

Ecophysiology of the benthic amphipod *Monoporeia affinis* in an open-sea area of the northern Baltic Sea: seasonal variations in body composition, with bioenergetic considerations

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ABSTRACT: A deep-living, open-sea population of *Monoporeia affinis* from the northern Baltic Sea was studied for seasonal variations in the gross biochemical, lipid class and elemental composition during 1991 to 1993. The seasonal cycle in the composition of this benthic, deposit-feeding amphipod was largely determined by the brief period of spring phytoplankton bloom sedimentation and the long-lasting deficiency of good-quality nutrition during late autumn-early spring. The level (% dry wt) of lipid was lowest in March–April (21 to 30 %, range: interannual variation), increased rapidly in early summer (27 to 43 %) and peaked in the autumn (38 to 44 %). Reciprocal to lipid, the level of protein was highest in the spring (19 to 29 %) and lowest in the autumn (17 to 23 %). Carbon and nitrogen levels followed closely the patterns of lipid and protein, respectively. Triacylglycerols were invariably the main lipid class (67 to 95 % of total lipids), while phospholipids formed 4 to 23 % and other classes <7 % each. Due to high variability in biochemical composition, the energetic value of the body matter of *M. affinis* showed great seasonal variation. Using body composition and previously determined metabolic rates, calculations showed distinct seasonal and life-cycle variability in the bioenergetic strategy of the amphipods. Interannual variability in the body composition of the amphipods was noted, especially between 1991 and the 2 following years. Previously recorded long-term oscillations in the abundance and biomass of *M. affinis* populations and the relation of these oscillations to pelagic events and sedimentation is discussed in the light of the present results.

KEY WORDS: *Monoporeia affinis* · Benthic amphipod · Baltic Sea · Biochemical composition · Lipid classes · Elemental composition · Bioenergetics · Seasonal variation

INTRODUCTION

The benthic amphipod *Monoporeia affinis* (previously *Pontoporeia affinis*; Bousfield 1989) feeds mainly on detrital organic matter present in the sediment and phytoplankton that reaches the bottom via sedimentation. On northern Baltic Sea soft-bottoms, *M. affinis* is usually the dominant macrobenthic species with densities reaching 10 000 ind. m⁻² and more (e.g. Ankar & Elmgren 1975, Andersin et al. 1978, 1984, Elmgren 1978). The amphipod is therefore a key species with regard to energy flow in these areas.

Monoporeia affinis is semelparous, reproducing usually in early spring, with a life-cycle varying between 1 and 4 yr (e.g. Segerstråle 1937, Andersin et al. 1984, Leonardsson et al. 1988). The abundance and biomass of *M. affinis* populations show long-term oscillations (Andersin et al. 1978, 1984); substantial evidence of a coupling between the intensity of algal blooms and the abundance and biomass of benthic amphipod populations has been obtained from lakes (Johnson & Wiederholm 1992, Fitzgerald & Gardner 1993) and from shallow, coastal areas of the Baltic Sea (Cederwall 1977, Elmgren 1978, Sarvala 1986).

A major biological feature of most sub-boreal, temperate aquatic environments is high seasonality in

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primary production; the consequences of this phenomenon are reflected through all levels of ecosystem organization and function. The nourishment of benthic deposit-feeders in open-sea areas is largely dependent on autochthonous food sources. However, because availability of such food varies widely throughout the year, benthic organisms must have efficient energy storage systems to be able to cope with long periods of poor food conditions. Consequently, the bioenergetic strategy of *Monoporeia affinis* is likely to be strongly governed by environmental conditions, and, furthermore, biochemical composition of the amphipods is likely to reflect food availability.

Lipid accumulation is the most widespread long-term energy storage strategy in aquatic crustaceans and their reproductive potential is largely dictated by lipid content (e.g. review by Sargent & Henderson 1986; also Gatten et al. 1980). Environmental nutritional conditions directly regulate the breeding success of individuals and, subsequently, population dynamics. Lipid (mainly triacylglycerols) is also the major energy storage component in *Monoporeia affinis* (Hill et al. 1992, Lehtonen 1995) and its North American counterpart *Diporeia hoyi* [formerly *Pontoporeia hoyi* (Bousfield 1989), now distinguished as consisting of several species (M. Quigley pers. comm.); e.g. Gardner et al. 1985b, Gauvin et al. 1989, Quigley et al. 1989].

This study deals with the seasonal and interannual changes in the gross biochemical (lipid and protein), lipid class and elemental (carbon and nitrogen) composition of *Monoporeia affinis* from a deep-living, open-sea population in the northern Baltic Sea. The results of a parallel work on the metabolic characteristics of *M. affinis* (Lehtonen 1996) were used to determine the bioenergetic strategy of the species in the study area.

MATERIAL AND METHODS

Sampling. Seasonal samples of *Monoporeia affinis* were collected from RV 'Aranda' on 16 occasions between 17 January 1991 and 28 July 1993 from the Bothnian Sea open-sea station SR5 (northern Baltic Sea, 61° 05' 00" N, 19° 35' 99" E; salinity ~6‰) at the depth of 125 m, using a van Veen grab. The amphipods were rinsed from the sediment using sea water cooled to ambient bottom temperature (3 to 4°C), sieved gently on a small 0.5 mm mesh and transferred to the ship's cold laboratory (4°C), where they were allowed to clear their guts in a sand-bottom aquarium for 24 h. The amphipods were sorted by size to age classes [1+ and 2+ yr olds, and gravid females (~3 yr olds; analysed with eggs/embryos); the young-of-the-year

were not collected], placed into Eppendorf tubes and stored in liquid nitrogen. Analyses for dry weight, lipid, lipid classes, protein, carbon and nitrogen were carried out after lyophilization.

Analytical procedures. Total lipid: Lipids were extracted according to the micromethod developed by Gardner et al. (1985a), with small modifications (Lehtonen 1995). Briefly, lyophilized samples (5 to 15 mg dry wt) of pooled (2 to 15) individuals were Potter-homogenized in 500 µl chloroform:methanol (2:1). The homogenate was drawn into microcapillaries and centrifuged (11000 × g, 20 s) to separate tissue debris. The extract was washed once with 20% volume of 0.9% NaCl and centrifuged again to separate the lipid-containing chloroform column. Subsamples were placed into folio cups, chloroform was evaporated and the weighed residue taken as total lipid after the subtraction of the daily zero-sample value.

Lipid classes: An Iatroscan MK-5 analyzer (Iatron Laboratories, Japan) was used for lipid class analysis. The analytical procedure is described in detail elsewhere (Lehtonen 1995). In short, the lipid extracts (2 µl) were spotted on Chromarods (SIII) and developed in solvent systems of varying polarity. The following lipid classes were determined: triacylglycerols (TAG), free fatty acids (FFA), sterols/diacylglycerols (ST/DG), acetone-mobile polar lipids (AMPL; e.g. pigments) and phospholipids (PL).

NaOH-soluble protein: Lyophilized samples (6 to 10 mg dry wt) of individuals (2 to 10) were homogenized in 2 ml 0.5 N NaOH. Triplicate 0.5 ml samples were incubated for 1 h in a water bath (60°C). From these samples, duplicate 0.2 ml aliquots were diluted with 0.8 ml deionized water (to adjust pH suitable for analysis) and centrifuged (11000 × g, 2 min). NaOH-soluble protein was determined by the Coomassie blue method (Bradford 1976; BioRad kit) and the samples were measured spectrophotometrically (Perkin-Elmer Lambda 2 UV/VIS) at 595 nm against a BSA (bovine serum albumin) standard.

Carbon and nitrogen: Carbon and nitrogen levels of the amphipods were measured from duplicate 1 to 2 mg subsamples taken from lyophilized, mortar-homogenized, pooled samples (3 to 10 individuals). The analysis was performed using a Heraeus CHN analyser

Population data: Mean dry weights of individuals from different age classes at each sampling date were obtained from a population study carried out simultaneously. The population samples (5 box cores) were stored in 5% hexamin-buffered formalin for 3 mo prior to analysis, and the amphipods were measured for length, and wet and dry weight (oven-drying). However, this procedure was found to yield significantly lower dry weights compared to results from the lyo-

philization of freshly collected and frozen material, most likely because of the extensive drainage of body lipids to the formalin solution during storage. An experimentally determined correction factor of 1.58 was therefore applied to convert the 'formalin dry weights' to 'lyophilized dry weights'. The population data will be presented in another paper (A.-B. Andersin & K. K. Lehtonen unpubl.).

Bioenergetic calculations: A parallel study on the metabolism of *Monoporeia affinis* (Lehtonen 1996) was used for the bioenergetic calculations. A detailed description of the method used for the metabolic measurements is given in Lehtonen (1994). In brief, seasonal experiments were carried out by incubating amphipods in batches of 15 to 20 individuals per vial for 24 h. Consumed O_2 and excreted NH_4^+ were measured using Winkler titration and the phenolhypochlorite method of Solórzano (1969), respectively.

Metabolic and biochemical parameters were converted to energy equivalents as follows: $O_2 = 14.06 \text{ J mg}^{-1}$ (Gnaiger 1983), $NH_4^+ = 24.87 \text{ J mg}^{-1}$ (Elliott & Davison 1975), lipid = 39.35 J mg^{-1} and protein = 23.63 J mg^{-1} (Winberg 1971). The remaining body matter was assumed to be mainly chitin, ash and carbohydrates; carbohydrate energy value (17.18 J mg^{-1} ; Winberg 1971) was used to estimate the energy content of the 'rest' fraction.

Oxygen consumption rates were determined using the following equations: $\mu\text{l } O_2 \text{ d}^{-1} = 14.29W^{0.770}$ for October–April, $\mu\text{l } O_2 \text{ d}^{-1} = 18.32W^{0.774}$ for May–September and $\mu\text{l } O_2 \text{ d}^{-1} = 13.93W^{1.030}$ for gravid females ($W = \text{mg dry wt}$). To calculate NH_4^+ excretion by the individuals ($\mu\text{mol } NH_4^+ \text{ d}^{-1}$), intercept values of the excretion versus dry weight power function, calculated for each month using a fixed exponent of 0.750, were used. Daily values for both physiological rates were determined for a mean-size individual from each year cohort; changes in these rates due to growth and seasonal variations in intercept or slope values were obtained by linear interpolation between the sampling dates. Daily growth rates (mg d^{-1}) and the interrelated changes in the contents of the specific biochemical components (accumulation and depletion rates) were obtained in a similar way.

RESULTS

Seasonal variations in biochemical composition

Lipid levels and seasonal lipid dynamics

Lipid level (% dry wt) varied between 15 and 45%, with lowest levels in March–April (Fig. 1). In late May–mid-June, rapid accumulation of lipid began

and peak levels were recorded in August–September. Gravid females (present only in winter) always had lower lipid levels (15 to 20%) compared to juveniles.

The total lipid content of individuals (mg ind.^{-1}) showed a marked accumulation in both age groups in June–August, and a steady state in the 1+ yr olds and an extensive decline in the reproducing 2+ yr olds in November–March (Fig. 2). Accumulation rates were high in June–August, with annual peaks between 19.0 and $33.2 \mu\text{g d}^{-1}$ (Table 1). After the summer months, the lipid balance turned negative. Most notably, the reproducing generation (2+ yr olds) lost lipid at the rate of 3.6 to $14.0 \mu\text{g d}^{-1}$ until brood release. Compared to 1991 and 1993, an earlier peak in the lipid accumulation rate was seen in 1992. The accumulation rates of both 1+ and 2+ yr olds were distinctly lower in 1992 (16 June to 9 September) than in 1991 (17 June to 13 August), while the 2+ yr olds in summer 1993 (27 May to 28 July) had, again, a higher rate. These observations could denote either earlier or poorer sedimentation of the 1992 spring bloom compared to 1991 and 1993. However, since the rates are dependent on interannual variability in the weight of individuals and the variable length of sampling intervals, the interannual differences in the rates are only indicative.

The reproducing generation of the 1989 cohort lost 62 and 67 % of body lipid and TAG, respectively, between 13 August 1991 and 5 March 1992 (Fig. 2). In a similar way, 64 % of lipid (74 % of TAG) was depleted in the 1990 cohort between 9 September 1992 and 4 March 1993, while 41 % of the loss (40 % of TAG loss) had already occurred by 25 November 1992.

Lipid class composition

TAG were the major lipid class at all times of the year (67 to 95 % of total) and correlated significantly with the total lipid levels (Fig. 3d, Table 2). The PL level became more pronounced in winter and spring, due to reductions in the TAG pool. The neutral-to-polar lipid ratio (TAG+FFA+ST/DG in relation to AMPL+PL) was low in the spring and early summer (range 4.1 to 9.8) and peaked in late summer-early autumn (range 7.3 to 23.3). The only winter measurement (November 1992: 2+ yr olds: 12.4) showed that the ratio had already started to decline in early winter. The neutral-to-polar lipid ratio was invariably higher in the 2+ yr olds compared to the 1+ yr olds. Gravid females had a low ratio in March 1992 and 1993 (3.9 and 3.3, respectively), but a very high ratio (18.4) in November 1992, although the lipid level was low (22.8 %). The lowest TAG levels recorded were

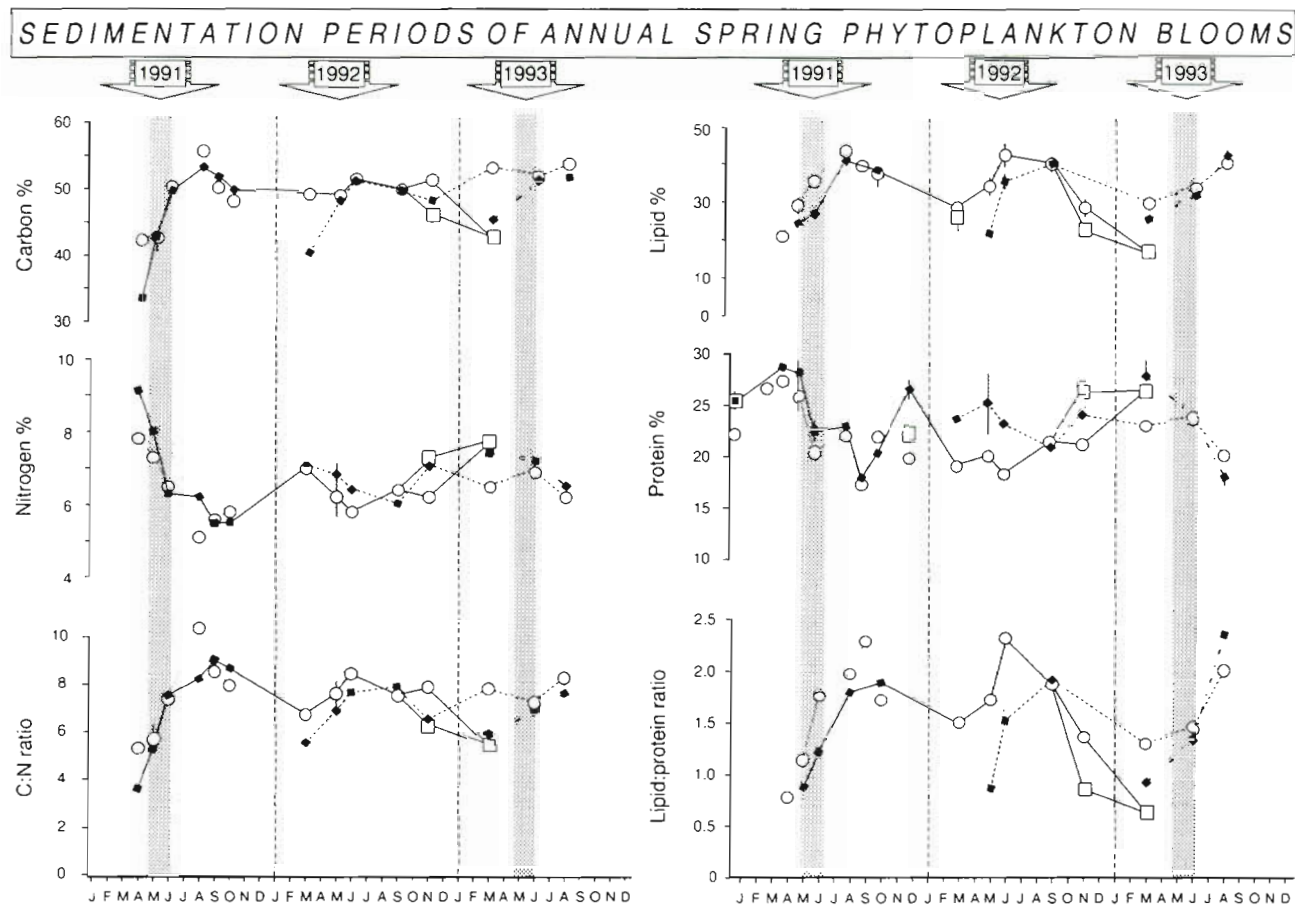


Fig. 1. *Monoporeia affinis*. Seasonal and interannual variations in the levels (% dry wt) of elemental (carbon and nitrogen) and biochemical (lipid and protein) constituents, molar C:N ratio and lipid:protein ratio. Standard deviation (\pm) is indicated by a vertical bar unless smaller than the symbol size. Shaded bars represent the periods of spring phytoplankton bloom sedimentation in 1991 and 1993 (FIMR unpubl. data). For 1992, the sedimentation period is based on assumption only. (■) 1+ yr olds; (○) 2+ yr olds; (□) gravid females. Cohorts: (.....) born 1989; (—) born 1990; (---) born 1991; (- · - ·) born 1992

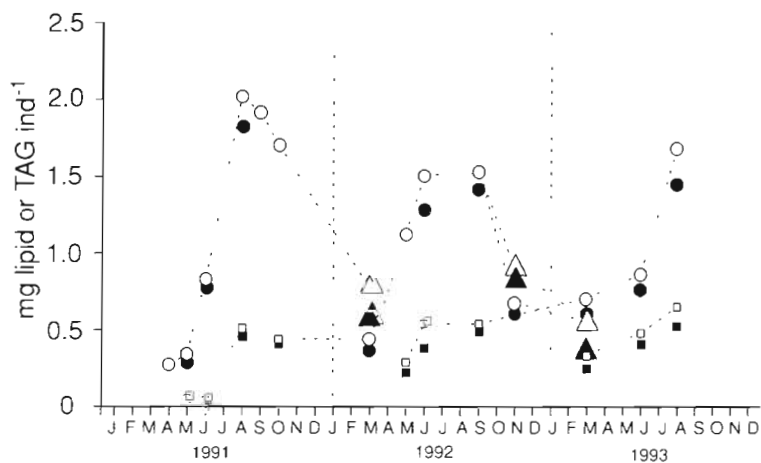


Fig. 2. *Monoporeia affinis*. Seasonal and interannual variations in the lipid (open symbols, broken line) and triacylglycerol (TAG, filled symbols, no line) content (mg ind^{-1}). Squares: 1+ yr olds; circles: 2+ yr olds; triangles: gravid females

those measured for gravid females in March 1993 (67.0%).

FFA and ST/DG together accounted for $<7\%$, which agreed with previous studies (Quigley et al. 1989, Hill et al. 1992). The markedly high FFA level in June 1992 samples (Table 2: 1+ yr olds: 11.6%) could be due to error in the storage or preparation of these samples causing partial hydrolysis, since similar levels were not detected in 1991 and 1993.

The level of AMPL is usually slightly elevated after the sedimentation of the spring bloom, indicating uptake of pigments. The amphipods also turned yellow, and the colour remained until the end of the summer. An increase in the pigment content of benthic macrofauna as a response to sedimentation is common (e.g. Ansell 1974,

Table 1. *Monoporeia affinis*. Lipid accumulation rates ($\mu\text{g d}^{-1}$) in different year cohorts, obtained by using linear interpolation of changes in dry weight and lipid level (% dry wt) between each sampling date, and calculating a mean daily rate for each period

Cohort born 1989	Lipid ($\mu\text{g d}^{-1}$)	Cohort born 1990	Lipid ($\mu\text{g d}^{-1}$)	Cohort born 1991	Lipid ($\mu\text{g d}^{-1}$)
1991		1991			
11 Apr–22 May	1.6				
22 May–17 Jun	20.0	22 May–17 Jun	1.9		
17 Jun–13 Aug	23.5	17 Jun–13 Aug	7.3		
13 Aug–24 Sep	-0.5	13 Aug–22 Oct	1.3		
24 Sep–22 Oct	-4.8	22 Oct–5 Mar (1992)	-1.4		
22 Oct–5 Mar (1992)	-14.0				
		1992		1992	
		5 Mar–28 May	1.8		
		28 May–16 Jun	33.2	28 May–16 Jun	10.6
		18 Jun–9 Sep	3.8	16 Jun–9 Sep	3.8
		9 Sep–25 Nov	-7.9	9 Sep–25 Nov	-2.4
		25 Nov–4 Mar (1993)	-3.6	25 Nov–4 Mar (1993)	-0.3
				1993	
				4 Mar–27 May	2.1
				27 May–28 Jul	19.0

Christensen & Kanneworff 1985). However, due to the low AMPL content, variations between measurements were high. For an unknown reason, individuals measured in March 1993 also had an elevated AMPL level. It is possible that AMPL in *Monoporeia affinis* is an indicator of the quality of the recently ingested food (i.e. fresh material relative to older, more refractory material), but the verification of this would need a more sophisticated study approach.

Protein

The level of protein ranged between 17.4 and 28.7%, mostly due to seasonality, but also to body size. Using the common factor 6.25 for converting nitrogen to protein, significantly greater protein values are obtained; Berges et al. (1993) pointed out that the Bradford method used here is a much less sensitive detector of small peptides and free amino acids than, for example, the method of Lowry et al. (1951), which yields up to 50% greater 'protein' values.

Carbon and nitrogen

Carbon (33.5 to 55.9%) and nitrogen (5.1 to 9.1%) levels followed the changes in the lipid and protein levels respectively, with significant correlations (Fig. 3a, b). The molar C:N ratio was lowest in April 1991 (3.7), while in March–May 1992 and 1993 the ratio was higher, coinciding with a higher lipid level. The ratio rose rapidly during the summer and annual peaks were recorded between August and November [generally >7, with the highest ratio in August 1991 (10.95)]. The C:N ratio correlated significantly with the lipid:protein ratio (Fig. 3c). Gravid females showed lower C:N ratios in comparison with the coexisting juveniles.

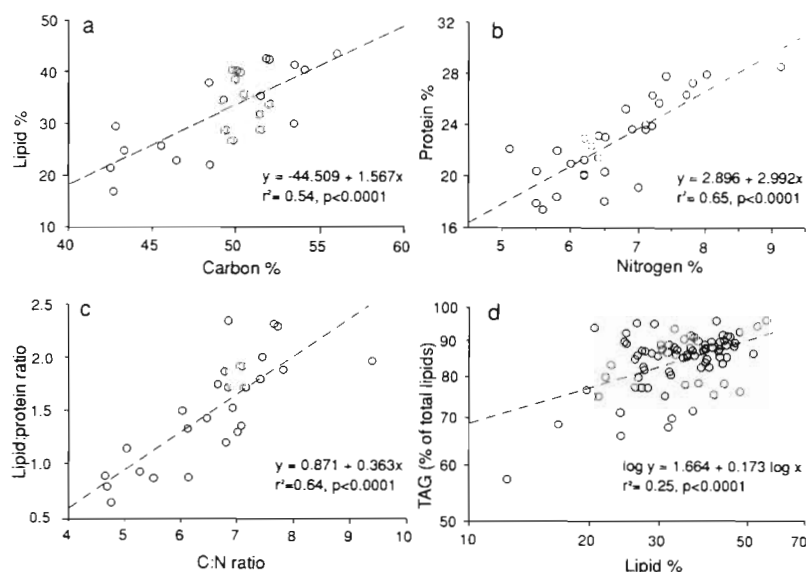


Fig. 3. *Monoporeia affinis*. Regression analyses on (a) carbon vs lipid; (b) nitrogen vs protein; (c) C:N ratio vs lipid:protein ratio; and (d) lipid (%) vs triacylglycerol (%). r^2 = coefficient of determination, p = significance at 95% level

Table 2. *Monoporeia affinis*. Seasonal variation in lipid class composition. Mean values \pm SD (italics). n = number of determinations; Weight = mean dry weight of measured individuals (mg); G = gravid females; TAG = triacylglycerols; FFA = free fatty acids; DG/ST = diacylglycerols/sterols; AMPL = acetone-mobile polar lipids; PL = phospholipids; NL:PL = neutral-to-polar lipid ratio

Date	Age	Weight	n	TAG	FFA	DG/ST	AMPL	PL	NL:PL
1991 22 May	2+	1.53	6	84.4 4.2	3.8 3.9	1.4 1.4	0.6 0.3	9.8 1.6	8.85 1.46
17 Jun	2+	2.39	6	88.2 1.3	1.2 0.9	<0.5	4.1 1.2	5.9 1.4	9.11 1.30
13 Aug	1+	0.39	3	90.9 1.3	<0.5	<0.5	1.5 0.5	7.7 0.9	10.13 1.42
13 Aug	2+	4.28	3	90.7 1.0	3.2 0.5	1.9 0.1	<0.5	4.1 0.7	23.31 3.97
1992 5 Mar	2+	1.20	4	83.7 3.6	1.6 1.6	1.9 1.2	<0.5	12.6 2.7	7.09 1.44
5 Mar	G	2.84	3	79.2 2.7	<0.5	<0.5	<0.5	20.3 23.0	3.90 0.62
28 May	1+	0.69	3	77.2 4.9	4.3 1.0	2.7 0.4	<0.5	15.1 2.7	5.75 1.48
28 May	2+	1.46	3	87.3 1.3	2.0 1.1	1.4 0.6	<0.5	8.9 0.4	9.82 0.43
16 Jun	1+	0.93	3	70.0 1.6	11.6 0.4	4.4 0.7	1.0 0.5	13.1 2.5	6.33 1.31
16 Jun	2+	2.67	3	84.6 1.6	4.7 1.0	2.3 0.8	0.5 0.1	7.9 0.5	3.89 0.34
9 Sep	1+	1.58	3	91.5 1.1	<0.5	<0.5	<0.5	8.4 1.1	11.01 1.72
9 Sep	2+	3.88	5	94.1 2.5	0.5 0.6	<0.5	0.5 0.1	4.5 1.5	20.82 6.04
25 Nov	1+	2.26	6	90.2 3.6	1.1 1.3	0.8 0.8	<0.5	7.6 2.2	12.43 3.30
25 Nov	G	4.31	2	94.7 0.8	<0.5	<0.5	<0.5	5.2 0.7	18.44 2.97
1993 4 Mar	1+	1.15	3	73.8 5.4	4.2 3.0	1.4 1.1	6.8 4.4	15.3 3.3	4.12 1.57
4 Mar	2+	1.52	6	86.7 2.7	1.8 1.1	<0.5	1.6 1.4	9.7 1.1	8.03 1.22
4 Mar	G	3.87	3	67.0 7.4	5.1 0.3	1.8 1.5	2.7 2.8	23.3 6.1	3.30 1.38
27 May	1+	1.55	3	84.7 2.8	1.7 0.1	<0.5	2.9 1.3	10.7 1.5	6.64 1.41
27 May	2+	2.61	3	87.4 1.5	1.1 0.2	<0.5	2.1 1.1	9.5 1.8	7.77 1.01
28 Jul	1+	1.52	6	81.1 5.1	4.0 1.5	2.0 0.7	1.0 0.7	12.1 3.0	7.32 2.57
28 Jul	2+	4.14	6	86.4 2.6	1.3 0.4	1.3 0.2	<0.5	11.0 2.3	8.54 2.05

Energy content and energetic value of body matter

Lipid formed the major energy component at all times, except in gravid females. The development in the energy content of mean-size individuals (J ind.^{-1}) showed very similar seasonal patterns between different cohorts (Fig. 4); the interannual variability was determined in general by differences in the size of the individuals (Andersin & Lehtonen unpubl.).

The energetic value of the body matter of *Monoporeia affinis* shows substantial seasonal fluctuations, with

highest values in late summer (28.2 J mg^{-1}) and lowest in spring (22.5 J mg^{-1}) (Fig. 5). The 2+ yr olds of the 1989 cohort showed, in 1991, markedly lower values in spring compared to the 2 following annual cohorts, but the peak values in summer were stable between the years. The energetic value of the 1+ yr olds is invariably smaller compared to the 2+ yr olds until the latter enter their reproductive phase. In comparison with cohort 1989, the gravid females of the 1990 cohort showed a more striking decline in energetic value as the moment of offspring release approached.

Energy dynamics

Fig. 6 shows the mean daily metabolic requirements of mean-sized individuals, the net accumulation rates of biochemical components and, in the case of net depletion of energy reserves, the contributions of specific components in energy metabolism. The 1+ yr olds of the 1990 cohort accumulated surplus energy between 17 June and 22 October 1991. Between 22 October and 7 December 1991, 47% of the metabolic energy was derived from the combustion of body components, mainly lipid (32%). In the 1+ yr olds of the 1991 cohort, body reserves supported 48% of energy needs between 9 September and 25 November 1992, but in this case all the energy was derived from lipids.

In the 2+ yr olds of the 1990 cohort, intensive accumulation of energy occurred between 16 June and 9 September 1992. Between 9 September and 25 November 1992, lipid stores supplied 60% of their metabolic requirements. In the 1989 cohort, however, lipid depletion accounted for only 15% of metabolic energy of 2+ yr olds at a corresponding time (24 September to

7 December 1991). Between 25 November 1992 and 4 March 1993, reserve lipid supported the metabolism of the now gravids of the 1990 cohort by only 26%, and the combustion of protein had intensified markedly (10% contribution to metabolic needs, seen also as an elevated NH_4^+ excretion rate of gravids; Lehtonen 1996). In the gravids of the 1989 cohort, however, lipid and protein accounted for 64 and 20%, respectively.

DISCUSSION

Effects of benthic nutritional conditions on *Monoporeia affinis*

The results indicate that the sedimentation of the spring bloom has a marked effect on the growth and composition of *Monoporeia affinis*, while the metabolic response (accelerated O_2 uptake and NH_4^+ excretion rates) is also distinct (Lehtonen 1996). Sediment nitrogen enrichment has been shown to enhance the growth and organic content of benthic invertebrates (Tenore 1977, Tsutsumi et al. 1990, O'Connor 1992). Studies carried out in parallel with the present study show that, at the study station in 1991 and 1993, 70 to 90% of the annual sedimentation of nitrogen and carbon occurred between early May and mid-June (Finnish Institute of Marine Research, FIMR, unpubl. data). Towards autumn and winter marked reductions in the C:N, nitrogen and chlorophyll *a* content of the settling material and in the sediment surface layer were observed. This data is in accordance with previous research on primary production, phytoplankton dynamics and sedimentation in the northern Baltic Sea (e.g. Lassig et al. 1978, Kuparinen et al. 1984, Leppänen 1988, Andersson & Rudehäll 1993, Heiskanen & Kononen 1994). Seasonality in the body composition and energetics of *M. affinis* is strongly influenced by pelagic processes,

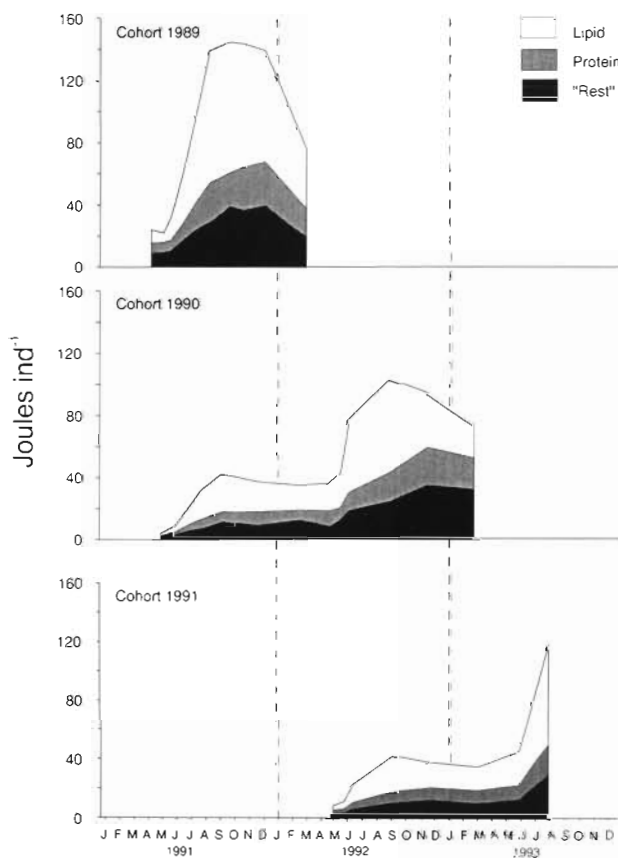


Fig. 4. *Monoporeia affinis*. Development in the energy content (J ind^{-1}) of mean-size individuals representing different year cohorts, fractionated to main biochemical constituents (lipid, protein and 'rest')

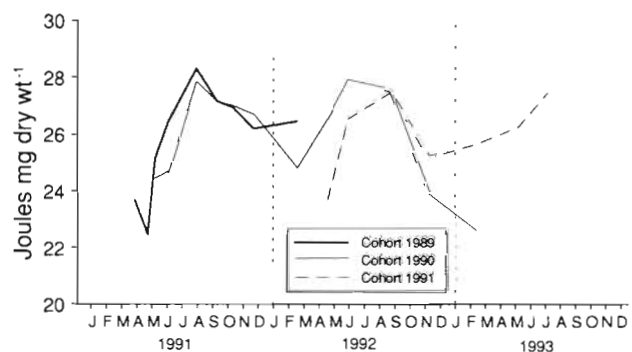


Fig. 5. *Monoporeia affinis*. Variations in the energetic value of the body matter (J mg dry wt^{-1}) of mean-size individuals representing different year cohorts

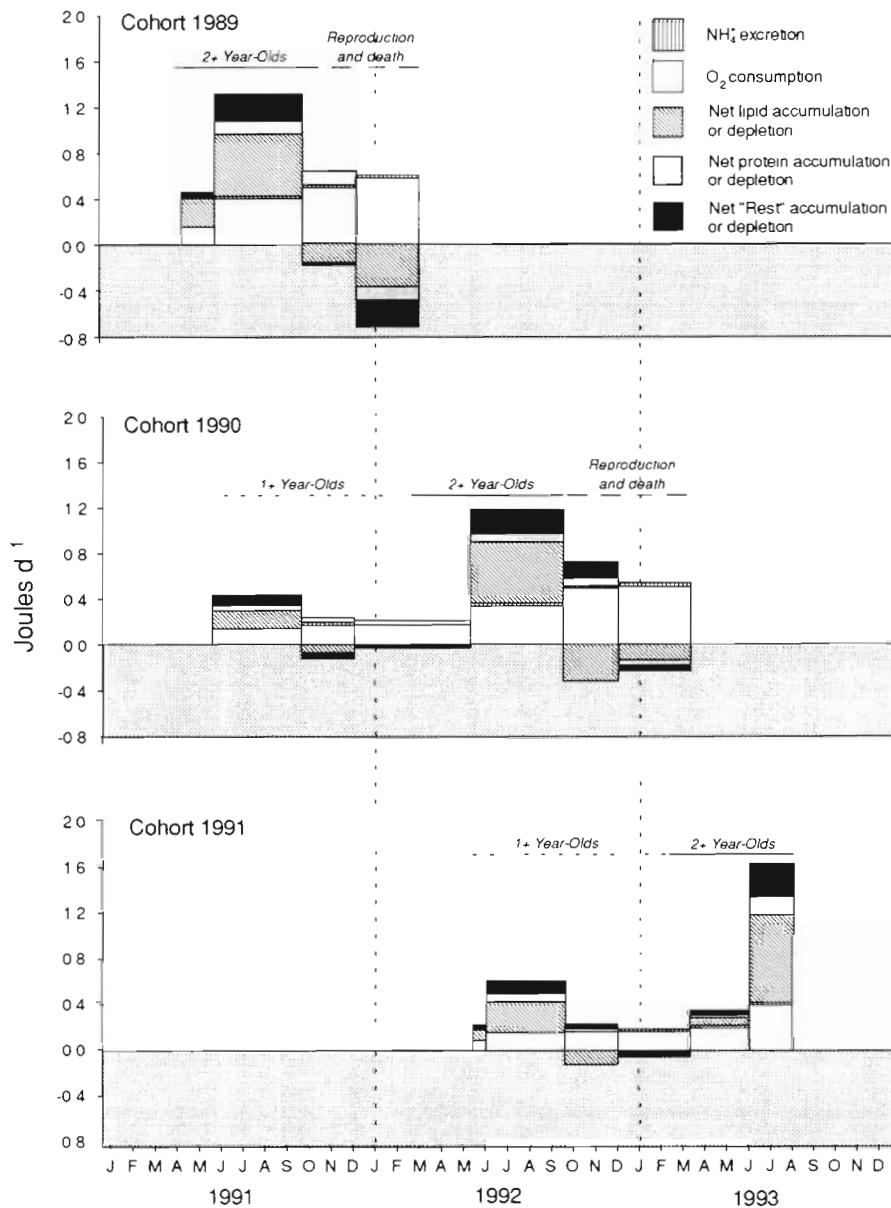


Fig. 6. *Monoporeia affinis*. Mean daily energy partitioning ($\text{J ind}^{-1} \text{d}^{-1}$) calculated for mean-size individuals from different year cohorts. The sum of O_2 consumption and NH_4^+ excretion represents the daily energetic requirements; net energy accumulation, fractionated to different biochemical components, shows the rate of surplus energy accumulation, while net energy depletion shows the combustion rate of body reserves for metabolic needs. Results from different sampling periods have been combined to represent the main seasonal periods in nutritive conditions in the environment and/or the life-cycle of the amphipods

which are observable in the benthic environment as changing nutritional conditions.

For zoobenthic species in general, the energetic value of the body matter of *Monoporeia affinis* falls at the high end of the scale (Griffiths 1977, Norrbin & Båmstedt 1984, Brey et al. 1988), even if an ash level up to 10% is assumed. This accords with the statement made by Slobodkin & Richman (1961) that organisms encountering periods of food scarcity during their life-cycle have high mean energy content. The results imply that the amphipods in the present study area have adopted an energy storage strategy which ensures maximum benefit from the short but intensive period of the spring phytoplankton sedimentation

Role of lipids in metabolism and reproduction

In *Monoporeia affinis*, lipids serve as a reserve of metabolic fuel and provide the main source of reproductive energy. A compilation of studies on *M. affinis*, *Pontoporeia femorata* and *Diporeia hoyi* (Table 3) shows that lipid levels in these closely related species are unusually high compared to other benthic crustaceans (review by Griffiths 1977; see also Clarke et al. 1985, Falkowski et al. 1989, Napolitano & Ackman 1989). In the present study, the seasonal range of 17 to 45% in the reproducing 2+ yr olds is wider than that reported by Hill et al. (1992) from a northern Baltic coastal population, but the maximum levels equal

those observed by Gardner et al. (1985a, b) and Gauvin et al. (1989) in Lake Michigan *D. hoyi*. The observed high lipid level of *M. affinis* secures a high reproductive potential as well as survival during poor food conditions.

Hill et al. (1992) recorded almost equal proportions of TAG and PL in *Monoporeia affinis* in the spring, while in the present study, TAG levels were always $\geq 70\%$ of total lipids. The lipid and TAG levels of the 1+ yr olds were always only slightly lower than in the 2+ yr olds entering the reproductive phase; this implies that a high lipid level in *M. affinis* is not necessarily coupled with reproduction, as juveniles evidently accumulate lipid for overwintering. A similar life-strategy has been demonstrated for juveniles of the deep-water prawn *Pandalus borealis* (Hopkins et al. 1993).

The production of eggs is related to the lipid content of individuals. In the study area, fertilization in *Monoporeia affinis* takes place in late autumn and the offspring are usually released before March (e.g. Segerstråle 1959, Andersin & Lehtonen unpubl.). The relation between lipid mass and body size seems to be a determining factor for the onset of the reproductive phase. It is suggested that the main reason why the 1+ yr olds at the study location do not reproduce despite a high lipid level is that the allocation of lipid for the development of reproductive tissue and eggs would result in serious starvation before brood release. Furthermore, low lipid content may reduce the viability of the offspring (Ouellet et al. 1992).

In this study, the lipid level of the 2+ yr olds declined in late autumn. Hill et al. (1992) also noted a decrease in lipid levels of both male and female *Monoporeia affinis*, as well as of *Pontoporeia femorata*, in October. Allocation of lipids and especially of TAG in the elaboration of reproductive tissue has also been shown in krill (Falk-Petersen et al. 1981). During maturation, reduced or halted feeding accelerates the depletion of body lipid for maintenance metabolism. After fertilization, the progressively increasing metabolism of the developing embryos further reduces the total lipid/TAG contents of the 'mother-brood complex'. In conclusion, lipid dynamics in *M. affinis* is intimately associated with the life strategy of the species.

Bioenergetic characteristics of the study population

During the periods when all the biochemical constituents studied show net accumulation (see Fig. 6), the sources of metabolic energy cannot be identified with the data obtained. However, the O:N ratio (O_2 consumption:NH₄⁺ excretion) is 50 to 60 during food abundance (Lehtonen 1994, 1996), denoting an almost

equal use of lipids and protein (e.g. Mayzaud & Conover 1988). These findings indicate that, in summer, substantial amounts of food protein are used to meet metabolic needs.

A high O:N ratio of >200 (Lehtonen 1994, 1996) observed in *Monoporeia affinis* during winter-spring indicates an almost exclusive use of lipids and carbohydrates. The bioenergetic calculations presented in Fig. 6 demonstrate that, although growth is completely ceased (Andersin & Lehtonen unpubl.), *M. affinis* obtains energy from the environment during winter-spring. This is most conspicuous in the 1+ yr olds, where depleted body reserves supported only 11 and 19% (cohorts of 1990 and 1991, respectively) of their metabolic needs during this period (Fig. 6).

That the gravids of the 1989 cohort relied completely on the use of body reserves (Fig. 6) supports the previous observations of a cessation of feeding at the onset of maturation in *Diporeia hoyi* (Moore 1979, Quigley 1988, Quigley et al. 1989). However, the gravids of cohort 1990 gained 60% of metabolic energy from the environment (Fig. 6), which confuses the proposed scheme.

Some of the aberrations in this bioenergetic model can be the result of loss of significant amounts of body material via ecdysis, most of the material belonging to the 'rest' fraction; however, it is probable that significant amounts of protein, lipid and chitin are resorbed from the old cuticle prior to moulting (Chandumpai et al. 1991 and citations within). Overestimation of the energy content of the 'rest' fraction, which also contains ash, can also cause bias, for example the observed 23% overshoot in energy loss in gravids of the 1989 cohort (Fig. 6).

Bioenergetic strategy in relation to life-cycle and long-term oscillations in amphipod populations

The life-cycle of *Monoporeia affinis*/*Diporeia hoyi* has generally been reported to be 1 to 2 yr (Segerstråle 1937, Green 1971, Winnell & White 1984, Siegfried 1985, Uitto & Sarvala 1991, Hill et al. 1992), but in the study area the population consists of at least 3 year classes (Andersin et al. 1984, Andersin & Lehtonen unpubl.). The longevity of the amphipods has been associated with depth and temperature (Segerstråle 1937, Moore 1979, Leonardsson et al. 1988), and trophic conditions of the environment (Siegfried 1985).

In contrast to shallow, coastal areas, growth of *Monoporeia affinis* in the study area is not temperature-regulated, since low temperature prevails throughout the season (2.5 to 5°C; Lehtonen 1996), slowing metabolism and reducing the catabolism of energy reserves. In addition, reduced respiration rate during adverse food conditions [Lehtonen 1996; equivalent to

Table 3. Reported lipid levels (% dry weight) of *Monoporeia affinis*, *Pontoporeia femorata* and *Diporeia hoyi*. F = females; M = males; A = adults (reproducing generation); J = juveniles [non-reproducing generation(s)]; G = gravids. From most studies, only the lowest and highest values are included

Species	Location	Age/Sex	Lipid (%)	Month	Depth (m)	Source
<i>D. hoyi</i>	Lake Cayuga	A	33.1	Jun	104	Green (1971)
<i>D. hoyi</i>	Lake Ontario	A?	24.1–32.5	?	?	Whittle &
	Lake Erie	A?	20.3	?	?	Fitzsimons (1983)
<i>D. hoyi</i>	Lake Michigan	J	37.4 ^a	Aug	24	Gardner et al. (1985a)
		J	28.7 ^a	Aug	45	
<i>D. hoyi</i>	Lake Michigan	J	18.3 ^a /45.0 ^a	Mar/Jun	29	Gardner et al. (1985b)
		J	18.3 ^a /43.0 ^a	Mar/Sep	45	
<i>D. hoyi</i>	Lake Michigan	J	16.4	Dec	45	Quigley et al. (1989)
		F	22.7	Dec		
		M	8.7	Dec		
<i>P. femorata</i>	Jeddore Harbour, Nova Scotia	M	12.0 ^b	Dec–Apr	4–16 ^c	Paradis & Ackman (1976)
<i>D. hoyi</i>	Lake Michigan	A	28.0/41.0	Dec/May	45	Gauvin et al. (1989)
<i>M. affinis</i>	Baltic Sea (coastal) - Askö area	J	11.0/19.0	Sep/Aug	30–40	Hill et al. (1992)
		A	13.0/27.0	Mar/Jul		
		F	19.0	Oct		
		M	18.0	Oct		
<i>P. femorata</i>		J	12.0/16.0	Aug/Oct		
		A	16.0/20.0–23.0	May/Rest of year		
		F	19.0	Oct		
		M	13.0	Oct		
<i>M. affinis</i>	Baltic Sea (open-sea)					
	- Bothnian Bay	A	13.7–16.8	Jun	70–112	Lehtonen (1995)
	- Bothnian Sea	A	33.0–37.2	Jun	77–212	
	- Gulf of Finland	A	24.4–32.7	Jun	51–60	
	- Bothnian Sea	J	22.0/41.5	May/Aug	125	This study
		A	21.4/43.8	Apr/Aug		
		G	16.8/26.8	Mar/Mar		
<i>P. femorata</i>	- Gulf of Finland	A	23.4–30.4	Jun	66–73	Lehtonen (1995)

^aRecalculated from ash-free dry weight (factor 0.87)

^bRecalculated from wet weight (assuming 75% water content)

^cCollected from stomachs of smelt *Osmerus mordax*

respiration measured under experimental starvation conditions (Lehtonen 1994)] further contributes to the conservation of energy. The varying life-cycles observed between coastal and open-sea *M. affinis* populations are probably a result of both nutritional and temperature conditions, which induce different bioenergetic strategies in populations inhabiting different sea areas.

Long-term oscillations (ca 7 yr cycle) in *Monoporeia affinis* populations (Andersin et al. 1978) almost certainly are connected to interannual variability in benthic nutritional conditions. The amphipods collected in winter and spring 1991 were smaller (2+ yr olds: mean dry wt ~1.0 mg, gravids: ~3.0 mg) than at a corresponding time in 1992 and 1993 (2+ yr olds: ~1.5 mg, gravids: ~4.5 mg) (Andersin & Lehtonen unpubl.). During spring 1992 and 1993, the seasonally characteristic biochemical condition of the amphipods was almost

identical and all the condition parameters studied indicated a healthier physiological state than in spring 1991. Evidently 1990 was nutritionally unfavourable for amphipods in this area.

In addition to the direct effects of interannual variability in the quantity and quality of sedimented particulate matter, interspecific relations (e.g. predation by demersal fish and the isopod *Saduria entomon*, processing of food by micro- and meiofauna) play a part in the population dynamics of *Monoporeia affinis*. Density-dependent regulation of population size, especially in nutrition-limited areas, may also be behind the oscillations. In considering the observed variability in the body condition of the amphipods, results indicate that there exists a physiological, lipid-related 'buffering capacity' in effect against years of limited food resources, caused by variations in the species composition and biomass of the spring bloom in the northern

Baltic Sea (e.g. Heiskanen & Kononen 1994). Assuming this scheme, a marked collapse in the population is likely only if 2 or more poor years follow successively. Together with environmental conditions, bioenergetic adaptations play an important role in the fluctuations in *M. affinis* populations.

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