples came were not subject to the selective pressure that produced the deviations in the other samples. In any case these results do not effect conclusions concerning breeding structure in *E. crystallorophias*.

Distribution of Alleles

Allelic frequencies for all polymorphic loci in both species are listed in Table 2. Application of χ^2 -contingency tests indicate that allelic frequency distributions at all loci in both species are homogeneous within the limits of sampling error.

Genetic Variation, Identity and Distance

Mean heterozygosity per locus (\overline{H}) was calculated for each sample set and as a measure of overall genetic variation in each species (Table 3). The estimate of \overline{H} for *E*. *superba* (0.118 ± 0.031) is in accordance with the estimate of Schneppenheim and MacDonald (1984). In fact, they calculated the mean individual heterozygosity, but if the same loci of each individual are analyzed the resulting values ought to be roughly identical (for explanations

Table 2. Allelic frequencies and frequency of heterozygotes. n = number of genes sampled

			E. superba					E. crystallorophias				
Locus a	lleles	Station 130/2	1274	249	DFB 83	1132	Total	1180	1207	279	191	Total
LDH ₁	n 76 90 100 125 H	100 0.010 - 0.720 0.270 0.400	100 - 0.010 0.710 0.280 0.500	100 0.010 0.730 0.260 0.300	100 - 0.710 0.290 0.340	100 0.720 0.280 0.320	500 0.004 0.002 0.718 0.276 0.372	100 1.000 	100 - - 1.000 -	100 1.000 	100 1.000 	400 - - 1.000 -
LDH ₂	n 76 82 100 112 124 H	568 0.007 0.023 0.965 0.005 0.067	494 0.008 0.982 - 0.002 0.036	324 0.012 0.012 0.969 0.006 - 0.049	600 0.018 0.008 0.967 0.007 - 0.067		1986 0.012 0.013 0.971 0.005 0.001 0.005	100 1.000 	100 1.000 	100 g 1.000 	, 100 - - 1.000 - - -	400 1.000
MDH	n 76 83 100 109 H	100 1.000 	100 1.000 	100 1.000 -	100 1.000 		400 1.000 	298 0.003 0.003 0.977 0.017 0.047	312 - 0.990 0.010 0.020	208 - 0.003 0.990 - 0.019	390 0.982 0.018 0.036	1208 0.001 0.003 0.984 0.012 0.031
ME ₂	n 100 H	100 1.000 -	100 1.000 -	100 1.000 -	100 1.000 —		400 1.000 -	100 1.000 	100 1.000 -	100 1.000 -	100 1.000 -	400 1.000 -
IDH ₁	n 100 H	100 1.000 -	100 1.000 	100 1.000 -	100 1.000 -		400 1.000 -	100 1.000 -	100 1.000 -	100 1.000 -	100 1.000 	400 1.000 -
IDH ₂	n 100 111 H	100 1.000 -	100 1.000 -	100 1.000 - -	100 1.000 		400 1.000 -	100 1.000 	100 - 1.000 -	100 - 1.000 -	100 1.000 	100 - 1.000 -
PGD	n 90 100 110 120 H							292 - 0.860 0.137 0.003 0.267	328 0.869 0.128 0.003 0.238	- - - -	390 0.003 0.813 0.174 0.010 0.313	1010 0.001 0.845 0.149 0.006 0.275
AO _I	п 100 Н							100 1.000 -	100 1.000 	100 1.000 -	100 1.000 -	400 1.000 -
AO ₂	n 100 H							100 1.000 -	100 1.000 	100 1.000 -	100 1.000 -	400 1.000 -
AAT _I	n 73 80 91 100 109 118 H	566 0.419 0.530 0.049 0.002 0.548	494 0.419 0.553 0.028 0.498	324 - 0.451 0.512 0.037 - 0.481	600 0.005 0.420 0.527 0.048 0.527		1984 0.001 - 0.427 0.531 0.041 0.001 0.514	100 	100 1.000 	100 1.000 	100 1.000 	400 1.000
AAT ₂	n 88 100 109 112 H							298 0.003 0.742 0.124 0.131 0.430	328 0.009 0.732 0.095 0.165 0.457	- - - -	390 - 0.721 0.138 0.141 0.415	1016 0.004 0.730 0.102 0.146 0.433

		E. superba				E. crystallorophias					
Locus a	lleles	Station 130/2	1274	249	DFB 83	Total	1180	1207	279	191	Total
ALAT	n	568	494	324	600	1986	100	100	100	100	400
	92	0.012	0.004	_	0.002	0.005	_	-	-		_
	96	_	0.014	0.006	0.008	0.007	_	_	_	—	
	100	0.972	0.976	0.985	0.988	0.980	1.000	1.000	1.000	1.000	1.000
	106	0.010	0.004	0.009	0.002	0.006	-	-	-	_	-
	112	0.005	0.002	-		0.002	-	-	-	-	-
	н	0.056	0.049	0.031	0.023	0.040	_		_		-
PK,	п	100	100	100	100	400					
• ••1	100	1.000	1.000	1.000	1.000	1.000					
	Н	_	_	_	_	_					
DK		4.00	100	100	100	400	100	100	100	100	400
PK_2	n	100	100	100	100	400	100	100	100	1.000	400
	90	1.000	1 000	1 000	1 000	1,000	1.000	1.000	1.000	1.000	1.000
	100 LI	1.000	1.000	1.000	1.000	1.000		-		_	_
	п	-	_	-	—	-	-	-	-	-	_
PGM	n	568	494	324	600	1986	292	328	208	384	1212
	92	_	0.002	0.019	0.016	0.007	0.048	0.043	0.043	0.040	0.043
	100	0.938	0.956	0.923	0.935	0.934			0.010	0.005	0.003
	102	—	—	-	-	-	0.003	0.006	0.005	0.003	0.004
	104	0.002	-	-	-	0.001	-	—	_	-	-
	108	0.053	0.043	0.052	0.053	0.050	0.949	0.045	0.928	0.930	0.940
	112	0.007	_	0.006		0.003	-	0.006	0.014	0.018	0.010
	Н	0.116	0.089	0.154	0.120	0.120	0.089	0.110	0.135	0.120	0.112
GDA_{2}	n	568	390	324	600	1882	100	100	100	100	400
-	92	0.011	0.005	0.003	_	0.005	_	_	_	_	_
	96	0.004	0.018	0.015	0.007	0.011	<u>·</u>		_	-	_
	100	0.943	0.912	0.948	0.942	0.939	1.000	1.000	1.000	1.000	1.000
	104	0.041	0.026	0.028	0.042	0.034	-	—	-	-	
	108	0.002	0.039	0.006	0.010	0.014	-	-	-	-	-
	Н	0.106	0.164	0.093	0.117	0.120	-	-	-	-	-
ACON	. n	100	100	100	100	400					
110017	100	1.000	1.000	1.000	1.000	1 000					
	н	_	_	_	_	_					
1 (51			40.4		600	1001			••••		
MPI	n	208	494	324	600	1986	296	328	208	390	1222
	80	-	-	-	-	-	0.003	-	_	_	0.001
	84	0.002	-	- 0.021	- 0.015	0.001	-	-	-	- 0.044	- 0.041
	92	0.032	0.028	0.031	0.015	0.026	0.047	0.024	0.058	0.041	0.041
	100	0.007	0.010	0.005	0.013	0.011	0.021	0.031	0.657	0.800	0.823
	100	0.930	0.925	0.003	0.028	0.931	0 125	0 1 2 5	0,105	0.154	0 1 2 1
	104	0.025	0.010	0.005	0.020	0.016	0.125	0.125	0.105	0.134	0.151
	112	-	-	_	_	0.010	0.003	_	_	0.005	0.002
	H	0.127	0.150	0.093	0.130	0.125	0.005	0 226	0.288	0.354	0.002
			40.1		~~~~	0.120	J.471	0.220	0.200	0.004	0.275
GPI	n	568	494	324	600	1986	298	328	208	390	1224
	80	-	-	_	-	-	0.007	0.009	0.005	0.008	0.007
	88	0.005	0.002	0.003	0.012	0.006	0.584	0.588	0.615	0.615	0.600
	100	0.625	0.646	0.627	0.630	0.632	0.409	0.399	0.370	0.374	0.389
	112	0.357	0.346	0.358	0.348	0.352	_	0.003		0.003	0.002
	136	0.002	-	0.003	-	0.001	-	-	-	-	-
	п	0.438	0.490	0.488	V.40/	0.481	0.537	0.573	0.606	0.487	0.542

concerning the differences in the standard errors see Fevolden and Ayala 1981). Their estimate of 0.099 ± 0.025 for the Atlantic Sector is similar to the value of Schneppenheim and MacDonald (1984) and our's. The comparison between samples of the Pacific and Atlantic Sectors is discussed by Schneppenheim and MacDonald. For *E. crystallorophias*, we found the same value as Fevolden and Ayala but with a higher standard error, due to the smaller number of loci examined.

As a further measurement of genetic differentiation pairwise comparisons of genetic identity and genetic distance between sample sets in each species (Tables 4 and 5) were calculated according to the method of Nei (1972). Sample 279 (*E. crystallorophias*) was excluded from genetic distance calculations because of the reduced number of loci screened (12) compared to other sample. In both species over 99% of observed allelic variation was common to each sample. Conversely, very small genetic

Table 3. Average heterozygosity (averaged over loci), \bar{H} and standard error, SE

Station	Ĥ	SE	Loci observed
E. superba			· · · · · · · · · · · · · · · · · · ·
130/2	0.125	± 0.048	15
1274	0.132	± 0.051	15
249	0.113	± 0.044	15
DFB 83	0.121	± 0.047	15
Mean	0.118	± 0.031	15
E. crystallord	ophias		
1207	0.096	± 0.043	17
1180	0.098	± 0.042	17
279	0.087	± 0.053	12
191	0.107	± 0.044	16
Mean	0.094	± 0.040	17

Table 4. Genetic distance (above diagonal) and genetic identity (belowdiagonal) between four samples of *Euphausia superba* (according toNei 1972)

Station	130/2	1274	249	DFB 83
130/2		0.0002	0.0002	0.0001
1274	0.9998		0.0003	0.0002
249	0.9998	0.9997		0.0002
DFB 83	0.9999	0.9998	0.9998	

Table 5. Genetic distance (above diagonal) and genetic identity (below diagonal) between three samples of *Euphausia crystallorophias* (according to Nei 1972)

Station	1207	1180	191
1207		0.0002	0.0002
1180	0.9998		0.0001
191	0.9998	0.9999	

distance estimates were found in each species (0.0001 to 0.0003 in *E. superba* and 0.0001 to 0.0002 in *E. crystal-lorophias*). Such low values are characteristic of genetic distance estimates expected between samples from a single interbreeding population.

Allele distributions at each locus were pooled over all samples for each species to provide a measure of genetic divergence between *E. superba* and *E. crystallorophias*. Estimates of genetic identity and genetic distance between these two species were 0.3780 and 0.9729, respectively, values which are similar to previous estimates of genetic divergence between *E. superba* and other members of the genus *Euphausia* (Ayala and Valentine 1979; Fevolden and Ayala 1981).

Discussion

The homogeneous distribution of alleles and electrophoretic phenotypes at eight polymorphic loci and the high values of genetic identity between *E. superba* samples from four different locations in the Southern Ocean sug-

gest that these samples belong to a single genetically homogeneous population which inhabits an area ranging at least from the Pacific side of the Antarctic Peninsula to the Scotia and Weddell Seas. These findings agree with the study of Schneppenheim and MacDonald (1984). Additional krill were analyzed from the eastern Weddell Sea off Cape Norvegia. The allele and phenotype distributions for even this outlying sample indicate no evidence of breeding isolation. Preliminary analyses of E. superba from the Indian Ocean sector of Antarctic waters (MacDonald and Schneppenheim 1983) indicated close genetic homogeneity within the sampled area and furthermore agreed closely with the data of Schneppenheim and MacDonald (1984) and the present study. Such results suggest that there is sufficient gene exchange between E. superba from all locations sampled to date to prevent the development of genetically distinct breeding populations.

There are two electrophoretic studies, however, which report results suggesting the existence of more than one *E. superba* breeding population. Fevolden and Ayala (1981) and Anderson (1982) postulate the existence of two discrete populations originating from the Bellingshausen Sea and the Weddell Sea respectively. This apparent discrepancy in the findings of different studies is discussed in detail by Schneppenheim and MacDonald (1984), and it illustrates the need both for further sampling and for standardized electrophoretic analyses to enable results to be directly compared.

E. crystallorophias is a neritic species and is confined mostly to Antarctic shelf waters. With a more limited distribution than *E. superba*, it would seem reasonable to expect *E. crystallorophias* to have a higher probability of exhibiting breeding isolation. However, little is known about the spawning grounds of this species and about the distribution of its larvae. Hempel et al. (1979) found eggs and nauplii in the western Bransfield Strait. Fevolden (1979) reported larvae in the southern Weddell Sea near the ice barrier in 1977. *E. crystallorophias* larvae have also been found in oceanic sectors of the Weddell Sea (Hempel and Hempel 1982), but the origin of these larvae is still unknown.

The homogeneous allele distributions of all *E. crystallorophias* samples analyzed in this study suggest that these animals were taken from a single interbreeding population. Given the water circulation pattern of the Weddell Sea gyre (Fig. 1) *E. crystallorophias* could indeed disperse between all sampled locations during their lifespan. Moreover, dispersal of ice krill from the Atlantic to the Pacific side of the Antarctic Peninsula is nevertheless quite likely as it is consistent both with the local oceanographic situation (Stein 1982) and with hypothesis on the dispersal of *E. superba* in this area based on recent biological and genetic data (Lubimova et al. 1980; Siegel 1982; Schneppenheim and MacDonald 1984; and this paper).

The Antarctic pelagic environment is under the unique regime of circumpolar currents (Deacon 1937). Such a current pattern would theoretically tend to promote long distance dispersal and circumpolar distributions for many pelagic organisms. The concept of a single circumantarctic breeding population of *E. superba* has proposed by Marr (1962) and discussed further by Everson (1981). However, it has been more fashionable in recent years to hypothesize at least four discrete breeding populations associated with cyclonic current systems in areas such as the Weddell Sea, the Prydz Bay region, the Ross Sea and the Bellingshausen Sea (Mackintosh 1973). Our findings and the results of other recent studies support the single population hypothesis. For its final test, further samples are required from the Ross Sea and the Bellingshausen Sea to complete the investigation.

Corresponding results – a homogeneous allellic frequency distribution in samples of the Antarctic amphipod *Themisto gaudichaudii* from South Georgia Island and the South Shetland Islands respectively suggest the single genetically homogeneous population hypothesis might be accepted for other comparable Antarctic pelagic organisms (Schneppenheim and Weigmann-Haass, in press).

The contribution that genetic studies can make to the development of rational fishery management plans is illustrated to some extent in this study. Our electrophoretic data suggest that E. superba and E. crystallorophias from the investigated area are each genetically homogeneous, and that observed differences in the morphology, growth rate and sexual maturity of stocks in different areas are influenced mainly by prevailing environmental factors such as temperature and food supply (Marr 1962; Mackintosh 1972; Fevolden 1979; Lubimova et al. 1980; Siegel 1982). Intensive local exploitation of krill should therefore result in only a temporary reduction of the stock size in a particular area, as recruiting individuals from other areas could be expected to replenish that stock in time. However the recovery of a depleted stock usually is a complex interaction of several factors, each of which is difficult to predict.

Furthermore, even short term fluctuations in the abundance of krill could precipitate changes in the population size of krill predators such as seals, penguins, whales and fish. Penguin rookeries and seal colonies are limited mainly to ice-covered continental coasts. These animals are dependant on nearby concentrations of krill, and fluctuations in their breeding success and total numbers appear to co-incide with fluctuations in krill availability. Regional aspects should therefore be taken into account for a future krill fishery, which could be better monitored by conventional morphometric methods of population analysis by size and maturity data which reflect the effects of local temperature and food supply.

Acknowledgements. We gratefully acknowledge the technical assistance of G. Janssen, the logistic support of the Alfred-Wegener-Institute and the many people who were involved in collecting material. We are very much indebted to Prof. Hempel, Dr. MacDonald and Dr. Grant for their valuable comments on the manuscript and Dr. Dieckmann for correcting the English version. This publication includes parts of the Ms thesis of S. Kühl.

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