Winter in a Svalbard Fiord Ecosystem

J.M. WESLAWSKI,[1] S. KWASNIEWSKI[1] and J. WIKTOR[1]

ABSTRACT. Data pertaining to the characteristics of an arctic fiord in winter were collected at the Polish Arctic Station situated in Hornsund at 77°N, 15°E on Svalbard. Winter in the fiord was defined in terms of climate (November-May), hydrology (January-March) and biology (November-March). The characteristic phenomena of winter in the fiord include a winter drop in the yearly biomass maximum to 0.1% for phytoplankton and 10% for zooplankton; a slowing of the growth rate among pelagic dominants such as *Pseudocalanus elongatus* and *Calanus finmarchicus*, as well as among the hyperbenthic dominants *Onisimus littoralis* and *Mysis oculata*; and heterotrophy or maintenance of metabolism among living phytoplankton cells found in the middle of the polar night in densities of 10-50 cells/L.

Since the life cycles of invertebrates are highly seasonal, no winter breeders were observed and 90% of the examined species were breeding according to a K strategy. Migration takes place among all seabirds in the area, but about 1% of the eiders, fulmars and kittiwakes overwinter, feeding in the open water of polynyas and crevices in the fast ice.

Key words: Arctic, winter ecology, fiord ecosystem, Svalbard, Hornsund fiord

RÉSUMÉ. Des données concernant les caractéristiques hivernales d'un fjord ont été recueillies à la station polonaise de l'Arctique située à Hornsund dans le Svalbard, à 77° de latit. N. et 15° de longit. E. L'hiver dans le fjord a été défini en termes de climat (de novembre à mai), d'hydrologie (de janvier à mars) et de biologie (de novembre à mars). Les phénomènes caractéristiques de l'hiver dans le fjord comprennent une baisse hivernale dans la biomasse annuelle maximale jusqu'à 0,1 % pour le phytoplancton et 10 % pour le zooplancton; un ralentissement du taux de croissance parmi les espèces pélagiques dominantes comme *Pseudocalanus elongatus* et *Calanus finmarchicus* ainsi que parmi les espèces hyperbenthiques dominantes, *Onisimus littoralis* et *Mysis oculata*; et une hétérotrophie ou maintien du métabolisme parmi les cellules vivantes du phytoplancton trouvées au milieu de la nuit polaire à des densités de 10 à 50 cellules/*l*.

Les cycles de vie des invertébrés étant extrêmement liés aux saisons, aucun animal se reproduisant en hiver n'a été observé, et 90 % des espèces examinées se reproduisaient selon une stratégie «K». La migration touche tous les oiseaux de mer de la région, mais environ 1 % des eiders, des fulmars et des mouettes tridactyles restent en hiver et se nourrissent dans l'eau libre des polynias et des fissures dans la banquise côtière.

Mots clés: Arctique, écologie de l'hiver, écosystème de fjord, Svalbard, fjord Hornsund

Traduit pour le journal par Nésida Loyer.

INTRODUCTION

Hornsund fiord is one of the most studied areas in Svalbard with respect to marine ecology (Fig. 1) (Swerpel and Weslawski, 1989). Polish expeditions working there have investigated the significance of seasonality to all processes observed in the marine ecosystem (Weslawski *et al.*, 1988). In summer, there is a high percentage of Atlantic organisms in the plankton, lending a subarctic character to the fiord. There is also a dense population of birds (Stempniewicz, 1990). In winter, the fiord changes to a high arctic marine locality with regard to ice cover and light regime. Since drastic changes from summer to winter landscapes are well known in temperate zones, we wanted to compare seasonal changes in Hornsund with those in the Baltic Sea.

For arctic animals, a long winter and a short productive period are the most demanding stresses (McLaren, 1963; Dunbar, 1968), but the majority of published reports have concentrated on early spring and summer seasons, which are the periods when the study region is most accessible. Some researchers, however, have dealt with an entire year, and information on the arctic winter can be found in Thorson (1936), McGinitie (1955), Grainger (1959), Prygunkova (1974), Chlebovitsh (1974), Smidt (1979), Andersen (1981) and Weslawski *et al.* (1988). The winter survival discussed here relates to how organisms manage the two major phenomena that dominate polar regions: 1) the short productive period during the year, and 2) the lack of light during the long polar night. Since the productive period of phytoplankton is directly dependent on light, the problem may be rephrased as: How do organisms survive the long period when food resources are limited?

This paper describes phenomena observed during winter in an arctic fiord of the northernmost Atlantic with special reference to life strategies and specific adaptations of the organisms.

STUDY AREA, MATERIALS AND METHODS

The data presented here were collected during two winterings at the Polish Polar Station in 1981/82 and 1984/85. The station is situated at 77°N, 15°E on the coast of Hornsund, the most southerly of the Svalbard fiords (Fig. 1). The area is under the direct influence of the Atlantic West Spitsbergen Current and coastal cold waters from the Sorkapp Current. Ice pack occurs at south Spitsbergen from December until May, and sometimes until August (Vinje, 1985; Weslawski and Adamski, 1987). The physical environment has been described by Swerpel (1985) and Rodzik and Stepko (1985) and the biological phenomena by Weslawski *et al.* (1988).

Two main sampling stations have been used: an outer one in Isbjornhamna (A) and an inner one in Burgerbukta (B) (Fig. 1). Air temperature was measured 2 m above ground level and monthly mean values were calculated from three measurements per day. Sea temperature was measured with reversing thermometers once a day at the surface and three times per month at a depth of 30 m. A bathythermometer was used simultaneously with the zooplankton hauls. Salinity was determined along with the temperature and samples were analyzed using the Winkler titration method. The thickness of the fast ice cover was measured without wind-driven snow. Primary production was measured in February and March

[1]Institute of Oceanology, Polish Academy of Sciences, 81-967 Sopot, Powstancow Warszawy 55, Poland
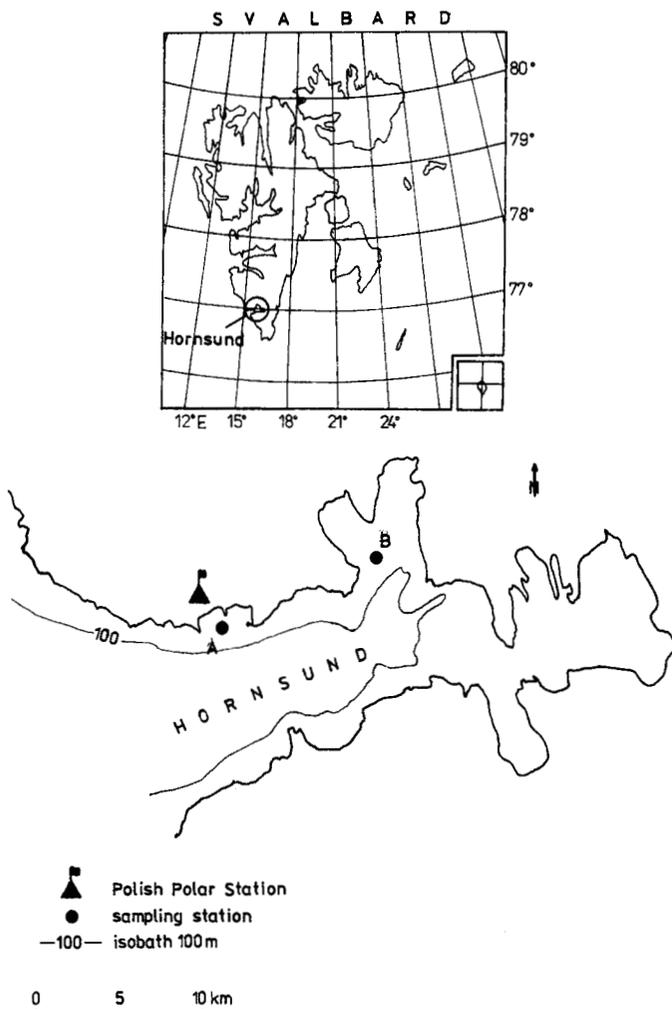
FIG. 1. Study area and sampling stations in winters 1981/82 and 1984/85.

in three repeated counts. The results were counted over again to record the number of individuals per litre. Zooplankton was sampled from 0-10, 10-25 and 25-50 m layers using a WP-2 net (mouth opening 0.25 m², mesh size 200 μm) equipped with a closing device (Zooplankton Sampling, 1968). Samples were weighed wet with 0.1 mg accuracy and preserved in 4% formaline, buffered with di-sodium-tetraborate. The laboratory analyses of the samples were carried out according to recommendations by Zooplankton Sampling (1968), Hernroth and Viljama (1979) and Hernroth (1985). Benthic fauna was collected with a light dredge (mouth opening 0.6 m per 0.3 m and 0.5 mm mesh size). Necrophages were collected from cylindrical (1 m length, 0.3 m in diameter and 1 mm mesh size) traps baited with carrion.

In all cases, crustacean length was measured from the tip of the rostrum to the end of the telson. To describe crustacean population structure, the following categories were used: juveniles (specimens of unidentifiable sex), immatures (secondary sexual features developed) and adults (fully mature males and females). Percentage of occurrence (or mean number of specimens per sample) was calculated as the total number of specimens divided by the number of all samples considered. Percentage of frequency was calculated as the number of samples with species x divided by the total number of samples considered.

Fish were collected when caught in the dredges, plankton nets or baited traps (Weslawski and Kulinski, 1989). Birds and mammals were observed along the northern coast of Hornsund, and their numbers were compared to summer abundances noted in Weslawski and Kwasniewski (1990).

Grad days were calculated as the total number of days at a given temperature. To avoid minus values, +2 was added to each temperature observed. Therefore 10 days with a temperature of −0.5 gave a value of 15 grad days.

RESULTS

Physical Phenomena

Winter in the fiord ecosystem has been defined in different ways (Table 1). The climatic winter in Hornsund is defined as the period when the mean daily temperature is below −2.5°C (Baranowski, 1977). Climatic winter lasted from October to May in both 1981/82 and from November to April in 1984/85 (Table 1).

Fast ice forms in October/November on shallow brackish bays and in December on inner fiord pools. In February, the ice cover is stable, reaching a thickness of 1.4 m in the inner

1985 using the ¹⁴C method described in Strickland and Parsons (1972); some of these results were published by Eilertsen et al. (1989). Chlorophyll a concentrations were measured in 2-5 L of water filtered on GF/C Whatman filters and analyzed according to Strickland and Parsons (1972) using a Specol 10 type spectrophotometer. Phytoplankton from 10 L water samplers was analyzed. This amount of water was sieved through 20 μm gauze to 2 ml volume and preserved in a 4% formaldehyde solution buffered with di-sodium-tetraborate. The 2 μl (microlitre) subsample was transferred to the microscopic plate and counted under the microscope

TABLE 1. Principal abiotic factors defining winter in Hornsund (data from 1984/85, outer station)

Factor	April	May	June	July	August	September	October	November	December	January	February	March
Air temp. (°C)	−10.0	−4.5	1.5	5.2	5.0	2.3	−3.6	−7.7	−12.3	−14.2	−12.6	−11.3
Water temp. (°C, 0 m)	−1.6	−1.0	1.5	2.0	2.3	0.0	−1	−1	−1.75	−1.88	−1.88	−1.55
Water temp. (°C, 30 m)	−1.9	−1.7	−0.7	0.0	1.5	2.0	1.7	1.9	2.0	1.1	−1.88	−1.88
Hours with daylight per month	530	744	720	744	682	347	18.3	2.0	0	0	3.5	84.9
Fast ice cover (cm) on inner basin	120-130	100-130	80-130	—	—	—	—	0-10	10-35	35-80	80-100	100-120
Salinity ‰ at 0 m	33.0	32.0	31.5	28.5	27.0	28.0	29.5	33.8	34.3	31.7	33.8	34.7
Number of grad days (0 m)	13.5	31.0	105.0	124.0	133.3	60	30	31	7.5	3.72	3.4	14
Number of grad days (30 m)	3.6	9.3	39.0	62.0	108.5	120.0	111	121	120	96.1	3.4	3.72

fiord basins, but not exceeding 0.5 m in the central fiord area. Winter fast ice usually breaks up by the end of April and disappears by June.

Hydrological winter is here defined as a period of cold water occurrence when the sea water temperature drops to its yearly minimum of –1.88°C. Hydrological winter started early in November in 1981/82, but not until late January in 1984/85.

Spring stratification of sea water begins in March/April and ends the hydrological winter. This is true for the innermost fiord basins with limited water exchange and durable fast ice cover. The outer part of the fiord is directly influenced by the open sea and is cooled later in the autumn and for a shorter time as compared to the inner fiord pools.

Light conditions in winter are stable. The polar night in Hornsund lasts from 11 November to 13 February, but continual darkness occurs only during three weeks in December. In January the first pale light appears on the horizon for about one hour.

Biological winter in the Hornsund marine ecosystem is defined here as the period between the autumn decrease of zooplankton biomass and the first signs of the spring bloom, or from about December to March/April (Table 2).

Net Phytoplankton

Very low densities were found in most of the samples examined, ranging mostly below 10 cells/L (Table 3). The cells were alive when collected, with bright orange (Ceratium) or green (Thalassiosira) chromatophores. The winter concentration of cells was about 1% of that observed in summer. The amount of chlorophyll *a* in the water was equally low throughout the winter (Table 2). Net phytoplankton was scarce, but non-detailed flagellates with 3-7 μm cell size were already numerous in late February, giving a significant primary production of 1 gC/m³/h (Table 2).

Zooplankton

The winter drop in the pelagic biomass and density ranged from 10 to 40% of the summer maximum. From some 40 planktonic taxa noted in summer samples, only 23 have been found in winter (Table 4). There were no pelagic larvae of benthic animals and no Hydromedusae or Tunicata. Winter plankton was dominated by small copepods, especially *Pseudocalanus* spp.

TABLE 2. Principal biological factors defining winter in Hornsund (data from 1984-85)

Factor	October	November	December	January	February	March
Mesozooplankton density n/L in 0-50 m water column	231-250	25-30	32-280	30-292	26-30	20-28
Mesozooplankton biomass mg/L in 0-50 m water column	50-177	12-318	15-320	20-121	12-40	4-10
Net phytoplankton count cells/L	<10	<10	50	20	20	50
Primary production mg C/m³/h	x	x	x	x	0.88	1.4
Chlorophyll *a* mg/m³	x	0.14	0.14	0.09	0.21	0.14

x indicates no data available.

TABLE 3. Phytoplankton cells found alive in net samples in winter 1984/85

Date of sample	Volume (L)	Species	Number of cells/L
27.11.84	3	*Ceratium arcticum*	*
		Thalassiosira sp.	*
27.11.84	3	*Protoperidinium depressum*	*
		Ceratium arcticum	*
28.11.84	1	*Ceratium arcticum*	*
		Thalassiosira sp.	*
11.12.84	4.5	*Thalassiosira* sp.	*
11.12.84	5	*Ceratium arcticum*	*
		Protoperidinium depressum	
11.12.84	7	*Thalassiosira* sp.	*
18.12.84	5	*Ceratium arcticum*	*
		Protoperidinium depressum	*
		filamentous algae fragments	*
27.12.84	5	*Protoperidinium depressum*	15
		Licmophora sp.	30
01.01.85	6	*Biddulphia* sp.	12
17.01.85	4.5	*Protoperidinium pellucidum*	*
		Protoperidinium depressum	17
		filamentous algae fragments	*
27.01.85	3.5	*Thalassiosira* sp.	*
		Ceratium arcticum	*
		Protoperidinium depressum	21
27.01.85	6	*Protoperidinium depressum*	12

* Densities >10 cells per L.

Metridia longa, Oncea borealis, Limacina helicina and *Oithona atlantica* were the only species more common in winter than in summer (Table 4).

The population structure of the two dominants (*C. finmarchicus* and *P. elongatus*) shows that both spend winter in older copepodite stages (Fig. 3). We have not found any naupliar stage in winter samples (Table 4; Fig. 2).

Slowing of growth in winter was observed in *Pseudocalanus* and *Calanus* populations. Although both species differ in breeding seasonality, their growth is restricted to the period from May to September. *Calanus* summer growth compared to winter stagnation was clear, while *Pseudocalanus* grew much slower, with only a slight summer increase (Fig. 3). The growth curves in Figure 4 were obtained by combining our data on the occurrence of developmental stages with length values of Spitsbergen copepod stages presented by Kanaeva (1962).

Stratified sampling at station B did not show any clear pattern of zooplankton biomass distribution. There was no correlation of zooplankton occurrence with temperature or time (Fig. 4). Zooplankton was distributed unevenly in the water column, with patches consisting of up to 70% of the biomass from the investigated station noted both at the surface and in the near bottom hauls (Fig. 4).

Benthos

The only regular benthic samples from winter were collected in traps baited with carrion. The set of taxa of benthic necrophages was very constant throughout the year, consisting of 10 taxa dominated by lysianassid amphipods (Table 5). The population structures of the two most common crustaceans, *Onisimus littoralis* and *Mysis oculata*, show a high percentage of immature specimens and juveniles during winter. The seasonality of breeding of Hornsund invertebrates (Tables 4 and 6) shows that the majority of benthic animals lay eggs in October and incubate eggs throughout the winter.

The smallest and youngest wintering benthic animals were juveniles of *Calliopius laeviusculus*, *Ischyrocerus anguipes* and *Hyperia galba* — all three species breeding exceptionally in summer, with juveniles hatching eggs in early autumn (Table 6).

The slowing of growth in winter was observed among all benthic animals but was much more evident for the omnivorous *M. oculata* than for the necrophagic *O. littoralis* (Fig. 5).

TABLE 4. Zooplankton occurrence in winter compared to summer (data from 1984/85 outer station)

| Taxon	Winter, 11 samples, occurrence n/m³	Summer, 34 samples, occurrence n/m³	Breeding status in Hornsund
Aglantha digitale	0.09	0.24	smallest specimens in June
Aeginopsis laurentii	0	0.21	?
Catablema vesicarum	0	0.03	?
Boungavilla supercilliaris	0	0.09	?
Euphysa flammea	0	0.15	?
Radhkea octopunctata	0	0.03	?
Mitrocomella polydiademada	0	0.09	?
Paratiara sp.	0	0.09	?
Beroe cucumis	0.09	0.74	smallest specimens in May
Martensia ovum	0	0.62	smallest specimens in May
Polychaeta larvae	0.09	8.1	peak of larvae occurrence in August
Lamellibranchiata larvae	0.09	1.85	peak of larvae occurrence in August
Clione limacina	0	0.09	smallest specimens in May
Limacina helicina	1.36	0.82	smallest specimens in May
Ostracoda spp.	0	3.6	smallest specimens in May
Cirripedia larvae	0.18	75	peak of larvae occurrence in June
Harpacticoida spp.	1.2	1.77	? at least 4 species
Calanus finmarchicus	0.4	45.5	both *C. finm.* and *C. glacialis*, naupli in May
Pseudocalanus elongatus	9.5	166.5	naupli in August
Microcalanus pygmaeus	2.6	3.4	?
Paraeucheta norvegica	0.09	0.15	?
Metridia longa	4.41	3.3	?
Heterorhabdus norvegicus	0.09	0.09	migrant with Atlantic waters
Acartia longiremis	1.73	1.9	?
Oithona similis	6.6	37.1	?
Oithona atlantica	3.91	0.91	?
Oncea borealis	0.82	0.59	?
Euphasidae larve	0	0.99	migrant with Atlantic waters not breeding in the area
Decapoda larvae	0.09	0.86	winter incubation of eggs, larvae hatched in April-May
Hyperia galba	0.09	0.15	summer incubation of eggs, juveniles in September
Themisto abyssorum	0	0.03	migrant with Atlantic waters not breeding in the area
Th. libellula	0.09	0.38	winter incubation of eggs, juveniles from March on
Gammarus juv.	0.27	0.21	winter incubation, juveniles from April/May
Mysis oculata	0.09	0.06	winter incubation, juveniles from April/May
Fritillaria borealis	0	1.94	migrant with Atlantic waters, juveniles in June
Oikopleura spp.	0	0.79	juveniles in June
Eukhronia hamata	0	0.24	migrant with Atlantic waters, juveniles in June
Sagitta elegans	0.46	1.03	juveniles in June
mean number of individuals per m³	148	367	
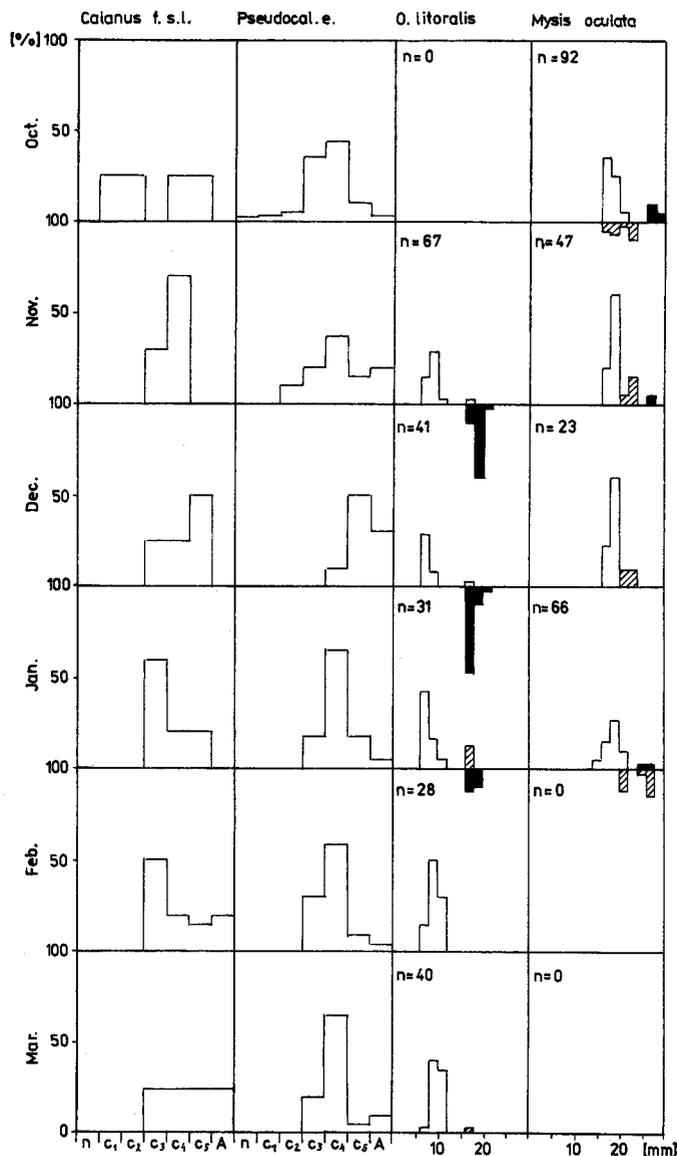
FIG. 2. Results from the stratified zooplankton sampling in the outer station. Temperature data from bathythermograph.

FIG. 3. Winter population structure of four dominant crustaceans in Hornsund. n – nauplii, c_1-c_5 – copepodit stages, A – adults, N – number of specimens measured.

Vertebrates

Scarce, mainly qualitative, information is available on the winter life of fishes in Hornsund (Table 7). The three most common species, sculpin (*Myxocephalus scorpius*), sea snail
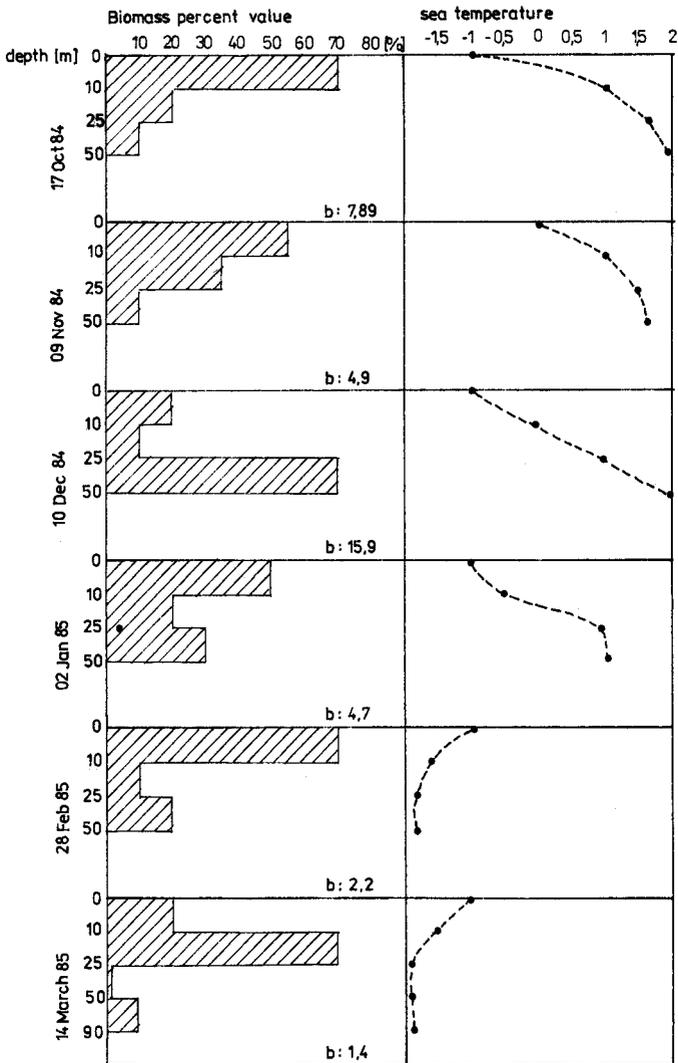

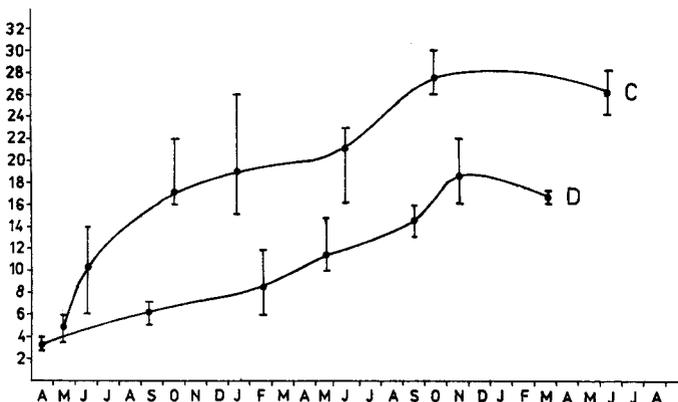FIG. 4. Growth curves of most common pelagic crustaceans in Hornsund. A - *Calanus finmarchicus*, B - *Pseudocalanus elongatus*.

FIG. 5. Growth curves of the most common benthic/hyperbenthic crustaceans in Hornsund. C - *Mysis oculata*, D - *Onisimus littoralis*.

(*Liparis liparis*) and polar cod (*Boreogadus saida*) all produce larvae in spring. The same is true for the migratory arctic char (*Salvelinus alpinus*) inhabiting lakes along the Hornsund coast.

Seabirds migrate from Hornsund in the beginning of autumn, usually in September. Only a few fulmars (*Fulmarus glacialis*), kittiwakes (*Rissa tridactyla*) and eiders (*Somateria mollissima*) winter in the fiord. Their number was estimated as 1-10% of the summer population (Table 7). By February, the majority of fulmars were already returning to their nesting cliffs. Wintering birds were commonly observed on water channels between the shore and fast ice.

Ringed seals (*Phoca hispida*) winter in the fiord, judging from the numerous breathing holes visible in December and January and animals resting on the ice in February and March. Bearded seals (*Erignathus barbatus*) have been observed in winter at the edge of the fast ice at the mouth of the fiord. Polar bears do not breed in the Hornsund area but migrate there in winter and spring. The peak of their migration appears to be in February, when as many as 40 bears were observed in 1982 (Table 7).

TABLE 5. Necrophagic invertebrates in Hornsund benthos

Taxon	Nov.-Feb. (n=16) F	O	March-May (n=41) F	O	Jun.-Aug. (n=21) F	O	Sep.-Oct. (n=6) F	O
Hyas araneus	0	0	7	0.15	14	0.9	33	2.3
Eupagurus pubescens	0	0	0	9	0.2	33	0.3	
Eualus gaimardi	6	0.06	15	0.02	0	0	67	2
Anonyx nugax	69	6	78	14	52	10	50	64
A. sarsi	94	50	36	0.4	100	120	33	0.7
Onisimus edwardsi	69	77	10	6.3	62	48	50	7
O. littoralis	50	11	22	7.4	33	14	17	17
Orchomene minuta	38	2.5	39	5	43	12	33	1
Gammarus spp.	6	0.8	10	1	19	1.6	0	0
Anaitides groenlandica	0	5	0.22	0	0	0	0	
number of taxa	7		9		8		8	

n — number of samples.
F — % frequency.
O — % occurrence.

TABLE 6. Life strategies related to wintering among plankton, hyperbenthos and fishes from Hornsund

Examples of species	Breeding season life span	Breeding strategy	Wintering part of population
Hyperia galba *Pseudocalanus* *Ischyrocerus a.* *Calliopius l.*	summer spawning 1-year life span	r K	juveniles
Calanus finm. *C. glacialis* *C. hyperboreus*	spring spawning 1.5 year	K	immatures, adults
Sagitta e. arctica *Mysis oculata* *Onisimus littoralis*	spring spawning 2.5 year	K	immatures, adults
Decapoda gen. *Gammarus wilkitz.* *Anonyx nugax* *Gammarus wilk.* *Myxocephalus* *Eupagurus pub.* *Boreogadus s.*	spring/summer spawning 3.5-year life span	K r	juveniles, immatures, adults

TABLE 7. Winter status of the most common marine vertebrates
from Hornsund

Taxon	Winter amount as % of summer maximum	Remarks on winter occurrence
Fish		
Boreogadus saida	? 100%	common, especially in ice holes
Liparis liparis	? 100%	found among laminariae
Myoxocephalus scorpius	? 100%	winter incubation of eggs laid among laminariae
Birds		
Alle alle	absent	
Uria lomvia	absent	small number in some years
Cepphus grylle	0.1-1%	as above
Fulmarus glacialis	0.1-1%	as above
Fratercula arctica	absent	
Rissa tridactyla	0.1%	wintering in small number in some years
Somateria mollissima	0.1-1%	as above
Larus hyperboreus	0.1%	as above
Mammals		
Phoca hispida	? 100%	common in the inner fiord basins
Erignathus barbatus	? 100%	common at fast ice edge
Phoca groenlandica	absent	
Delphinapterus leucas	absent	
Ursus maritimus	95% yearly observations in winter	absent in summer; migrating in winter in Hornsund, maximal count in February

DISCUSSION

Duration of Winter

Most of the factors discussed here are common for the temperate waters, where a seasonally changeable marine environment is typical. Table 8 compares the arctic, Baltic Sea and Antarctic regions with respect to several factors. The pelagic biomass drop in Hornsund is sharp, but not extremely so. The winter minimum in the Arctic ranges from 2 to 30% of the summer zooplankton maximum, in the Baltic it ranges from 10 to 12% and in Antarctica from 10 to 15%. Primary production in winter ranges similarily from 2 to 10% of summer values in arctic and Baltic localities (Table 8). A more pronounced difference among the regions is the length of the non-productive (or less productive) periods during a year. It ranges from 50 to 90% in the Arctic and Antarctic, but is only 25% in the Baltic Sea (Table 8). In some arctic localities, winter is defined as a non-productive period lasting from 25 to 90% of the year. In Hornsund, where pronounced year-to-year variations were observed, the climatic winter may last from 140 to 210 days per year (Weslawski and Adamski, 1987), as compared to 210-280 days per year in Franz Josef Land (Averincev, 1989). Among the abiotic factors that determine the duration of the biological winter, light is considered a key factor, since both phytoplankton and zooplankton grow and develop well at low sea temperatures (Clarke, 1988). Water stratification is not necessary to start the spring bloom in the Arctic (Eilertsen et al., 1989), as was commonly supposed.

TABLE 8. Winter characteristics of the Arctic, Antarctic and Baltic seas

Factor and region	Spring/summer values	Winter values	% of winter to summer value	Locality	References
Chlorophyll a					
Arctic	200 mg/m²	<10/m²	<5%	Frobisher Bay	Grainger, 1979
	4 mg/m³	0.15 mg/m³	4%	Hornsund	Weslawski et al., 1988
Antarctic	2 mg/m³	0.3 mg/m³	15%	S. Shetlands	Lipski, 1987
	0.8 mg/m³	0.1 mg/m³	13%	Open ocean	El Sayed, 1984
	19 mg/m³	0.23 mg/m³	1.2%	Signy Island	Clarke et al., 1988
Baltic	75 mg/m²	5 mg/m²	6.7%	Central Baltic	Lindahl, 1977
Primary production					
Arctic	1200 mgC/m²/d	10	0.8%	Frobisher Bay	Grainger, 1979
	1000	<200	<20%	Disco Bay	Andersen, 1981
	2000	<10	<0.5%	Hornsund	Eilertsen et al., 1989
Baltic	900	20	2.2%	Baltic Sea	Lindahl, 1977
Net phytoplankton density					
Arctic	10⁷/dm³	10³	0.01%	Baltic Sea	Eilertsen et al., 1981
	2 × 10⁵/dm³	5 × 10³	2.5%	White Sea	Chlebovitsh, 1974
	10⁴/dm³	10/dm³	0.1%	Hornsund	this paper
Antarctic	10⁷	10⁵	1%	S. Shetlands	Ligowski, 1986
Baltic	2 × 10⁹	7 × 10⁸	35%	Baltic Sea	Wiktor, unpubl. data
Zooplankton density					
Arctic	13 000/m³	2000	15%	White Sea	Prygunkova, 1974
	360-800	20-200	1-40%	Hornsund	this paper
Antarctic	155 ml/1000 m³	44	28%	South Georgia	Atkinson and Peck, 1988
Baltic	1031 ml/m³	85 ml/m³	8%	Baltic Sea	Chojnacki et al., 1973
Duration of productive period (days/year)					
Arctic	150	210	58%	W. Greenland	Andersen, 1981
	180	180	50%	W. Greenland	Smidt, 1979
	120	240	66%	Arctic (general)	Subba Rao and Platt, 1984
	30	330	92%	Frobisher Bay	Grainger, 1979
	60	300	83%	Hornsund	Weslawski et al., 1988
Antarctic	210	150	42%	Signy Island	Clarke et al., 1988
Baltic	270	90	25%	Baltic Sea	Renk et al., 1986

Drop in Pelagic Biomass

A drop in pelagic biomass is commonly reported from all arctic localities (Table 8). This phenomenon is caused by the dying of older organisms after summer or autumn breeding and the lack of larvae and juveniles. Some plankters apparently undergo a dormant stage of life, either wintering on the bottom as spores (Eilertsen, 1987) or perhaps inhabiting the ice (Horner and Murphy, 1985), but in any event disappearing from the pelagic environment. The winter minimum of pelagic biomass may range from 10% of summer values for zooplankton to less than 0.01% among phytoplankton in the Arctic (Eilertsen et al., 1981). The sharpest drop is usually observed in phytoplankton biomass, and since the continual darkness of the polar night is responsible for the death of most phytoplankton, year-to-year variations in the amount of wintering phytoplankton are unlikely. The amount of zooplankton surviving the winter may vary from year to year (Smidt, 1979). The lack of euphausiids in winter samples from Hornsund reflects the migrant character of Thysanoessa inermis in this area. T. inermis does not breed up north (Lomakina, 1978) and is carried by warm Atlantic waters along the West Spitsbergen Current. The same is true for Eukhronia hamata and Themisto abyssorum. As was shown by Mandel (1976), the flow of Atlantic waters in winter is much weaker along the Spitsbergen coast and farther from the shore, causing the Atlantic plankton transport to coastal waters in winter to be severely diminished. The sharp winter drop in pelagic biomass in Hornsund is comparable to that of high arctic rather than subarctic localities (Table 8).

Slowing of Growth Rate and Starvation

Inadequate light conditions do not entirely eliminate phytoplankton in winter. In subarctic northern Norway a considerable amount of phytoplankton occurs in winter (Eilertsen et al., 1981), and in the White Sea five diatom species were reported in densities between 10 and 100 cells/L in winter (Chlebovitsh, 1974). Phaeocystis pouchetii was reported from the subarctic and arctic pelagic waters all year around and appears to be especially adapted to low irradiance (Eilertsen, 1987). Some microscopic algae are able to survive the dark winter by reducing metabolism, as was observed by Hamilton et al. (1968), Fournier (1970), Horner and Alexander (1972) and Antia (1976). Since the food base is limited and temperature is low in winter, the obvious consequence is the slow growth rate, as was noted for the four most common crustaceans from Hornsund.

Similar observations were collected for the Antarctic by Clarke (1985). Poor winter nutrition necessitates the maturation on inner energy resources of C. finmarchicus (Tande et al., 1985). Some Antarctic copepods do not feed in winter but rely on inner resources (Clarke et al., 1988). The absence of winter zones in the scales of arctic char (Gullestad, 1974) also reflects the winter period of starvation and inhibited growth.

Change in Ecological Niche

The presence of live algae in darkness may suggest heterotrophy, as was reported from a subarctic lake in Sweden by Rodhe (1955), who found numerous flagellates in the winter plankton. Dunbar (1968) has suggested that feeding on the dissolved organic matter is a common winter adaptation among phytoplankton, but this suggestion has been criticized and a reduced metabolism has been observed as more common for diatoms wintering in sea ice (Horner and Alexander, 1972). However, Protoperidinium sp. observed in Hornsund was reported to be heterotrophic (Gaines and Taylor, 1984). The suspended matter present in winter may support selective feeding by otherwise filtering herbivores (Digby, 1954). Scavenging or necrophagy is expected to be a convenient method of feeding in winter and is regarded as adaptive in polar and deep-sea regions (Arnaud, 1970; Dahl, 1979). However, Presler (1986) reports a more diversified necrophagic fauna in summer as compared to winter in an Antarctic fiord. Among necrophages we have observed in Hornsund, lysianassid amphipods were specialized in carrion feeding, and no seasonal pattern was found. The absence or scarcity of pelagic food in winter may drive plankton-feeding carnivores to feed on benthic fauna. For example, ringed seals feed on krill in summer but take benthic shrimps in winter in Spitsbergen fiords (Weslawski et al., in prep.).

Migration — Change of the Habitat for Winter

Since coastal arctic biota are extremely cold and food is limited in winter, one may expect a seasonal migration to deeper, warmer waters, or at least out of the harshest areas. In Hornsund, however, the winter downward migration was not prominent due to the shallow depths of the basin. Vertical migration was considered to be a successful metabolic advantage and adaptation of planktonic organisms (McLaren, 1963; Dunbar, 1968). In arctic localities most plankters living in surface waters in summer descend to a greater depth in winter (Smidt, 1979; Tande et al., 1985). Seasonal migration in this case might be simply explained as an avoidance of minimal temperatures. The autumn cooling occurs downward from the surface, and spring heating also starts from the surface. Thus winter migration to deeper waters diminishes the contact with overcooled water by 1-3 months (Table 1). Since fiord basins are equally cooled from the surface to the bottom in winter, avoidance of cold water is only possible for a limited time. In contrast, the shelf waters of west Spitsbergen are winter cooled in the surface layer only; below the 50 m depth constant positive temperatures occur all year around (Atlas Arktiki, 1985). Thus, on the Spitsbergen shelf, the downward migration of zooplankton entirely prevents contact with cooled water. This explains the high adaptive value of seasonal migration in open sea and its low adaptive value in arctic fiords. Polar cod is one of the few species migrating to the surface and to shallow waters in winter (Andriashev, 1954; Craig et al., 1982). Arctic char is another typical migrator. In Hornsund most juveniles of the year leave fresh water before a second wintering (Gullestad, 1974). Plankton-feeding seabirds leave Hornsund and spend the winter on the open sea out of the ice zone (Brown, 1984).

Species Life History Related to the Winter

Winter food limitation reduces the number of young produced. Since food occurs in abundance once a year in late spring, the high seasonality of the life history is expected as there is only one period of reproduction per year. In Hornsund all the observed animals breed once a year and no winter breeders were found. The lack of larvae and

younger stages in the winter plankton has also been reported in Alaska (Horner and Murphy, 1985). Wintering in older stages was reported for *C. finmarchicus* from the Barents Sea (Davis, 1976; Tande *et al.*, 1985) and for *Sagitta elegans* from Greenland (Ussing, 1938; Dunbar, 1941). Larvae of benthic fauna were absent in Greenland winter plankton (Smidt, 1979; Andersen, 1984).

The very limited list of species breeding in winter and larvae observed in winter plankton is shown in Table 9. To fit the spring bloom a herbivore should release larvae just before or during the productive period. There are two ways to achieve this. The r strategy means that numerous small eggs are laid in early spring and hatch in late spring. In a K strategy, a few large eggs are laid in autumn and long-lasting incubation occurs throughout the winter, with hatching in the spring. In an arctic environment, such large young are better fitted both for the wider feeding possibilities and more favourable energy budget (Thorson, 1936; Marshall, 1953; McLaren, 1966; Dunbar, 1968). Table 6 illustrates the typical predominance of the K breeding strategy among arctic animals. Polar cod is among the few exceptions, spawning in mid-winter and producing larvae in spring (Craig *et al.*, 1982).

CONCLUSIONS

Long-lasting, limited production is a dominant characteristic of the arctic winter. Hornsund fiord is similar in winter character to a typical high arctic region. The adaptive strategy for organisms is to gather sufficient inner resources during the short productive period to avoid winter starvation. This strategy involves breeding once a year using a K strategy and vertical migration. These adaptations have also been observed in the Antarctic ecosystem (Clarke, 1979; Picken, 1980; Clarke *et al.*, 1988).

The polar marine ecosystem is some 4 Ma years old in the Antarctic (Knox and Lowry, 1977), while arctic polar biota are not older than 0.7 Ma years (Herman and Hopkins, 1980). Organisms inhabiting the Antarctic polar ecosystem have developed numerous physiological adaptations to live in cold water, such as antifreeze bodies and the white blood of some fish (Rakusa Suszczewski, 1980). There are no such adap-

tations among arctic fauna. On the other hand, both old and young polar populations have developed similar features related for winter survival. The presence of these features in temperate waters as well indicates that the observed phenomena are characteristic of seasonally changeable ecosystems.

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TABLE 9. Examples of winter occurrence of larvae and invertebrates spawning during winter in the Arctic

Taxon	Region	Author
Polychaeta		
Autolytus alexandri	N. Barents Sea	Averincev, 1989
Bivalvia		
Hiatella striata	NW Greenland	Andersen, 1984
Mya truncata	E. Greenland	Thorson, 1936
Pteropoda		
Clione limacina	Beaufort Sea	McGinitie, 1955
Helicina limacina	E. Greenland	Ussing, 1938
Copepoda		
Metridia longa	White Sea	Prygunkova, 1974
Microcalanus pygmaeus	E. Greenland	Ussing, 1938; Digby, 1954
Microsetella norvegica	White Sea	Prygunkova, 1974
Oithona similis	E. Greenland	Digby, 1954
	White Sea	Prygunkova, 1974
Oncea borealis	E. Greenland	Digby, 1954
	White Sea	Prygunkova, 1974
Pseudocalanus minutus	E. Greenland	Digby, 1954
Amphipoda		
Parathemisto libellula	Ungava Bay	Dunbar, 1957

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