A-58

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Life cycle and production of *Onisimus litoralis* (Crustacea Amphipoda): The key species in the Arctic soft sediment littoral

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Abstract

The common Arctic species *Onisimus litoralis* (Krøyer, 1845) was collected in the littoral of the Svalbard archipelago from 1984 to 1997 with various kinds of sampling gears. The species was noted in 49 of the 180 investigated localities with mean density of 192 indiv. m^{-2} and mean biomass of 2.1 g ww m^{-2}. Its occurrence was generally limited to waters less than five meters in depth, thus this common species has a very narrow distribution and is susceptible to any environmental stress that may occur in the intertidal. *O. litoralis* is a dominant macrobenthic taxon of the tidal flats, constituting up to 95% of the total fauna density. In such habitats it can reach high abundance and biomass of 6000 indiv. m^{-2} and 42 g ww m^{-2} respectively. Studied population of *O. litoralis* had a 2.5-year life-span with a single brood incubated from November to April/May. Finding several large spawned – out females (exceeding 20 mm) in late summer confirmed their greater longevity. This species is represented by a typical K breeding strategy with 30–60 large (0.9mm diameter) eggs laid by 17mm long females. Its production is estimated between 6.4 and 19.3 kJ m^{-2} yr^{-1} in the Svalbard intertidal flats.

Key words: Arctic, littoral, Lysianassidae, Amphipoda

1. Introduction

The genus *Onisimus* is currently represented by some 26 species restricted in their distribution to the northern boreal, Arctic waters and Caspian Sea (Gurjanova 1951, Just 1980, Palerud, Vader 1991, Lowry, Stoddart 1993). One of the most common species of this group is *Onisimus litoralis*, referred to as *Pseudalibrotus litoralis* in the older literature (Holmquist 1965, Gurjanova 1951). This species is commonly found in the intertidal waters of the Arctic

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(Holmquist 1965, Węsławski 1990), but it may also occur under the fast ice cover in coastal areas (Bradstreet, Cross 1982, Boudrias, Carey 1988, Gulliksen, Lonne 1991). Since it inhabits easy accessible localities, *O. litoralis* has been the subject of numerous physiological and biochemical studies (Szaniawska, Wołowicz 1986a, b, Opaliński, Węsławski 1989, Shea, Percy 1990, Węsławski, Opaliński 1997). The only published information on the biology of this species comes from research conducted in the northern temperate Gulf of St. Lawrence (Sainte-Marie *et al.*1990) and the low Arctic Beaufort Sea (Boudrias, Carey 1988). Its feeding habits were studied in detail by Carey, Boudrias (1987) and Sainte-Marie *et al.* (1989, 1990). There is a lack of information on the biology, feeding and production of this species from the high Arctic. *O. litoralis* is a food source for waders (*Calidris* spp.), Black guillemots (*Cephhus grylle*), eiders (*Somateria* spp.) and Arctic terns (*Sterna* spp.) (Bradstreet 1980, Stempniewicz, Węsławski 1992). The aim of the present study is to describe the life cycle and estimate the biomass and density of this species in the Svalbard archipelago.

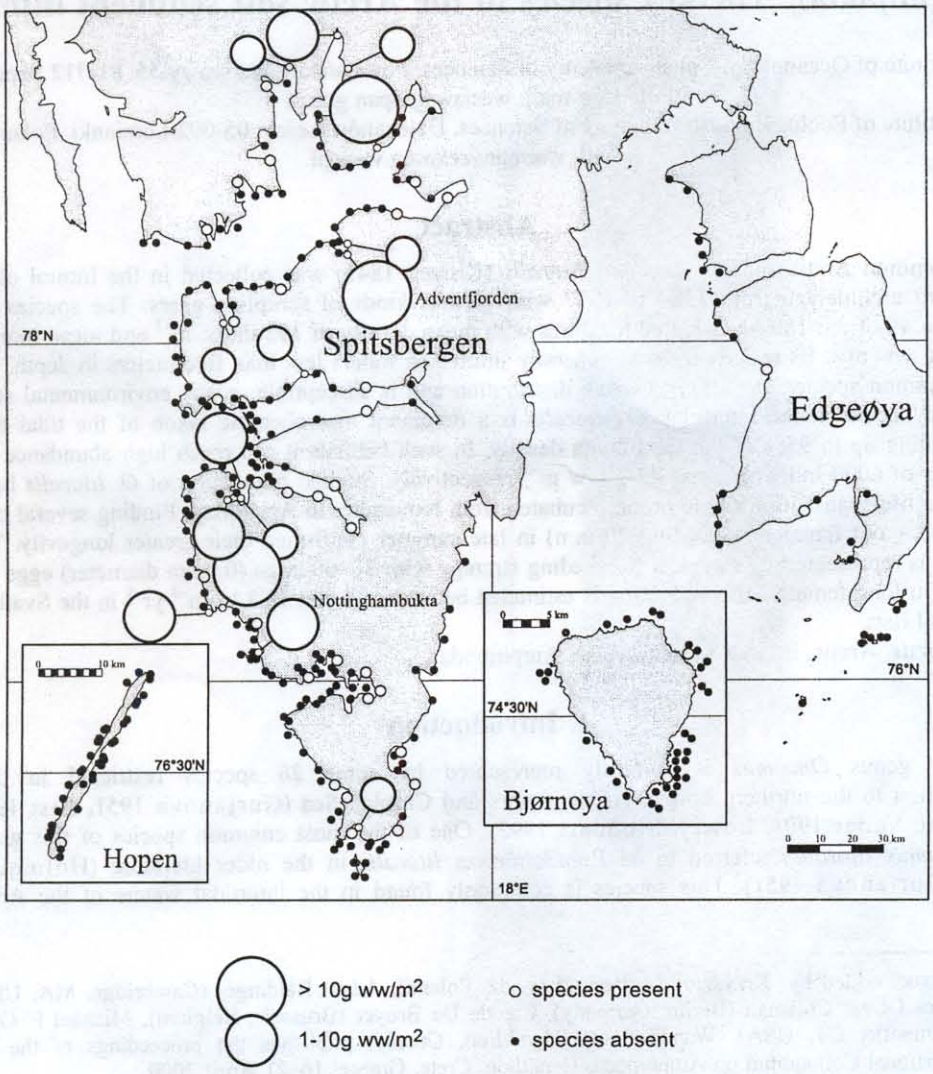

Fig. 1. Occurrence of *O. litoralis* in the littoral of Svalbard archipelago

2. Materials and methods

O. litoralis was collected with various kinds of sampling gear over a large area of Svalbard from 1984 to 1997 (Węsławski *et al.* 1997, Fig. 1). Data for population studies were taken from quantitative samples collected with a tube 30 cm in diameter inserted to a depth of 20 cm into the sediment. Samples were collected monthly, during low tide in two tidal flats (Nottinghambukta at 77°N in 1984–85 and Adventfjorden at 78°N in 1996–97). The specimens were sieved on 0.5mm screens, preserved in 4% formaldehyde and analysed some months later in the laboratory. Specimen length was measured from the tip of the head to the tip of the telson to the nearest 0.1 mm. The wet weight was determined to within 1mg of accuracy after gently blotting the specimen on filter paper and dry weight was determined after drying in 65°C for 24 hours. Individuals were classified either as juvenile (no secondary sexual characteristics), immature (early oostegites in females and copulatory papillae in males) or adult (setiferous oostegites in females and elongated antennulae in males). Eggs were removed from the marsupium, counted and measured to the nearest 0.01 mm. Female volume was estimated as $nd^2 \times L$ (d – the height of the fourth pereon segment, L – body length). Egg volume was estimated as $4/3nr^3$ (r – mean from the long and short egg radius). The following equations and coefficients were adopted:

1 cm^3 assimilated O_2 = 4.687 kcal, 1 g assimilated O_2 = 3.28 kcal, 1 kcal = 4.186 kJ (Remmert 1985). Productivity efficiency = 36.2% for detritophagic invertebrates, net production = productivity efficiency × O_2 assimilation (Krebs 1997).

The measurements of oxygen consumption of animals were carried out in October 1996 at the University Studies on Svalbard (UNIS), Longyearbyen. Animals were collected from nearby Adventfjorden tidal flat. Oxygen consumption of single individuals of *O. litoralis* were measured using closed vessel method. Oxygen concentration was measured by WTW OXI 3000 oxygen meter; a vessel with capacity of 100 cm^3 was used. The measurements were done in natural conditions, i.e. the temperature of –0.8°C and salinity 34 PSU. Energetic value of animals was determined at the Institute of Ecology Polish Academy of Sciences, using a micro-bomb calorimeter, model elaborated by Klekowski, Bęczkowski (1973).

3. Results

Distribution, density and biomass

O. litoralis was found in 49 of the 180 investigated localities on Spitsbergen and in single localities on other islands of the archipelago (Fig. 1). Maximum densities were about 6000 indiv. m^{-2}, but most commonly 192 indiv. m^{-2} with a biomass ranging to 42 g ww m^{-2} (Tab. I).

Table I. Mean and maximal values of the biomass and density of *Onismus litoralis* along the Svalbard coast

	Biomass (g ww m^{-2})	Density (indiv. m^{-2})	Estimated energy value (kJ m^{-2})
Mean	2.1	192	8.4
Maximal	42	6000	167.4
SD	2.0	188	
n= 42 samples			

Place in coastal assemblages

O. litoralis was found in different habitats, but its share in the littoral assemblages changes depending on the substrate character (Tab. II). In places with numerous stones, other amphipods (*Gammarus setosus* and *G. oceanicus)* are more abundant, among intertidal vegetation *Ischyrocerus* spp. and small polychaetes compose the bulk of the biomass. *O. litoralis* accounts up to 95% of the macrofauna density in soft bottom tidal flats (Tab. II)

Table II. Position of *Onisimus litoralis* in coastal assemblages of Spitsbergen, F% – frequency of occurrence, D% – abundance contributions, n= number of localities examined

	Soft bottom tidal flats	Stones and mud shallows	Intertidal mud and gravel with macrophytes	Shallow sublittoral gravel	Shallow sublittoral macrophytes
	n=12	n= 60	n= 6	n=30	n=25
F %	100	50	30	20	20
D %	95	20	10	20	10

Breeding

Some of the biological parameters analysed for this species are shown in Table III. The minimum size of females with a brood was 12.5mm, the maximum 19.5. The number of eggs in a brood pouch ranged from 30 to 60, and the egg diameter was consistently large – with a mean of 0.9 mm. The life cycle of *O. litoralis* was analysed in the Nottinghambukta tidal flat population and shows that the first females with eggs in their marsupium were found in November (Fig. 2). Eggs were incubated for 5–6 months, and the first juveniles hatched in April/May. Juveniles grow until autumn and spend winter as immature specimens, reach adult size by next autumn, hence, closing the life cycle in 2.5 years (Fig. 3). There were some females in the resting stage (large oostegites with poor setation) exceeding 20mm in length, with one record specimen of 25 mm collected in July. The size difference between the smallest (12.5 mm) and the largest (25mm) adult female may suggest a second brood and a 3.5 year life span in some specimens.

Bioenergetical parameters

Animals used for oxygen consumption measurements were juveniles of 13 mm and 70 mg wet weight, females of 16 mm and 79 mg ww and males of 15 mm and 86 mg wet weight. The average consumption for all sex and age categories was 18 mm^3 $ind.^{-1}$ h^{-1} and metabolic rate (wet weight basis) 0.227 mm^3 mg^{-1} h^{-1} (Tab. IV and V). Energetic value of *O. litoralis* was 15.1 J mg^{-1} dry weight basis and 3 J mg^{-1} wet weigh basis (Tab. VI).

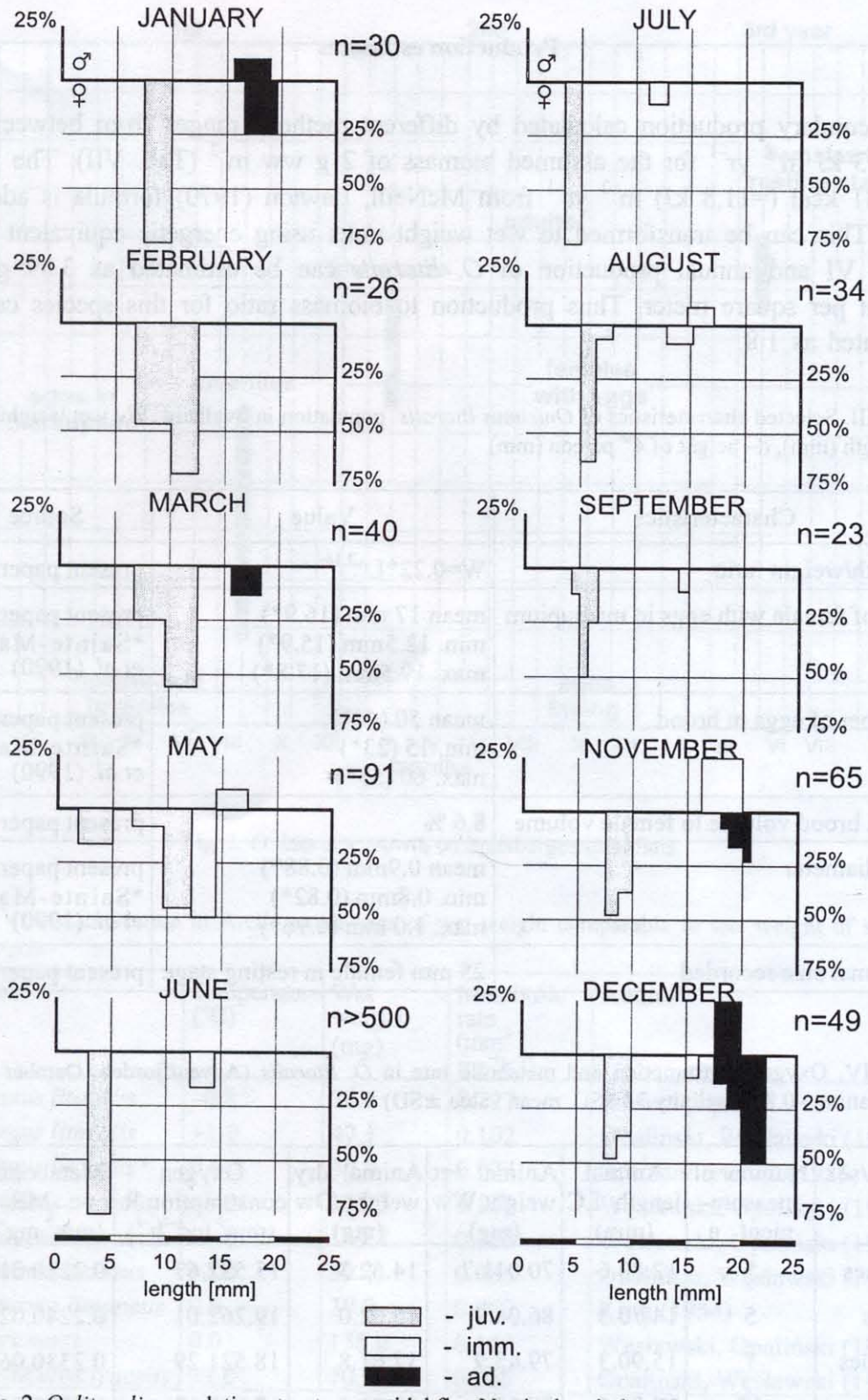

Fig. 2. *O. litoralis* population structure on tidal flat, Nottinghambukta. N – number of animals analysed, males above, females below the axis

Production estimates

Secondary production calculated by different methods ranges from between 6.4 to 19.3 kJ m^{-2} yr^{-1} for the assumed biomass of 2 g ww m^{-2} (Tab. VII). The value of 2.81 kcal (=11,8 kJ) m^{-2} yr^{-1} from McNeill, Lawton (1970) formula is adopted here. This can be transformed to wet weight units using energetic equivalent from Table VI and annual production of *O. litoralis* can be estimated as 3.89 g wet weight per square meter. Thus production to biomass ratio for this species can be estimated as 1.8.

Table III. Selected characteristics of *Onisimus litoralis* population in Svalbard. W– wet weight (mg), L– length (mm), d– height of 4th pereon (mm)

Characteristics	Value	Source
Length/weight ratio	W=0.22*L^2.14	present paper
Size of female with eggs in marsupium	mean 17 mm (16.9*) min. 12.5mm (15.9*) max. 19.5mm (17.8*)	present paper, *Sainte-Marie *et al.* (1990)
Number of eggs in brood	mean 50 (44*) min. 15 (23*) max. 60 (55*)	present paper, *Sainte-Marie *et al.* (1990)
Mean brood volume to female volume	8.6 %	present paper
Egg diameter	mean 0.9mm (0.88*) min. 0.8mm (0.82*) max. 1.0 mm (0.96*)	present paper, *Sainte-Marie *et al.* (1990)
Maximal size recorded	25 mm female in resting stage	present paper

Table IV. Oxygen consumption and metabolic rate in *O. litoralis* (Adventfjorden, October 1996, temperature: –0.8°C, salinity 34 PSU, mean value ±SD)

Stage/sex	Number of measure-ment n	Animal length LC (mm)	Animal wet weight Ww (mg)	Animal dry weight Dw (mg)	Oxygen consumption R (mm^3 $ind^{-1}h^{-1}$)	Metabolic rate MR (mm^3 mg^{-1} h^{-1})
Juvenes	5	12.80.6	70.011.7	14.62.3	15.582.67	0.2230.014
Males	5	14.70.3	86.04.9	15.02.0	19.262.01	0.2240.028
Females	7	15.90.3	79.45.9	12.61.8	18.521.29	0.2330.061
All	17	14.90.5	78.64.4	13.91.1	17.881.10	0.2270.036

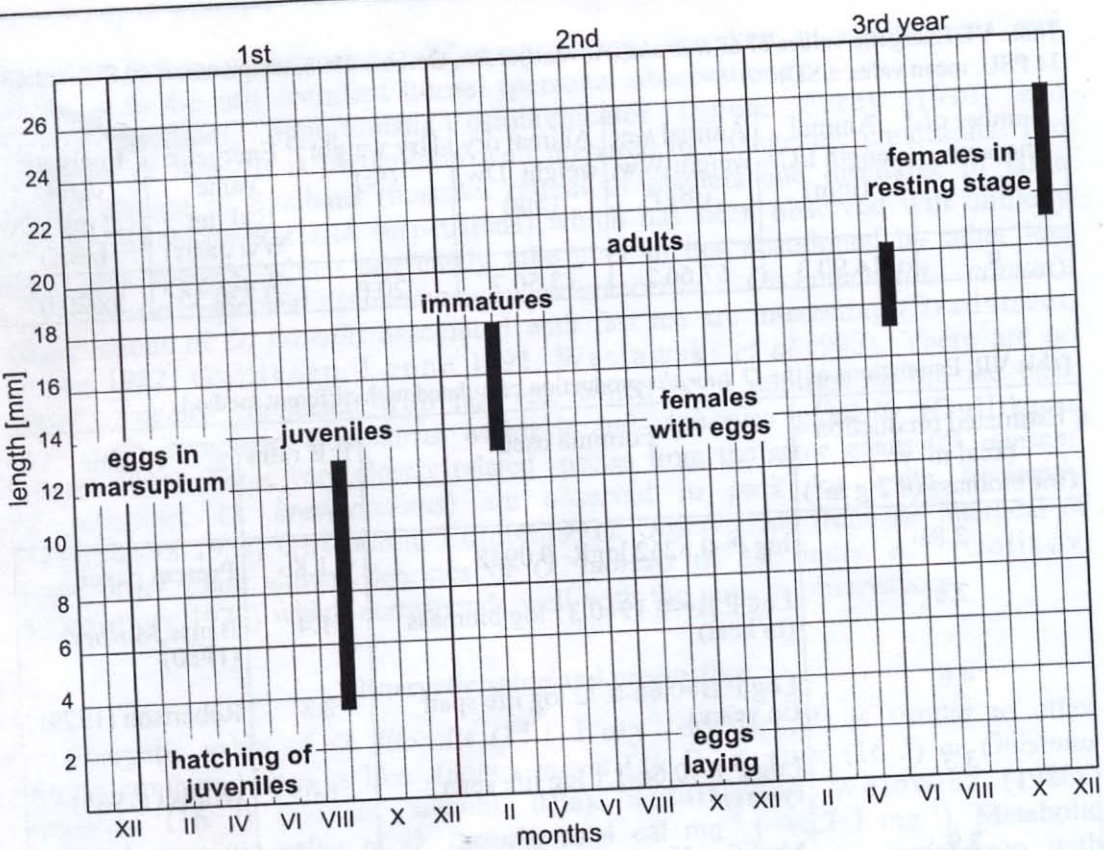

Fig. 3. *O. litoralis* growth on Spitsbergen tidal flats

Table V. Metabolic rate in Arctic amphipods of wet weight comparable to wet weight of studied *O. litoralis*

Species	Temperature (°C)	Wet weight (mg)	Metabolic rate ($mm^3 mg^{-1}h^{-1}$)	Author
Onisimus litoralis	–0.8	78.6	0.227	Present paper
Onisimus litoralis	+1.0	47.1	0.102	Opaliński, Węsławski (1989)
*Onisimus litoralis**	0.0	30.0	0.077	Scholander *et al.* (1953)
Gammarus oceanicus	–1.0	128.5	0.189	Węslawski, Opaliński (1997)
Gammarus setosus	–1.6	149.7	0.126	Węsławski, Opaliński (1997)
Gammarus setosus	+2.0	59.1	0.085	Opaliński, Węsławski (1989)
Gammarus limaneus	0.0	30.0	0.060	Krog (1954)
Anonyx sarsi	0.0	155.0	0.149	Węsławski, Opaliński (1997)
Paroediceros lynceus	+2.0	70.9	0.055	Opaliński, Węsławski (1989)

*in original paper *Pseudalibrotus litoralis*.

Table VI. Energetic values of *O. litoralis* (Adventfjorden, October 1996, temperature: –0.8°C, salinity 34 PSU, mean vales ±SD)

Number of measure-ment	Animal length LC, (mm)	Animal wet weight Ww, (mg)	Animal dry weight Dw, (mg)	Dry weight (%)	Energetic value (cal mg^{-1} Ww basis)	Energetic value (cal mg^{-1} Dw basis)
9	14.90.3	67.66.2	13.50.7	20.0	0.720.35	3.620.07

Table VII. Estimations of the *O. litoralis* production calculated with different methods

Estimated production (kcal m^2 yr^{-1}) (for biomass of 2 g m^{-2})	Formula used	P:B ratio	Author
2.81	log P=0.8262 logR- 0.0948	1.8	Present paper
2.8	Log P:B=-0.19+0.37 log biomass (in kcal)	1.4	Banse,Mosher (1980)
4.6	Log P:B=0.66-0.72 log life span (in years)	2.3	Robertson (1979)
3.3	Log P:B=0.66-1.1 log life span (years)	1.65	Wildish (1984)
2.9	Modified Hynes method	1.5	Wildish (1980)
1.54	$P_{(t1-t2)}$=EN*dw	0.77	Crisp (1971)

4. Discussion

Position in littoral assemblages

O. litoralis was attracted by baited traps exposed at a shallow depth, which suggests that this species takes carrion or is a facultative carnivore (Sainte-Marie *et al.* 1989, 1990, Węsławski 1990, Legeżyńska *et al.* 2000). On the other hand, gut analyses performed on specimens collected from the Longyearbyen tidal flat in late June, shows the presence of microphytobenthic diatoms (Węsławski, Wiktor, unpubl.). Data from ice associated *O. litoralis* suggest that this species is an opportunistic omnivore (Carey, Boudrias 1987, Sainte-Marie *et al.* 1989). There are few consumers from the higher trophic levels that feed on Arctic littoral. Small waders (*Calidris maritima, C. alpina, Charadrius hiaticula*) comprise, at best, concentrations of up to 1000 individuals in the Longyearbyen tidal flat, while in other places at one time from several to dozens of birds can be observed.

However, when waders occur, *Gammarus* spp. is taken in stony areas and *Onisimus* in the soft sediment littoral (personal observations).

The intertidal, opportunistic osmoregulator (Shea, Percy 1990) and omnivore *O. litoralis* is particularly well prepared to changeable conditions. The coastal change in Svalbard (massive retreat of glaciers and discharge of large amounts of freshwater and suspensions) which has been observed will unlikely affect this species, which can easily take over niches abandoned by other less opportunistic species (*Gammarus, Ischyrocerus, Orchomenella minuta*). Observations of *O. litoralis* associated with fast ice are interesting (Bradstreet, Cross 1982, Gulliksen, Lonne 1991, Węsławski *et al.*1993). There are no specific species connected with fast ice, which is in contrast to the ice pack biota with sympagic *Gammarus wilkitzkii* and *Apherusa glacialis* (Gulliksen, Lonne 1991). Three very closely related species from the same genus (*O. nanseni, O. pelagicus, O. brevicaudatus*) are observed in pack ice quite frequently (Gurjanova 1951, Gulliksen, Lonne 1991). Observations from the intertidal of Franz Josef Land shown densities of *O. litoralis* of 200 indiv. m^{-2} (Golikov, Averintzev 1977) which corresponds well with the present observations.

Energetic value and production

Energetic value of *O. litoralis* (15.1 J mg^{-1} dry weight) is similar to other Arctic amphipod species like *Anonyx nugax* (16 J), *A. sarsi* (16 J) or *Onisimus edwardsi* (16 J) (authors' unpubl. data). Szaniawska, Wołowicz (1986a) reported energetic value of *O. litoralis* as 4 cal mg^{-1} (=16.7 J mg^{-1}). Metabolic rate of *O. litoralis* measured in present paper is higher in comparison with literature data for this species and other species from Arctic littoral/ tidal flat zone (Tab. V). This difference can be a result of differences in temperature and season in which measurements were done. Calculated annual production of *O. litoralis* depends on metabolic rate value which was used for calculations. If we use lower metabolic rate, e.g. 0.102 mm^3 mg h (Opaliński, Węsławski 1989) the P value will be 6.4 kJ m^2 yr^{-1}. Both calculated production values: 11.7 and 6.4 are in the range of literature data on this subject (Tab. VII).

Breeding

O. litoralis exhibits a life cycle typical for medium sized Arctic amphipods with one brood in a lifetime, a long winter incubation of large eggs and a 2.5 year life cycle (Kuznetsov 1964, Steele, Steele 1975). This typical K breeding strategy seems to be universal in both Arctic and Antarctic benthic crustaceans and fishes (Thorson 1950, Clarke 1980). Holmquist (1965) reports 19 mm long ovigerous female which is larger than the average from Svalbard, while Boudrias, Carey (1988) and Sainte-Marie *et al.* (1990) present data which are very similar to those presented in this study (Tab. III). The reproductive effort (percent of brood volume to female volume) of *O. litoralis* females is relatively low (8.6%), when compared with other amphipods

from Spitsbergen, where this figure ranges from 5 to 30% (authors' data). Large eggs and large female size were found to be typical patterns for brackish water and winter breeding amphipods in general (Nelson 1980, Van Dolah, Bird 1980). Size of mature females (13.5 mm) found in the low Arctic (70°N, Boudrias, Carey 1988) was smaller than size at maturity observed in present study. The April-May release of juveniles was similar in Beaufort Sea and Spitsbergen. The breeding seasonality, fecundity and size of ovigerous females from the southernmost population of *Onisimus* (47°N, Sainte-Marie *et al.* 1990), were very consistent with that which is shown in the present study (78°N). This is in contrast with variable biota and food types utilised by this opportunistic species.

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