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Life cycles of some Arctic amphipods

Jan Marcin WĘSŁAWSKI and Joanna LEGEŻYŃSKA

Instytut Oceanologii Polskiej Akademii Nauk, Powstańców Warszawy 55, 81-712 Sopot, Poland
<weslaw@iopan.gda.pl>

ABSTRACT: Life cycles, number of eggs per female, minimal adult female length and reproductive costs are presented for 18 species of Amphipoda from the West Spitsbergen area, 77–79°N. Fifteen species incubated eggs during the polar night and released their offspring in early April. Three species incubated eggs from late spring till late summer. The appearance of the youngest juveniles, indicating the hatching period, is presented for 63 species. Most of the species studied were *K* strategists, with large eggs of over 1 mm diameter; only one species (*Hyperoche medusarum*) was *r* – strategist.

Key words: Arctic amphipods, breeding, life cycles, eggs incubation.

Introduction

Amphipods are a speciose group and constitute an ecologically important component of polar fjords ecosystems (Jażdżewski *et al.* 1995). Spitsbergen amphipods have been relatively well recognised from the faunistic point of view (Stephensen 1935–40, Palerud and Vader 1991, Gulliksen *et al.* 1999), and ecology (Lagardere 1968, Węsławski 1990, Jażdżewski *et al.* 1995, Legeżyńska 2001). Except for ice-associated taxa (sympagic) (Poltermann 1997) and intertidal species (Węsławski *et al.* 2000) there is no published data on the breeding biology or production of Svalbard amphipods. Breeding of amphipods from other Arctic regions is not well known; there are some data from the southern Barents Sea (Kuznetsov 1964, Tzvetkova 1977), Canadian Arctic, and Greenland (Dunbar 1957, Steele 1967, 1972; Steele and Steele 1970, 1972, 1973, 1975 a, b, c, 1978). Some data on Arctic amphipods (16 species also known from Svalbard area) are presented in the extensive review by Sainte-Marie (1991). Most of the above-cited studies were based upon a seasonally limited material (usually collected in summer) and contained only a few adult females. The growing concern of the consequences of climate warming for the Arctic ecosystem involves an understanding of the biology of key species, since the poikilotherm animals' development is directly temperature-related. The present paper contains some new data on breeding parameters of common coastal species, aimed at resolving the question – what is the diversity of breeding strategies in the Amphipoda of the Svalbard region? May they be changed when exposed to elevated sea temperatures?

Materials and methods

Gravid females were collected using different sampling gear (grabs, dredges, and hand nets) during a year-round expedition to Hornsund (South West Spitsbergen) in 1984/85 and during several summer trips to Kongsfjorden (Norh West Spitsbergen) in the years 1996–2000. Amphipod length was measured from the tip of the rostrum to the end of the telson to 0.1 mm accuracy. Wet weight was taken from animals preserved in 4% formaldehyde, after gently washing them in tap water and blotting on filter paper 6 to 12 months after collection. Egg diameter was calculated as a mean value from two measurements of the longest and shortest diameter, from at least 5 eggs measured to 0.01 mm accuracy. Wet formaline weight of 10 eggs was measured to an accuracy of 0.1 mg, then calculated for the single egg. The effect of formaline preservation on crustaceans' weight and volume have been analysed by Opaliński (1991), who found fresh weight to formaline weight difference of 1%; our unpublished data on fresh and preserved amphipods shown to 1 to 5% difference.

Reproductive effort (%RR) was calculated after Wildish (1982) as the percentage share of brood volume to female volume. Female volume was calculated after measuring the depth of body (d) as the body height at the 4th pereion segment. Altogether 152 gravid females were measured (Table 1).

Study area

Hornsund (77°N) and Kongsfjorden (79°N), where the materials were collected, are both medium-sized West Spitsbergen fjords facing the Greenland Sea. The waters from coastal current (South Spitsbergen Current) and coastal waters of West Spitsbergen fill the fjords. Surface layer is less saline, up to 30 PSU, whereas in the near bottom layer, below 20 m depth, salinity is stable and does not fall below 34 PSU. Maximal summer temperature (August) may reach 8°C in tidal pools, and in open fjord waters is up to 6°C. Very cold water (–1.88°C) is formed in autumn (November–December) during freezing of the water surface; this dense and cold water sinks down and fills the semi-enclosed basins in the inner fjord areas. During the spring melt the water column is heated from the surface and seasonal picnocline is formed (Swerpel 1985, Węsławski *et al.* 1991, Piechura 1993, Piechura and Walczowski 1996, Svendsen *et al.* 2001). The seasonality of physical phenomena and primary production in examined fjords is presented by Węsławski *et al.* (1988), Eilertsen *et al.* (1989) and Wiktor (1999).

Table 1

Reproduction parameters of examined egg-bearing females, Hornsund, Kongsfjorden, Svalbard.

Taxon	number of ovigerous females	min-max length of ovig. female	mean length of ovig. fem.	min-max wet weight ovig. fem	mean wet weight ovig. fem	min-max number of eggs per fem.	mean number of eggs per fem.	egg diameter	wet weight of single egg
	n	mm	mm	mg	mg	n	n	mm	mg
Acanthostepheia malmgreni	5	31–36	33.2	693–990	808		85	1.2	0.85
Ampelisca eschrichti	1	37			676		12	1.6	1.04
Anonyx nugax	1	44			1900	87		1.3	0.74
Anonyx sarsi	6	20–30	27.5	548–630	589	20–30	25	1	
Calliopius laeviusculus	7	12–18	15				62	0.85	
Gammarellus homari	8	19–36	28.4	245–739	424	20–133	49	1.5	0.7
Gammarus oceanicus	33	18–32.5	26.4	158–512	331	16–152	78	0.77	0.16
Gammarus setosus	23	19–30	26	200–350	287	30–117	70	0.77	0.16
Goesia depressa	3	8–11	9.25	12.5–18	15.6		9	0.6	0.07
Hyperoche medusarum	4	7– 9.5	8.5	11.4–31.5	23.5	160–500	320	0.23	0.003
Ischyrocerus anguipes	16	8.5–9	8.9	8–13	10.4	8–9	8	0.78	0.1
Monoculodes packardi	1	5.8			14		30	0.45	
Onisimus caricus	5	22–26	25		287	5–18	12	1.4	1.8
Onisimus edwardsi	6	11–12.5	12				39	0.7	
Onisimus litoralis	6	12.5–19.5	17			15–60	50	1	
Orchomenella minuta	15	6–9	7	5–34	20	4–15	8	0.7	
Paroediceros lynceus	11	18–24	20.9	147–312	227.8	200–300	220	0.7	0.1
Weyprechtia pinguis	1	25			360		157	1.02	0.29

Table 2

Some data on breeding seasonality of Amphipoda of the Svalbard area.

Taxon	Egg bearing females	Smallest observed juveniles	Females with empty marsupium
Ampeliscidae			
Ampelisca eschrichti Kröyer, 1842	August	3 mm, July	August
Byblis gaimardii (Kröyer, 1846)			
Haploops tubicola Lilljeborg, 1855			July
Corophiidae s.l.			
Goesia depressa (Goes, 1866)			July
Neohela monstrosa (Boeck, 1861)			July
Unciola leucopis (Kröyer, 1845)		3 mm, July	
Isaeidae			
Protomedeia grandimana Bruggen, 1905			July
Dexaminidae			
Atylus carinatus (Fabricius, 1793)	October	4 mm, June	
Iphimediidae			
Acanthonotozoma serratum (Fabricius, 1780)			August
Eusiridae s.l.			
Apherusa glacialis (Hansen, 1887)	May	3 mm, July	
Apherusa sarsi Shoemarker, 1930		4 mm, July	
Apherusa tridentata (Bruzzellius, 1859)		3.5 mm, July	
Calliopius laeviusculus (Kröyer, 1838)	Jan.–May, June–July	3 mm, June	
Eusirus cuspidatus Kröyer, 1845			August
Halirages fulvocinctus (M. Sars, 1858)			July
Rhachotropis aculeata (Lepechin, 1780)			July
Rhachotropis inflata (G. Sars, 1882)			July
Rhachotropis helleri (Boeck, 1871)			July
Rhachotropis macropus G. Sars, 1893			August
Rozinante fragilis (Goes, 1866)			July
Epimeriidae			
Paramphithoe cuspidata (Lepechin, 1780)			August
Gammarellidae			
Gammarellus homari (Fabricius, 1779)	October–April	2.5 mm, April	May
Gammaracanthidae			
Gammaracanthus loricatus (Sabine, 1821)			August
Gammaridae			
Gammarus oceanicus Segerstrale, 1947	October–April	2.5 mm, April	May
Gammarus setosus Dementieva, 1931	October–April	2.5 mm, April	May
Gammarus wilkitzkii Birula, 1897	April	3 mm, May	June
Weyprechtia pinguis (Kröyer, 1838)		5 mm, July	July
Ischyroceridae			
Ischyrocerus anguipes Kröyer, 1838	May– July	2 mm, July	July
Lysianassidae s.l.			
Anonyx laticoxae Gurjanova, 1962		3 mm, April	
Anonyx nugax (Phipps, 1774)	November–June	3 mm, April	
Anonyx sarsi Steele et Brunel, 1968	November–April	3 mm, April	
Aristias sp.			July
Hippomedon propinquus (G.Sars, 1890)			July
Lepidepecreum umbo (Goes, 1866)		2mm, July	July
Menigrates obtusifrons (Boeck, 1861)		3mm, July	

Table 2 – continued.

Onisimus brevicaudatus Hansen, 1886		3 mm, May	
Onisimus caricus Hansen, 1886	September–May	3 mm, July	
Onisimus edwardsi (Kröyer, 1846)	November–May	4 mm, July	
Onisimus glacialis G. Sars, 1900		4 mm, July	
Onisimus litoralis (Kröyer, 1845)	November–April	2.5 mm, May	June
Orchomenella minuta (Kröyer, 1846)	December–May	2 mm, May	June
Stegocephalidae			
Stegocephalus inflatus Kröyer, 1842	June	3 mm, August	August
Stenothoidae			
Metopa bruzelii (Goes, 1866)			July
Synopiidae			
Syrrhoe crenulata Goes, 1866		3 mm, July	
Caprellidae			
Caprella septentrionalis Kröyer, 1838	November–May	3 mm, June	July
Hyperiidae			
Hyperoche medusarum (Kröyer, 1838)	June–August		August
Themisto abyssorum (Boeck, 1871)	December–March		
Themisto libellula (Lichtenstein, 1822)	December–March	3 mm, Feb.	July
Melitidae			
Melita dentata (Kröyer, 1842)			July
Melita formosa Murdoch, 1866			July
Melita palmata (Montagu, 1804)			July
Odiidae			
Odius carinatus (Bate, 1862)			July
Oedicerotidae			
Acanthostepheia malmgreni (Goes, 1866)	November–April	5 mm, July	August
Arrhis phyllonyx (M. Sars, 1858)	June	2.5 mm, June	July
Monoculodes borealis Boeck, 1871		2.5 mm, June	July
Monoculodes longirostris (Goes, 1866)			July
Monoculodes packardi Boeck, 1871	November–May	2.5 mm, July	July
Paroediceros lynceus (M. Sars, 1858)		2.5 mm, June	June
Phoxocephalidae			
Harpinia serrata G. Sars, 1879		2.5 mm, July	August
Phoxocephalus holbolli (Kröyer, 1842)			July
Pontoporeiidae			
Pontoporeia femorata Kröyer, 1842	June	2.5 mm, July	July
Pleustidae			
Parapleustes bicuspis (Kröyer, 1838)	May	3 mm, June	July
Parapleustes monocuspis (G. Sars, 1893)	May	3 mm, June	July
Pleustes panoplus (Kröyer, 1838)	May		
Pleusymtes glabroides Dunbar, 1954	May		

Results

Indirect evidence of hatching was observed for 20 species – namely constituting observations of newly-hatched juveniles and females with empty marsupium (Table 2). Most of the species observed incubated eggs in winter, from November till April–May; summer incubation of eggs was observed in two species (pelagic *Hyperoche medusarum* and phytal inhabitant *Ischyrocerus anguipes*). There were indications that one species (*Calliopius laeviusculus*) may have two breeding periods per year, since some females were found to incubate eggs in December–April and some in May–September. The examined species represented different life strategies; extremes were *Orchomenella minuta*, a small species laying 4 to 15 large eggs, while the equally small *Hyperoche medusarum* lays a large number (150–500) of very small eggs (Table 1). Medium-sized amphipods (*Onisimus litoralis* and *Paroediceros lynceus*) also differed in terms of eggs' number (60 to 250 respectively), whereas large species (*Anonyx nugax, Acantostepheia malmgreni*) represented similar breeding patterns with not numerous large eggs (Table 1). Reproductive effort measured after the Wildish (1982) method, divided all species into two groups – the first with low reproduction costs in the range of 1–10% (*Gammarus* spp., *Anonyx* spp., *Hyperoche medusarum*), and the second group of high reproductive costs ranging from 15 to 30% (*Weyprechtia pinguis, Gammarellus homari, Monoculodes packardi*) – Table 1. The relation of breeding costs to *K* or *r* strategy was not clear, as both types of strategies represented low and high reproductive costs (Table 1). Sex ratio divides the species studied into three groups, those with the balanced (1:1) ratio (*e.g. Gammarus* spp.), species with female predominance (*e.g. Onisimus edwardsii*), and species with strong male predominance (*e.g. Calliopius laeviusculus*) – Table 3.

Table 3

Sex ratio in examined populations, Hornsund, Svalbard, summer season.

Species	males	females	sex ratio	mean
Gammarus setosus	136	120	1.13	
Gammarus oceanicus	185	199	0.93	
				0.9
Caprella septentrionalis	44	58	0.76	
Gammarellus homari	68	125	0.54	
Orchomenella minuta	38	80	0.48	
Onisimus edwardsi	67	148	0.45	
				0.5
Anonyx nugax	28	10	2.80	
Anonyx sarsi	87	45	1.93	
Onisimus litoralis	117	43	2.72	
Caliopius laevisculus	51	14	3.64	
Paroediceros lynceus	240	133	1.80	
Monoculodes borealis	14	4	3.50	
Pleustes panoplus	34	16	2.13	
				2.6

Discussion

Most of papers on the biology of subpolar and polar marine invertebrates report strong seasonally correlated breeding as a typical pattern (Dunbar 1957, Kuznetsov 1964, Steele 1967, 1972; Steele and Steele 1972, 1975c; Thurston

1972, Clarke 1979). A stable physical environment, and well marked peak of seasonal vegetation followed by long months of low food availability (Węsławski *et al.* 1988, 1990; Węsławski 1994, Wiktor 1999) are all factors in favor of a single, well-timed brood per year. The variability of year-to-year sea surface temperature, presence or absence of sea ice, changeable freshwater inflow, *etc.* (Piechura and Walczowski 1996, Węsławski and Adamski 1987, Beszczyńska *et al.* 1997) may directly influence the intensity or the length of the algal bloom. These factors would not change the scheme of high Arctic primary production with a single bloom, governed by the solar cycle. This stability and low productivity regime, have been considered as promoting an *A* strategy in "adverse" conditions (a follow-up of *r* and *K* strategies concept Greenslade 1983). In Amphipoda it would a favor long life span, late maturity, and low reproductive costs (Sainte-Marie 1991).

Duration of life might be estimated after an analysis of the length frequency for a given population. Considering that polar amphipods breed once in a lifetime (Dunbar 1957, Kuznetsov 1964, Steele and Steele 1975, Tzvetkova 1977, Kosz-teyn *et al.* 1995) and breeding is strongly seasonally timed *i.e.* once per year (present data) we may attribute each of the length frequency peaks for separate year cohort (Table 4). A summary of the life cycles for the species studied is given in Fig. 1, which shows small species with a 1 year life span and the largest with over 4 years life expectancy. A long life span was also observed for a high Arctic ice-associated species – *Gammarus wilkitzkii* (Tzvetkova 1977, Polterman 1997). Southern-boreal populations of some of the species observed usually show a shorter life span and often two broods per year (Kuznetsov 1964, Segerstrale 1967, Jażdżewski 1970, Steele and Steele 1973, 1975b, 1976; Sainte-Marie 1991, Koszteyn *et al.* 1995, Beare and Moore 1998). Other taxa of Peracarida in the Svalbard area, like mysids and decapods, show similar patterns in breeding (Węsławski 1987, 1989).

The minimal size of mature females plays a key role in the number of eggs laid in amphipods (Steele and Steele 1975a). Females of amphipods observed in the Svalbard area belong to the largest specimens known in their species. The same is true for the egg diameter (mean 0.6 mm) when compared to the 0.4 mm mean egg diameter for temperate populations of amphipods (Van Dolah and Bird 1980, Nelson 1980, Wildish 1982). The size of egg is related to the incubation temperature and its duration in marine poikilotherms (Marshall 1953). As was estimated by Steele and Steele (1975) a gammaridean egg of 1.00 mm diameter needs some 120 days for incubation in cold temperate sea. This value is in accordance with the incubation time presented here (about 150 days). A larger egg size yields even longer incubation time, as was observed in Antarctic lysianassoid amphipods (Thurston 1972). The largest specimens of egg-bearing females in our collection were found in August (*Anonyx nugax, Ampelisca eschrichtii* and *Acanthostepheia malmgreni*), when their eggs diameter ranged to 1.5 mm – comparable to the size of decapod eggs incubated for 9–10 months in Antarctica (Clarke 1979).

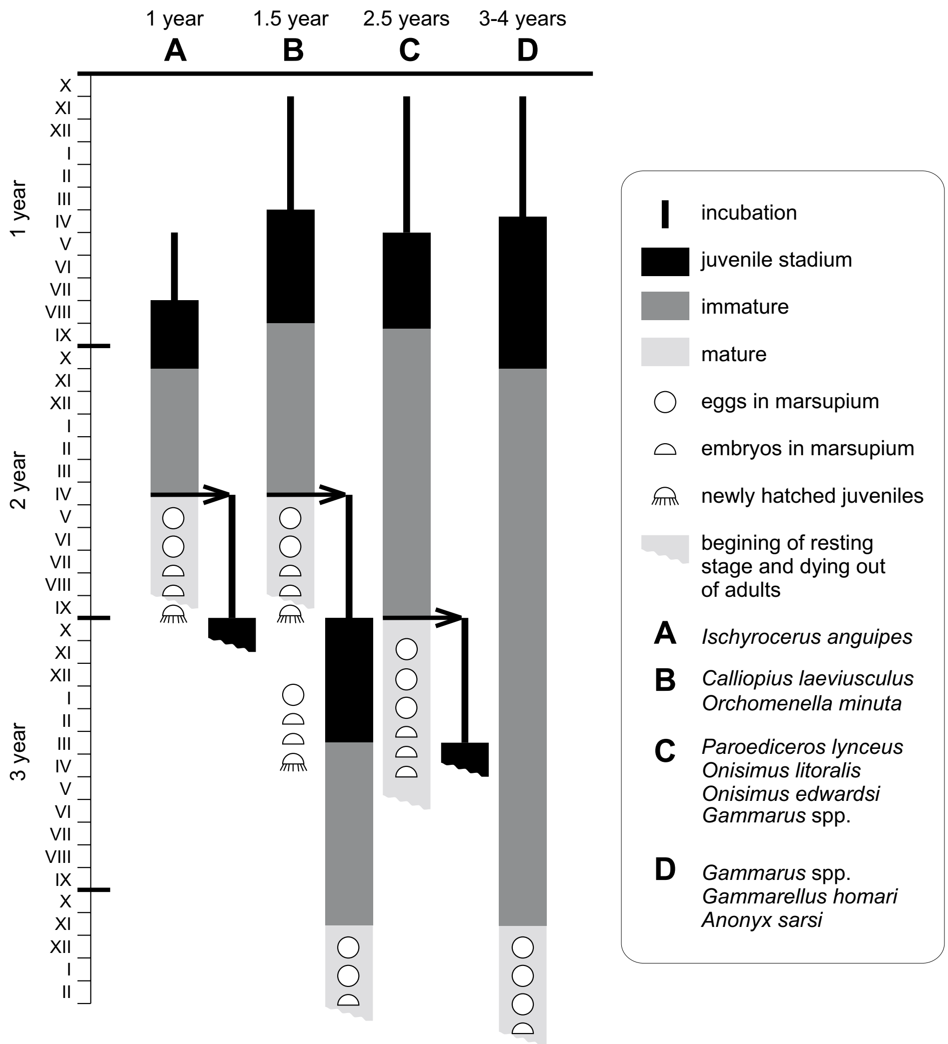

Fig. 1. Life history diagrams of Svalbard amphipods.

The only clear example of *r* strategy in our collection was the small, pelagic, summer-breeding *Hyperoche medusarum*. Abundant early autumn zooplankton may serve as a predictable food source for the rapid development of *H. medusarum* juveniles.

The calculation of reproductive costs in Svalbard amphipods shows twice higher costs (mean of 11.2%), when compared to southern counterparts (mean of 5.6%, Wildish 1982). The present review of the breeding biology of Svalbard amphipods shows little variance in strategies and confirms the view of the domination of *K* (or *A* sensu Greenlade 1983) strategy in cold water crustaceans (Clarke 1979, 1980, Sainte-Marie and Brunel 1983, Sainte Marie 1991). Since the breeding of

Table 4

Estimated life span and lenght frequency for some of the examined species in summer, Svalbard.

length mm	estimated age	*Caprella septentrionalis* n = 38; August	*Gammarellus homari* n = 86; September	*Gammarus setosus* n = 30; June	*Paroediceros lynceus* n = 257; June	*Anonyx nugax* n = 73; July	*Onisimus edwardsi* n = 90; July	*Onisimus caricus* n = 84; July	*Anonyx sarsi* n = 90; July
4	1st year			5	60				
5	1st year			25				3.6	
6	1st year		10	20				12.0	
7	1st year							5.0	
8	1st year				10	6.8	2.2	5.0	2.2
9	1st year					6.8	38.9	3.6	10.0
10	1st year	3.4					45.6	7.1	12.2
11	2nd year						13.3	6.0	12.2
12	2nd year	12.3						3.0	2.2
13	2nd year							3.0	0.0
14	2nd year	16.8	10	5	10			3.0	0.0
15	2nd year					1.4		1.2	1.1
16	2nd year	25.1		5	10	8.2			2.2
17	2nd year					5.5		1.2	1.1
18	2nd year	12.3	15	15		5.5		4.8	1.1
19	2nd year					2.7		16.0	3.3
20	2nd year	23.5	15	8	10			9.5	10.0
21	2nd year					1.4		8.3	17.8
22	2nd year	3.4	20	7		1.4		4.0	14.4
23	2nd year							6.0	5.6
24	2nd year		20			5.5		1.2	3.3
25	2nd year					9.6			1.1
26	3rd year	3.4	4			8.2			
27	3rd year					1.4			
28	3rd year		2	5		2.7			
29	3rd year					1.4			
30	3rd year		2	5		1.4			
31	3rd year								
32	3rd year								
33	3rd year					1.4			
34	3rd year		2			1.4			
35	4th year					2.7			
36	4th year					4.1			
37	4th year					9.6			
38	4th year					2.7			
39	4th year					2.7			
40	4th year					4.1			
41	4th year					1.4			

most of the species observed is synchronised with algal development, which in turn is fully controlled by the solar cycle (Wiktor 1999), it seems unlikely that the predicted temperature increase will change the life patterns of Svalbard amphipods. Even with slightly faster eggs' incubation there is only a narrow window in time when juveniles may be released to find abundant food in High Arctic latitudes.

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References

BEARE D.J. and MOORE P.G. 1998. The life histories of the offshore oedicerotids *Westwodilla caecula* and *Monoculodes packardi* (Crustacea: Amphipoda) from Loch Fyne, Scotland. — Journal of Marine Biological Association of United Kingdom, 78: 835–852.

BESZCZYŃSKA-MÖLLER A., WĘSŁAWSKI J.M., WALCZOWSKI W. and ZAJĄCZKOWSKI M. 1997. Estimation of glacial meltwater discharge into Svalbard coastal water. — Oceanologia, 39: 289–297.

CLARKE A. 1979. On living in cold water: *K* strategies in Antarctic benthos. — Marine Biology, 55: 111–119.

CLARKE A. 1980. A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. — Biological Journal of Linean Society, 14: 77–92.

DOLAH VAN, R.F. and BIRD E. 1980. A comparison of reproductive parameters in epifaunal and infaunal gammaridean amphipods. — Estuarine, Coastal and Shelf Science, 11: 593– 604.

DUNBAR M.J. 1957. The determinants of production in northern seas. A study on the biology of *Themisto libellula*. — Canadian Journal of Zoology, 35: 797– 819.

EILERTSEN H.Ch., TAASEN J.P. and WĘSŁAWSKI J.M. 1989. Phytoplankton studies in the fjords of West Spitsbergen. Physical environment, production in spring and summer. — Journal of Plankton Research, 11: 1245–1260.

GULLIKSEN B., PALERUD R., BRATTEGARD T. and SNELI J.A. 1999. Distribution of marine benthic macro-organisms at Svalbard (including Bear Island) and Jan Mayen. — Research Report for DN 1999, 4: 1–148.

GREENSLADE P.J.M. 1983 Adversity selection and the habitat templet. — American Naturalist, 122: 352–365

JAŻDŻEWSKI K. 1970. Biology of Crustacea Malacostraca in the Bay of Puck, Polish Baltic Sea. — Zoologica Poloniae, 20: 423–484.

JAŻDŻEWSKI K., WĘSŁAWSKI J.M. and DE BROYER C. 1995. A comparison of the amphipod faunal diversity in two polar fjords: Admiralty Bay, King George Island (Antarctic) and Hornsund, Spitsbergen (Arctic). — Polskie Archiwum Hydrobiologii, 42: 367–384.

KOSZTEYN J., TIMOFEEV S., WĘSŁAWSKI J.M. and MALINGA B. 1995. Size structure of *Themisto abyssorum* Boeck and *Themisto libellula* (Mandt) populations in European Arctic seas. — Polar Biology, 15: 85–92.

KUZNETSOV V.V. 1964. Biologija massovykh i najbolee obycnykh vidov rakoobraznykh Bielogo i Barentsogo moriej. Moskva–Leningrad, Nauka; 241 pp.

LAGARDERE J.P. 1968. Les crustacees de l'Expedition Francaise RCP 42 au Spitsberg (été 1966). — Bulletin Centre Études des Recherches Scientifiques, Biarritz, 7: 1–36.

LEGEŻYŃSKA J. 2001. Distribution patterns and feeding strategies of lysianassoid amphipods in shallow waters of an Arctic fjord. — Polish Polar Research, 22: 173–186.

MARSHALL N.B. 1953. Egg size in Arctic, Antarctic and deep sea fishes. — Evolution, 7: 328–341.

NELSON W.G. 1980. Reproductive patterns in gammaridean amphipods. — Sarsia, 65: 61–71.

PALERUD R. and VADER W. 1991. Marine Amphipoda Gammaridea in North- East Atlantic and Norwegian Arctic. — Tromura Naturvitenskap, 68: 1–97.

PIECHURA J. 1993. Hydrological aspects of the Norwegian-Barents confluence zone. — Studia i Materiały Oceanologiczne, 65: 197–222.

PIECHURA J. and WALCZOWSKI W. 1996. Interannual variability in the hydrophysical fields of the Norwegian-Barents Seas confluence zone. — Oceanologia, 38: 81–98.

POLTERMANN M. 1997. Biology and ecology of cryopelagic amphipods from Arctic Sea ice. — Berichte zur Polarforschung, 225: 1–170.

SAINTE-MARIE B. 1991 A review of the reproductive bionomics of aquatic gammaridean amphipods: variation in life history traits with latitude, depth salinity and superfamly. — Hydrobiologia, 223: 189–227.

SAINTE-MARIE B. and BRUNEL P. 1983. Differences in life history and success between suprabenthic shelf populations of *Arrhis phyllonyx* (Amphipoda Gammaridea) in two ecosystems of the Gulf of St. Lawrence. — Journal of Crustacean Biology, 3: 45–69.

SAINTE-MARIE B., LAMARCHE G. and GAGNON J.M. 1990. Reproductive bionomics of some shallow water lysianassoids in the St. Lawrence Estuary, with a review on the fecundity of the Lysianassoidea (Crustacea, Amphipoda). — Canadian Journal of Zoology, 68: 1639–1644.

SEGERSTRALE S. 1967. Observations of summer breeding populations of the glacial relict *Pontoporeia affinis* Lindstr. (Crustacea, Amphipoda), living at greater depths in the Baltic Sea with notes on the reproduction of *P. femorata* Kroyer. — Journal of Experimental Marine Biology and Ecology, 1: 55–64.

STEELE D.H. 1967. The life cycle of the marine amphipod *Stegocephalus inflatus* Kroyer in the Northwest Atlantic. — Canadian Journal of Zoology, 45: 623–628.

STEELE D.H. and STEELE V.J. 1970. The biology of *Gammarus* (Crustacea, Amphipoda) in northwestern Atlantic. II. *Gammarus setosus* Dementieva. — Canadian Journal of Zoology, 48: 659–671.

STEELE D.H. and STEELE V.J. 1972a. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. V. *Gammarus oceanicus* Segerstrale. — Canadian Journal of Zoology, 50: 801–813.

STEELE D.H. 1972b. Some aspects of the biology of *Gammarellus homari* (Crustacea, Amphipoda) in the northwestern Atlantic. — Journal Fisheries Research Board of Canada, 29: 1340–1343.

STEELE D.H. and STEELE V.J. 1973. Some aspects of the biology of *Calliopius laeviusculus* (Kroyer) (Crustacea, Amphipoda) in the northwestern Atlantic. — Canadian Journal of Zoology, 51: 723–728.

STEELE D.H. and STEELE V.J. 1975a. Egg size and duration of embryonic development in Crustacea. — International Revue Gesellshaft Hydrobiologie, 60: 711–715.

STEELE D.H. and STEELE V.J. 1975b. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. XI. Comparison and discussion. — Canadian Journal of Zoology, 53: 1116–1126.

STEELE D.H. and STEELE V.J. 1975c. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. IX. *Gammarus wilkitzkii* Birula, *Gammarus stoerensis* Reid, and *Gammarus mucronatus* Say. — Canadian Journal of Zoology, 53: 1105–1109.

STEELE D.H. and STEELE V.J. 1978. Some aspects of the biology of *Pontoporeia femorata* and *Pontoporeia affinis* (Crustacea, Amphipoda) in the northwestern Atlantic. — Astarte, 11: 61–66.

STEPHENSEN K. 1935–40. The Amphipoda of N. Norway and Spitsbergen with adjacent waters. — Tromsø Museum Skrifter, 3: 1–525.

SVENDSEN H., BESZCZYŃSKA-MOLLER A., HAGEN J.O., LEFAUCONNIER B., TVERGERG V., GERLAND S., ORBAEK J.B., BISCHOF K., PAPUCCI C., ZAJĄCZKOWSKI M., AZZOLINI R., BRULAND O., WIENECKE C., WINTHER J-G. and DALLMANN W 2002 The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. — Polar Research, 21: 133–166.

SWERPEL S. 1985. The Hornsund fjord water masses. — Polish Polar Research, 6: 475–496.

THURSTON M.H. 1972. The Crustacea Amphipoda of Signy Island, Southern Orkney Islands. — British Antarctic Survey, Scientific Reports, 71: 1–133.

TZVETKOVA N.L. 1977. Some peculiarities of ecology, growth and production of two species of gammarids (Amphipoda, Gammaridea) in high latitudes of the Arctic. — Issledovanija Fauny Morej, XIV (XXII): 291–298.

WĘSŁAWSKI J.M. 1987. Occurrence and ecology of Decapoda Crustacea from Spitsbergen. — Polish Polar Research, 8: 121–134.

WĘSŁAWSKI J.M. 1989. Occurrence and life cycle of *Mysis oculata* (Crustacea) from Spitsbergen. — Polskie Archiwum Hydrobiologii, 36: 207–215.

WĘSŁAWSKI J.M. 1990. Distribution and ecology of coastal waters amphipods from Southern Spitsbergen. — Polskie Archiwum Hydrobiologii, 37: 503–519.

WĘSŁAWSKI J.M. 1994. Genus *Gammarus* (Crustacea, Amphipoda) from Svalbard and Franz Josef Land. Distribution and density. — Sarsia, 79: 145–150.

WĘSŁAWSKI J.M. and ADAMSKI P. 1987. Cold and warm years in South Spitsbergen coastal marine ecosystem. — Polish Polar Research, 8: 95–106.

WĘSŁAWSKI J.M. KWAŚNIEWSKI S. and WIKTOR J. 1990. Winter in a Svalbard fjord ecosystem. — Arctic, 44: 115–123.

WĘSŁAWSKI J.M., OPALIŃSKI K.W. and LEGEŻYŃSKA J. 2000. Life cycle and production of *Onisimus litoralis* (Crustacea, Amphipoda): the key species in the Arctic soft sediment littoral. — Polskie Archiwum Hydrobiologii, 47: 585–596.

WĘSŁAWSKI J.M., JANKOWSKI A., KWAŚNIEWSKI S., SWERPEL S. and RYG M. 1991. Summer hydrology and zooplankton in two Spitsbergen fjords. — Polish Polar Research, 12: 445–460.

WĘSŁAWSKI J.M., ZAJĄCZKOWSKI M., KWAŚNIEWSKI S., JEZIERSKI J. and MOSKAL W. 1988. Seasonality in an Arctic fjord ecosystem. — Polar Research, 6: 185–189.

WIKTOR J. 1999. Early spring microplankton development under fast ice covered fjords of Svalbard, Arctic. — Oceanologia, 41: 51–72.

WILDISH D.J. 1982. Evolutionary ecology and reproduction in gammaridean amphipods. — International Journal of Invertebrates Reproduction, 5: 1–19.

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