



Annual routines and life history of the amphipod *Onisimus litoralis*: seasonal growth, body composition and energy budget

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ABSTRACT: The scheduling of life history events over the year is a central characteristic of organisms in seasonal environments. Here, we report on seasonality in growth rate and cellular energy allocation, as well as timing of maturation, egg production and brood release, through a full annual cycle of *Onisimus litoralis*, a lysianassoid amphipod dominating soft bottoms in the intertidal zone in the high Arctic. We observed that *O. litoralis* follows a semelparous 2 yr life cycle, with growth and development mainly taking place in summer, but with slow growth also in winter, which with the lack of energy reserves suggests that it feeds year-round. The importance of the spring bloom of phytoplankton in fueling growth and development is reflected in carbohydrate and protein content. Relatively stable lipid content and no build-up of energy stores prior to egg production indicate income breeding. Seasonal differences in energy consumption are apparent, with higher consumption in summer, but as a result of increased energy content during summer, the energy budget remains relatively stable during the whole year. The life history observed is similar to that of previous studies, but our observations do not support iteroparity, which has been suggested by others. Parental care, through a 'start pack' of energy to the offspring and the ability to time the brood release to favorable conditions, add flexibility to the life history strategy. Easy access to the species and a good understanding of its biology support further use of *O. litoralis* as an indicator species for environmental change in the Arctic.

KEY WORDS: Seasonality · Timing · Energy allocation · Benthos · Intertidal · Arctic · Monitoring

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INTRODUCTION

In seasonal environments organisms schedule their activities in close connection to the annual cycle, and many invertebrate species have a life cycle duration corresponding to a number of annual cycles, such as annual, 2 yr, and 3 yr life cycles. Seasonality in food availability is perhaps the most common selective force leading to annual routines, the regular scheduling of activities such as breeding, growth or migrations; but variation in predation risk, competition and physical factors such as light regime, temperature or ice condi-

tions are involved as well (McNamara & Houston 2008). The development of annual routines can be assumed to be shaped by natural selection to maximize the organisms' fitness (McNamara & Houston 2008). In marine systems, a well known case of seasonal feeding and growth is that of zooplankton grazing on the highly seasonal phytoplankton bloom, with marked seasonality in food availability also for the predators on zooplankton (Varpe & Fiksen 2010). The annual routines of both predator and prey clearly reflect this situation, for instance through the evolution of seasonal migrations and energy storage.

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As growth and development are generally slow in the cold polar environments, organisms living there often have long life cycles and usually a single breeding period per year (Peck et al. 2006). There is a trade-off between reproduction and growth, because large parents usually produce more offspring, whereas growth to a large size comes with the costs of being exposed to predators and potentially harsh environmental conditions for a longer period of time (Stearns 1992). A key question in seasonal environments is therefore: Is it worth spending an additional year in order to reap the benefits of growth or energy storage through one more feeding season, or is it more profitable to put all resources into reproduction as early as possible (Varpe et al. 2009)? To answer this, an understanding of the potential for growth through the year is needed.

The energy budget (energy intake vs. metabolism) plays a fundamental role in the ability of organisms to survive, grow and reproduce (Calow & Sibly 1990). Cellular energy allocation (CEA) was developed by De Coen & Janssen (1997) as a biomarker for toxic stress, measuring the metabolic balance of an organism. A change in the energetic status may impact the ability to respond to environmental stress, both natural and anthropogenic, and therefore make the organisms more susceptible to stress in periods when their energy supplies are low, linking physiological processes to population responses (Calow & Sibly 1990). Using CEA in field conditions can additionally provide information on the physiological status of organisms and energy fluxes in the ecosystem (Verslycke et al. 2004a).

Benthic fauna are fueled by vertical flux of organic material from the water column, originating both from primary and secondary production. In the Barents Sea, the main flux of organic matter to the sea floor is connected with the spring bloom of ice algae and phytoplankton, since the primary production exceeds the rate of pelagic consumption during the bloom (Wassmann et al. 2006). In Arctic glacial bays, turbid freshwater runoff during the melting period enhances flocculation of organic matter with inorganic particles, thus generating an additional peak in the vertical flux of organic carbon to the benthos (Zajączkowski et al. 2010). These 2 annual events are of great importance for fueling the benthic fauna, and are reflected in the life history of many species (Węśławski & Legeżyńska 2002, Legeżyńska 2008, Nygård et al. 2009). Processes taking place during the winter may also influence the vertical flux of organic matter and could potentially be of importance for the benthic fauna (Berge et al. 2009).

There are few studies from the highly seasonal Arctic where sampling has the temporal resolution to investigate annual routines in sufficient detail, a situation caused mostly by logistic constraints. Yet, the Arc-

tic is currently changing rapidly and there is a need for model organisms and baseline values that can be used to study how animals respond to these changes (Post et al. 2009). In addition, most methods for monitoring effects of pollution have been developed for temperate species, whereas Arctic species may have differing life history strategies and therefore respond differently to stressors. We propose that the circumpolar amphipod *Onisimus litoralis* could serve as a model organism for studying environmental change in the Arctic. It is easily accessible as it lives on the soft sediments in the intertidal zone during the entire year. Furthermore, a clear 2 yr life cycle has been reported, both from the European (Węśławski et al. 2000) and the American (Boudrias & Carey 1988) Arctic, allowing distinct cohorts to be followed in observational studies. Finally, as for all peracarids, the species displays parental care by carrying the modest number of relatively large eggs for almost half a year, which allows direct observations of individual fecundity.

Here we report from such a study on *Onisimus litoralis* focusing on the timing of growth, maturation and reproduction as well as seasonal patterns in body composition and energy budget. Four main questions are addressed: (1) Do we also find the characteristic 2 yr life cycle in our study system Adventfjorden, and is there evidence for iteroparous individuals as suggested by Węśławski et al. (2000)? (2) When does structural growth of *O. litoralis* take place? Given its omnivorous and scavenging foraging mode, we expected only weak seasonality in growth. (3) Does *O. litoralis* rely on energy stores during parts of its life cycle, such as lipid reserves as an adaptation to periods of food limitation, or protein and lipid stores used for maturation or egg production, so called capital breeding (Jönsson 1997, Varpe et al. 2009)? (4) Seasonal differences in the metabolic rate can be expected due to temperature dependency, but do they induce seasonality in the energy budget of *O. litoralis*? With these questions, we focus on individual states, a prerequisite for understanding the potential for flexible responses to change and for an understanding of how the separate events in annual routines are related and influence each other.

MATERIALS AND METHODS

Study species and sampling. The *Onisimus* species are lysianassoid amphipods, which are commonly known to be scavengers with an omnivorous diet; however, some species-specific specialization in feeding is known (Carey & Boudrias 1987, Arndt et al. 2005, Legeżyńska 2008). They are high-latitude species, many with a circumpolar distribution (Vader et al.

2005), common in shallow waters and the intertidal zone, with some species also occurring in the sea ice environment (Holmquist 1965). *Onisimus littoralis* (Krøyer) is a major component of the shallow soft bottom fauna in Arctic coastal areas, e.g. on Svalbard, up to 95% of the macrofauna on tidal flats consists of *O. littoralis* (Węśławski et al. 2000). It has a 2 yr life cycle, is known to utilize sea ice during the spring for feeding and release of young, and has an omnivorous diet mainly consisting of diatoms, meiofauna and crustaceans (Carey & Boudrias 1987, Boudrias & Carey 1988, Węśławski et al. 2000).

The study took place in the inner part of Adventfjorden, Svalbard, Norway (78° 13.5' N, 15° 40.5' E). Adventfjorden is a glacial bay with seasonal variation in temperature, salinity, freshwater input and occasional sea ice cover, described in more depth by Zajaczkowski et al. (2010). Quantitative sampling of *Onisimus littoralis* was conducted monthly for a period of 12 mo (July 2007 to June 2008). However, due to harsh weather conditions no samples could be obtained in January, and only a qualitative sample was obtained in September. The samples were collected at low tide in water depths around 30 cm, using a pipe (26 cm in diameter, 0.053 m² area) that was pushed down in the sediment. The top 5 cm of the sediment were dug out and sieved through a 1 mm meshed sieve, and a dip net was used to catch the animals escaping in the water. Five replicate samples, 5 to 10 m away from each other, were taken every month. Qualitative samples for the CEA analysis were collected with a hand net. In addition, samples collected in May and June 2007 using baited traps, with the bait unavailable for the amphipods, were used for the CEA analyses.

When presenting results according to season, we consider April to May as spring, June to August as summer, September to October as autumn and November to March as winter. Only 1 measurement of the body constituents and the energy budget was done on the 0+ year class in summer (June), whereas the 1+ year class was measured monthly in summer. In autumn, body constituents and energy budget were measured once per year class: the 0+ year class in September and the 1+ year class in October.

Laboratory analyses. The quantitative samples were stored in ethanol. Length was measured from the front of the head to the tip of the telson along the dorsal contour with an accuracy of 0.1 mm. The gender was determined according to Boudrias & Carey (1988), using presence of genital papillae for identifying males and presence of oostegites for identifying females. Elongated second antenna was used to indicate maturity among males, whereas setose oostegites indicated mature females. If no secondary sexual characteristics

were observed, the specimen was considered juvenile. Specimens were weighed for wet weight, dried at 60°C for 24 h for dry weight, and finally combusted at 450°C for 3 h for weighing the ash-free dry weight (wet and dry weights are presented in the supplement, available at www.int-res.com/articles/suppl/m417p115_supp.pdf). The weighing was done with an accuracy of 0.1 mg, without correcting for the preservation effects. The daily growth rate was calculated using the mean value of the month, subtracting the mean value of the previous month and dividing by number of days between the sampling dates. Animals for the CEA analysis were sorted alive, packed individually in aluminum foil, shock frozen and stored at -80°C until they were processed. Since determination of sex of living amphipods is difficult without damaging the animals, sex separation was only done for mature individuals. The larger stages of *Onisimus littoralis* could be analyzed individually, while for smaller stages, samples had to be pooled to get enough material for the analysis.

The CEA analyses, total carbohydrate, protein and lipid content, and activity of the electron transport system (ETS) were conducted following the methods used by De Coen & Janssen (1997) with minor modifications. Briefly, the samples were thawed on ice and homogenized in a buffer solution (3 ml buffer per 0.2 g sample). Aliquots of 300 µl for protein and carbohydrate analyses, 200 µl for lipid analyses and 150 µl for ETS analyses were reserved. Carbohydrate content was determined by spectrophotometrically measuring absorbance at 490 nm using a glycogen standard. Protein content was determined with Bradford's reagent (Bradford 1976), and absorbance was measured at 595 nm using bovine serum albumin as standard. Lipids were extracted according to Bligh & Dyer (1959) and measured at 340 nm using tripalmitine as standard to determine the content. The ETS activity was measured according to the method of Owens & King (1975), modified by De Coen & Janssen (1997). Fifty µl of the homogenate was added to 100 µl buffered substrate solution and 50 µl NAD(P)H solution. To start the reaction, 100 µl iodonitrotetrazolium chloride (INT) was added and the absorbance was measured kinetically at 490 nm for 10 min to monitor the formation of formazan. All measurements were done in triplicate.

Quantifying the energy reserves available and the energy consumption at cellular level, CEA can be used to reflect the energy budget of an organism, making it possible to link the results to levels of higher ecological relevance (De Coen & Janssen 2003, Smolders et al. 2004). The energy content was calculated using the energetic equivalents for carbohydrates (17 500 mJ mg⁻¹ glycogen), proteins (24 000 mJ mg⁻¹ protein) and lipids (39 500 mJ mg⁻¹ lipid) (Gnaiger 1983). The sum of the energy content of the 3 constituents represents

the available energy (E_a) in the CEA calculations. The ETS activity was first transformed into oxygen consumption based on the stoichiometrical relationship that for each 2 mol formazan formed 1 mol of O_2 was consumed, and then into energy consumption (E_c) using the oxyenthalpic equivalent of $484 \text{ kJ mol}^{-1} O_2$ (Gnaiger 1983). In this study, the CEA was calculated as the proportion of E_a to E_c . Thus, a decline in the CEA-value indicates either a reduction in E_a or an increase in E_c (Verslycke et al. 2004a).

RESULTS

The abundance of *Onisimus litoralis* varied greatly among the sampling periods, with the highest densities ($>1000 \text{ ind. m}^{-2}$) recorded in August and February and lowest abundance in November (Table 1). The highest biomass of *O. litoralis* in both wet weight and dry weight was recorded in February as >40 and $>5 \text{ g m}^{-2}$, respectively.

The length distribution (see Fig. S1 in the supplement at www.int-res.com/articles/suppl/m417p115_supp.pdf) shows a clear division into 2 cohorts, confirming the previously observed 2 yr life cycle (Boudrias & Carey 1988, Węśławski et al. 2000), with similar timing of reproduction and brood release (Fig. 1). However, our study does not support iteroparity as suggested by Węśławski et al. (2000). Many dead females from the 2+ year class were found in May after the brood release, which suggests a semelparous strategy. The size of egg-bearing females ranged from 18.5 to 22.6 mm. The brood size varied from 12 to 61, with an average number

of 42 ± 15 (mean \pm SD), with eggs having an average diameter of $1.15 \pm 0.26 \text{ mm}$ and mean wet weight of $0.52 \pm 0.21 \text{ mg}$.

Growth, body constituents and energy budget

Spring

The newly released juveniles (0+ year class) were small, 4 to 5 mm long, and their biomass was low. The 1+ year class did not show any growth or change in weight during the spring (Figs. 2 & 3), but the first individuals showed signs of developing into immature adults. The carbohydrate levels of the 1+ year class were at the highest level of their lifespan, and the protein levels started to increase from the low levels in winter. There was no change in the lipid content, but a high variation among individuals was observed during the spring (Fig. 4).

The total energy content only increased slightly during the spring and a high variation in energy content was seen, especially in May (Fig. 5). The energy consumption was relatively high in April, but decreased in May to approximately the same level as in winter,

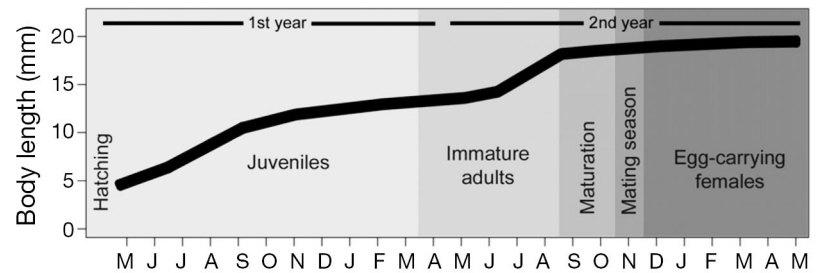


Fig. 1. *Onisimus litoralis*. A conceptual model illustrating the 2 yr life cycle

Table 1. *Onisimus litoralis*. Abundance and biomass (mean \pm SD), based on the quantitative sampling on the tidal flat in Adventfjorden, Svalbard, Norway. Abund = abundance, Wwt = wet weight, Dwt = dry weight. Dates are given as dd.mm.yr

Sampling date	1st cohort			2nd cohort		
	Abund (ind. m^{-2})	Wwt (g m^{-2})	Dwt (g m^{-2})	Abund (ind. m^{-2})	Wwt (g m^{-2})	Dwt (g m^{-2})
03.07.2007	663.0 \pm 219.8	3.1 \pm 1.3	0.4 \pm 0.2	75.3 \pm 23.1	5.0 \pm 1.9	0.8 \pm 0.3
15.08.2007	1002.0 \pm 395.2	10.7 \pm 4.6	2.0 \pm 0.8	94.2 \pm 85.3	7.9 \pm 7.2	1.4 \pm 1.3
24.09.2007	no data	no data	no data	no data	no data	no data
30.10.2007	169.5 \pm 192.5	2.5 \pm 2.9	0.8 \pm 0.8	3.8 \pm 8.4	0.3 \pm 0.7	0.1 \pm 0.1
19.11.2007	41.4 \pm 73.4	1.0 \pm 1.8	0.2 \pm 0.3	–	–	–
17.12.2007	252.4 \pm 74.9	6.1 \pm 1.8	1.0 \pm 0.5	11.3 \pm 16.8	1.5 \pm 2.1	0.2 \pm 0.3
21.01.2008	no data	no data	no data	no data	no data	no data
26.02.2008	1179.1 \pm 744.0	37.3 \pm 24.2	5.2 \pm 3.4	18.8 \pm 23.1	3.0 \pm 3.9	0.3 \pm 0.4
14.03.2008	312.7 \pm 224.7	10.2 \pm 6.9	1.2 \pm 0.9	–	–	–
25.04.2008	184.6 \pm 189.5	7.4 \pm 7.2	1.1 \pm 1.1	–	–	–
21.05.2008	252.4 \pm 164.0	0.1 \pm 0.0	0.1 \pm 0.0	730.8 \pm 300.0	28.5 \pm 14.2	3.9 \pm 1.7
10.06.2008	591.4 \pm 338.7	0.2 \pm 0.2	0.1 \pm 0.1	79.1 \pm 80.4	3.3 \pm 3.6	0.4 \pm 0.4

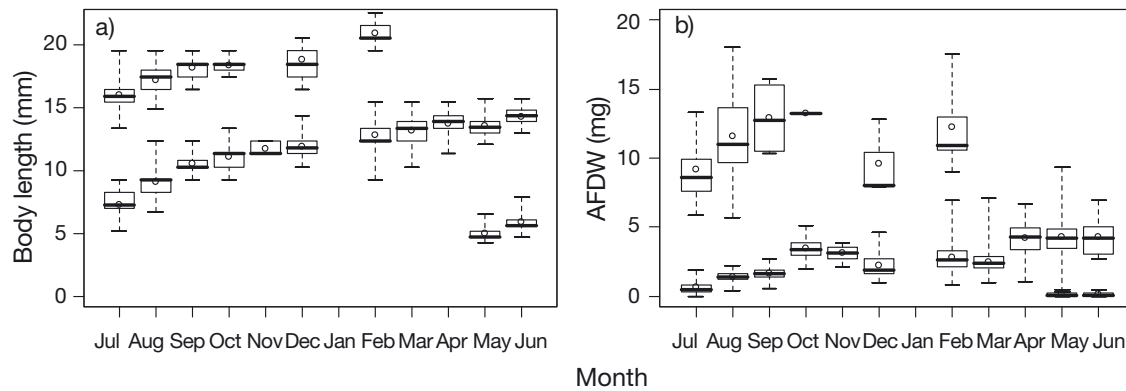


Fig. 2. *Onisimus litoralis*. (a) Length and (b) ash-free dry weight (AFDW) of the 2 cohorts. The line shows the median value. The box represents the second and third quartile of observations, while the whiskers include the full range of observations. The circle shows the mean value

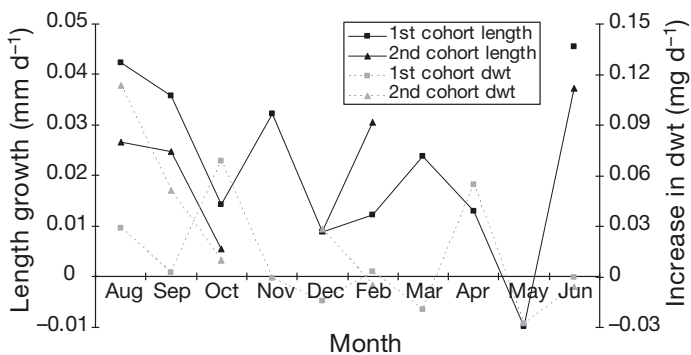


Fig. 3. *Onisimus litoralis*. Growth rate indicated as daily length growth and daily increase in dry weight (dwt) since previous sampling, separating the 2 cohorts. Note the shift in cohorts in June

albeit with high variation. This pattern in available energy and energy consumption resulted in a comparably low CEA value in April and a relatively high value in May.

Summer

The 0+ year class showed a fast growth during the summer and had doubled in length by the end of the summer (Fig. 2). A corresponding increase was seen in the weights; wet weight, dry weight and ash-free dry weight increased steadily through the summer (Fig. 2, see Fig. S2 in the supplement at www.int-res.com/articles/suppl/m417p115_supp.pdf). The 1+ year class also grew fast (particularly in weight units) during the summer (Fig. 3). For example, the dry weight was almost tripled from June to August (Fig. S2). The carbohydrate content in the 0+ year class was around 6 mg g^{-1} wet weight (Fig. 4), which was comparable to

the level in the 1+ year class. In summer, the carbohydrate content in the 1+ year class decreased from the high levels observed in spring. Proteins increased in the 1+ year class during the summer and reached the highest values in July. The 0+ year class had protein values comparable to the 1+ year class in June. The lipid content of the 0+ year class was very high (Fig. 4), indicating that juveniles got a 'start pack' of energy from their mother. The 1+ year class had a relatively stable level of lipids through the summer, with a slight peak in July. The high variation observed in the lipid content in the spring was still seen in June, but was remarkably smaller in July and August.

Concurrent with the high lipid content in the 0+ year class, the energy content also peaked in June. The 1+ year class also had a high energy content in the summer. The energy consumption was high in small juveniles in June. In the 1+ year class, the energy consumption in June was on the same level as in May, but increased markedly in July and was also high in August. The increase in both energy content and energy consumption in summer resulted in a quite stable CEA value through the summer. The high energy consumption in June was also compensated for by a high energy content in the 0+ year class, which could be seen as CEA values comparable to those of the 1+ year class in summer (Fig. 5).

Autumn

The 0+ year class continued growing in the autumn, but at a slower rate compared to the summer. No change was seen in the wet weight, but both the dry weight and ash-free dry weight increased remarkably (Figs. 2 & S2). The length growth and increase in weight in the 1+ year class ceased as the individuals

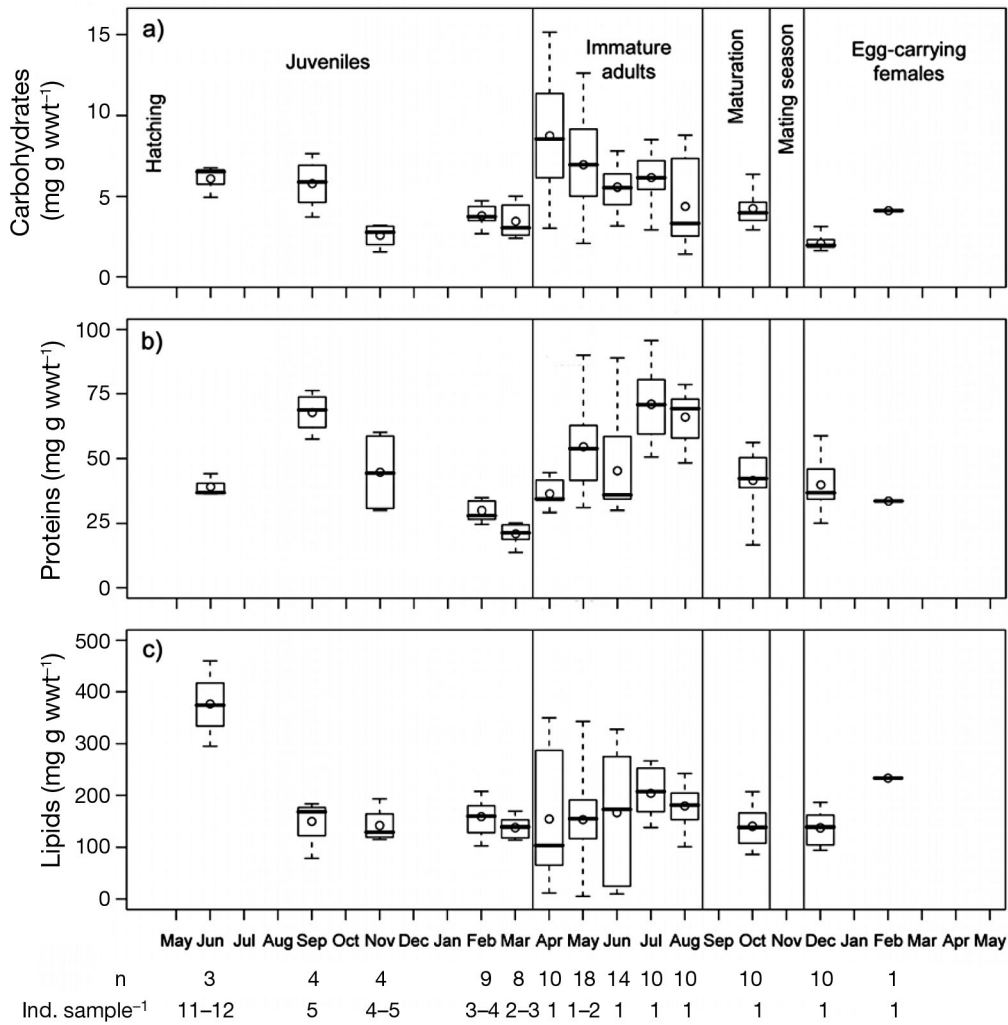


Fig. 4. *Onisimus littoralis*. Variation in the body composition throughout the lifespan. Content of (a) carbohydrates, (b) proteins and (c) lipids. The line shows the median value. The box represents the second and third quartile of observations, while the whiskers include the full range of observations. The circle shows the mean value. Vertical lines separate the development stages. wwt = wet weight, n = number of samples

started maturing in the autumn (Figs. 2 & 3). In both the 0+ and the 1+ year classes, the carbohydrate content had decreased slightly from the summer values. The protein content of the 0+ year class in September was high, almost as high as the maximum value for the 1+ year class in July. In October, the 1+ year class protein content had decreased from the high late summer values back to values comparable to the spring and early summer. The high lipid levels observed in June in the 0+ year class had decreased by 60% by September. However, the absolute amount of lipids per individual had increased even if the lipid content relative to wet weight was more than halved. For the 1+ year class, the lipid content decreased slightly and was at a level comparable to the spring values (Fig. 4).

The energy content in autumn was lower than during summer. The energy content of the 0+ year class halved from June to September, whereas the decrease in the 1+ year class was less and the values were similar to those observed in the spring (Fig. 5). Energy consumption was quite high in autumn in both year classes, which resulted in a relatively low CEA value for the autumn period.

Winter

There was a small length increase in the 0+ year class indicating growth also in winter. A slight increase in the wet weight was observed through the winter,

energy consumption after reproduction and the egg-carrying female had a very low energy consumption in February. The CEA value in winter was quite similar to the CEA values observed in spring and summer, apart from the 1+ year class female in February that had a very high CEA value (Fig. 5).

DISCUSSION

Life strategy

In this study, we identify a 2 yr semelparous life cycle of *Onisimus litoralis*, well in accordance with earlier studies in the Beaufort Sea (Boudrias & Carey 1988), in the Saint Lawrence Estuary (Sainte-Marie et al. 1990) and on Svalbard (Węśławski et al. 2000, Węśławski & Legeżyńska 2002). However, our study does not provide any evidence for iteroparity as suggested by Węśławski et al. (2000). Mating and egg production presumably take place in November, and the eggs are carried through the winter, hatch and are released in April to May, confirming the findings of Węśławski et al. (2000). No increase in energy stores is seen prior to egg production, indicating that *O. litoralis* can be categorized as an income breeder (Jönsson 1997, Varpe et al. 2009), relying on concurrent food intake for egg production. However, as shown by Casas et al. (2005), organisms can be income breeders for some nutrient classes and capital breeders for others. Although *O. litoralis* seems to be an income breeder for lipids and carbohydrates, the pattern for proteins, with high late summer values prior to maturation, could indicate more of a capital breeding strategy for this nutrient. The fate of proteins, if they are invested in gonad production or used for metabolism, remains unknown, and future studies on these aspects are needed to fully understand the reproduction strategy of *O. litoralis*.

The clear division into 2 cohorts, the unity in length among mature females and the lack of records of surviving females after the brood release, support semelparity for *Onisimus litoralis*. Węśławski et al. (2000) found some large females during summer and a wide length range of egg-carrying females, indicating a possible third year for at least some of the females. A 3 yr strategy could emerge as a result of poor resource availability, delaying growth and development, thus restricting the females to reach maturity in the second autumn and postpone egg production until the third year (3 yr semelparous strategy), or a rather conservative investment in reproduction the second autumn, securing resources to survive after brood release and grow bigger to produce a larger brood the next year (3 yr iteroparous strategy). Both alternatives would add flexibility to the life strategy and may be an adaptation

to environmental stochasticity. The 2 yr semelparous life cycle we found in Adventfjorden assumes that sufficient resources are available to produce a large brood and complete the life cycle in 2 yr. Finally, the absence of 3-yr-olds observed during our study may alternatively have been caused by higher mortality (for instance predation) than during the study by Węśławski et al. (2000).

Having a modest sized brood, survival of the early life stages is critical for a successful recruitment of *Onisimus litoralis*. Parental care is performed by the mother carrying the eggs and hatched juveniles. Timing the brood release to favorable conditions, when food is available for the juveniles, is also important for a successful start to their life (Boudrias & Carey 1988). The high lipid content of the newly released juveniles indicates a start pack received from the mother, as it is unlikely that newborn juveniles would grow lipid reserves instead of prioritizing structural growth. With a warmer climate, a reduction in ice cover and earlier ice breakup is expected in the Arctic (Stirling & Parkinson 2006), leading to an earlier or absent ice algal bloom, as well as an earlier onset of the spring bloom of phytoplankton (Zajączkowski et al. 2010). This is likely to have a negative effect on *O. litoralis*, since the eggs might not hatch in time for the juveniles to be released in synchrony with the early bloom, but the start pack of energy that the juveniles receive from the mother could buffer such a mismatch or other unfavorable conditions. However, further studies on the early life stages (eggs and newly released juveniles) with higher time resolution are needed to fully understand the role of lipids and importance of timing of the brood release.

Growth and body constituents

Growth is fastest during summer, which is revealed both in length and weight increase, as well as in protein content. Seasonal variations in production in polar environments are expected due to physical factors like light conditions restricting primary production, and therefore the availability of food for secondary producers. Being omnivorous, *Onisimus litoralis* is not solely dependant on the spring bloom of ice algae and phytoplankton, although this is important for newly released juveniles (Boudrias & Carey 1988), but also utilizes other food sources such as phytodetritus and meiofauna, and scavenges on macrofaunal crustaceans (Carey & Boudrias 1987). A broader and more flexible diet allows a longer feeding season and less extreme annual routines (Atkinson 1998). In Adventfjorden, and probably also in most *O. litoralis* habitats, glacial rivers bring suspended particles in summer that

restrict the euphotic zone, favoring heterotrophs, and increasing the sedimentation of organic particles through flocculation (Zajaczkowski et al. 2010). Additionally, freshwater input to glacial bays in summer causes zooplankton mortality due to osmotic shock (Zajaczkowski & Legeżyńska 2001, Eiane & Daase 2002), facilitating foraging for benthic scavengers (Legeżyńska 2008). The increased flux of organic material to the bottom in summer seems to be of prominent importance for the 1+ year class of *O. littoralis* for somatic growth, maturation and preparation for reproduction, and is mirrored in increased protein content, a tripling of the dry weight and raised energy content. The increase in protein in summer may also indicate a switch in diet towards zooplankton carcasses. The importance of the input of organic material to the bottom in summer has also been shown for other *Onisimus* species, for example *O. caricus*, which releases its juveniles during this time (Nygård et al. 2009).

Continuous feeding throughout the year is indicated by a constant length growth, even though the growth rate varies seasonally. However, the ash-free dry weight shows stagnation and even decreases in winter. This shows a change in feeding behavior or food quality during winter, restricting the energy intake, since the energy consumption is also low during winter. Different strategies for overwintering have been observed among amphipods. *Monoporeia affinis* and *Pontoporeia femorata* build up lipid reserves that they utilize during winter (Lehtonen 1996, 2004), whereas *Onisimus affinis* relies on available food resources throughout the year and does not gather energy reserves for the winter (Percy 1979). *O. littoralis* does not show any storage of lipids in summer and autumn to use as an energy source in winter, but the decrease in protein content in winter may indicate a consumption of proteins in addition to continuous feeding to cover metabolic costs. Being an omnivorous scavenger, it can also find food in adverse conditions during winter. Large carrion can serve as an important bonus to the diet, but due to its scarcity and unpredictability, in addition to the feeding behavior of *O. littoralis*, the diet needs to be more flexible (Sainte-Marie et al. 1989). Kaufman et al. (2008) report slower isotopic turnover in late summer relative to spring, based on experiments, leading to a slower growth and metabolic turnover rates. This is likely caused by a seasonally differing diet, but they also note that the actual growth and metabolic turnover rates are probably underestimated in late summer, since these experiments were performed at a lower temperature than that observed in the field.

The juveniles' start pack of lipids is used during the first months, and the lipid content thereafter decreases to a base level, from which no large deviation takes

place during the rest of the lifespan. The importance of the spring bloom in primary production is apparent for the 1+ yr cohort. They exploit it for developing into adults, and this can be seen in an increase in energy content from April onwards. The high variation observed could be explained by individual success in finding food and surviving through the winter and, hence, variation in individual development. Since lipids make up the most of the body mass of *Onisimus littoralis* and energy content is also highest in lipids compared to proteins and carbohydrates, the total energy content of *O. littoralis* closely follows the pattern of lipid content.

Energy budget

A seasonal pattern in the energy consumption of *Onisimus littoralis* is apparent, with elevated values in the summer. Similar seasonal differences have been observed in the metabolic rates of other Arctic littoral and sublittoral amphipods (Węśławski & Opaliński 1997). Both temperature and salinity changes alter the metabolism of Arctic amphipods (Percy 1975, Aarset & Aunaas 1990a,b). Metabolism generally increases with elevated temperature, while salinity changes alter osmoregulation, leading to higher energy demand at low salinities. In Adventfjorden, the surface water varies from -1.8°C in winter to around 8°C in summer, while the salinity drops from 34.7 in winter to <5 in summer (Zajaczkowski et al. 2010). For the sympagic amphipod *O. glacialis*, a Q_{10} value of 3.6 has been measured in the range of 0 to 10°C (Aarset & Aunaas 1990b), while the benthic *O. affinis* shows a more temperature-insensitive metabolism (Percy 1975). An increase in the metabolism in *O. littoralis* due to temperature shifts is expected, but the exact relationship between temperature and metabolism is not known. *O. littoralis* is a euryhaline hyperosmotic regulator and tolerates large variations in salinity, but needs energy for osmoregulation at low salinities (Shea & Percy 1990). *O. glacialis* showed a 3-fold increase in metabolism when transferred from a salinity of 35 to 5 (Aarset & Aunaas 1990a), while *O. affinis* is rather insensitive to variations between salinities of 10 and 25 when pre-adapted to lower salinities (Percy 1975). Based on our data, the driver for elevated energy consumption in summer can not be pin-pointed, but most likely it is a combination of temperature-dependent metabolism and energy-consuming osmoregulation. Further experimental work needs to be carried out to investigate the effect of different environmental parameters on energy consumption. After mating has taken place, the energy consumption drops, probably because the available energy is directed towards development of

eggs and females become less active during the incubation of the eggs.

The CEA value is relatively stable throughout the year, and consequently also through the lifespan of *Onisimus litoralis*. Only the gravid female shows deviation from the otherwise stable pattern. The CEA value reflects the high energy consumption in summer accompanied by high energy content, while in winter, when metabolism is low, the energy available is also low. This shows that there is no particular period during the lifespan of *O. litoralis* when sufficient excess energy is obtained for a build-up of energy reserves. Instead, it seems likely that the energy is utilized for growth and development at the same rate as it is acquired. Hence, if energy stores are assumed to cause resistance to stress, there is no time of the year when *O. litoralis* is particularly pre-adapted to cope with increased metabolic stress. Since the egg-carrying female was analyzed with the eggs, the high CEA value could indicate that the excess energy is in the eggs and used for their development, rather than for the usage of the female itself.

CEA has proven to be useful as an indicator of stress, both *in situ* and in laboratory experiments, for a number of pollutants in temperate areas (e.g. Verslycke et al. 2003, 2004a,b, Smolders et al. 2004). It has also been used as a biomarker to experimentally study effects of oil-related compounds in some Arctic benthic species, among them *Onisimus litoralis* (Olsen et al. 2007, 2008). However, species-specific responses were observed, restricting a generalization of the use of CEA as a biomarker. The method, therefore, has to be tested and evaluated for individual species. Identification of natural baseline values could serve as a first step in such an evaluation, as has been done here for *O. litoralis*. With the baseline data available, further experimental work can be performed to test and validate the use of CEA as a biomarker for pollution-induced stress in Arctic species.

Annual routines and selection pressures

Few studies on amphipod life histories in the Arctic have had sufficient seasonal resolution. To our knowledge, the only studies on Arctic amphipod life history traits with year-round sampling in addition to the present work are the ones on *Onisimus litoralis* and 4 other lysianassoid amphipods by Sainte-Marie et al. (1990), on *O. litoralis* by Węśławski et al. (2000), on *O. caricus* by Nygård et al. (2009) and the work by Węśławski & Legeżyńska (2002) where the breeding parameters of several common coastal species are presented. It is however clear that there are annual routines that seem to follow the same patterns among Arc-

tic amphipods. Most of the species studied lay eggs in autumn or early winter, to incubate them through the winter and release the hatched juveniles in spring or summer (Węśławski & Legeżyńska 2002, Arndt & Beuchel 2006, Nygård et al. 2009). Annual routines in growth and development are observed in *O. litoralis*, with the main growth occurring in summer, and the ontogenic development taking place during summer and autumn leading up to reproduction in early winter.

There are several selection pressures influencing the evolution of these annual routines. Physical conditions, food availability and predation pressure are important factors that are likely to affect different life stages, parents and offspring, differently. The variation in light conditions, temperature and, near-shore, salinity, creates environmental seasonality and has both direct and indirect effects on growth, development and reproduction of amphipods. Temperature dependence in development is commonly known (Peck et al. 2006, Ingólfsson et al. 2007), and is also likely to influence the growth and development of *Onisimus litoralis*. Salinity variation, and freshening of the surface water in summer adds an energetic cost to the amphipods through increased osmoregulation (Aarset & Aunaas 1990a, Shea & Percy 1990), but this is compensated through increased energy intake. As light drives the seasonality in primary production, the food availability and energy transfer to higher trophic levels also follow this seasonality (Søreide et al. 2010). The offspring is released when primary production is highest, while the older stages can utilize other types of food during the rest of the year. Predation by seasonally migrating shorebirds (Luukkonen 2009) and other seabirds (Bradstreet 1980) is increased during summer, and egg-carrying females would be easy and valuable prey for the birds compared to small juveniles. This may have caused egg production to start when the migrating birds have left and the brood release to occur before their return. Predation by fish and seals in the littoral zone has not been studied, but is presumably less seasonal.

The annual routines identified in this study (seasonality in body composition, growth pattern, and timing of reproduction) increase the understanding of the seasonal population dynamics, the timing of annual routines and the individual variation in condition. The individual condition of specimens can be used to evaluate their ability to cope with stress and to predict their reproductive output (McNamara & Houston 1996), both of importance when trying to predict how organisms respond to a change in their environment.

Climate warming and increasing anthropogenic activities (oil industry, mining, shipping) in the Arctic, will induce changes in the environment. Baseline data, such as provided in this study, are needed to assess

how these changes affect organisms. Easy access to *Onisimus litoralis* and a relatively good understanding of its biology supports the use of this species in further work, as we monitor and study the responses of the Arctic biota to its dynamic and changing environment.

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