KARI K. LEHTONEN

Ecophysiology of two benthic amphipod species from the northern Baltic Sea

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Academic dissertation

To be presented, with the permission of the Faculty of Science of the University of Helsinki, for public criticism in the lecture room of the Division of Animal Physiology (Arkadiankatu 7) on January 16th, 1998, at 12 o'clock noon.
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This thesis is based on the following papers, which are referred to by their respective Roman numerals:


V  Lehtonen K.K. Physiological condition of the amphipods *Monoporeia affinis* (Lindström) and *Pontoporeia femorata* Krøyer as an indicator of variations in benthic nutritional conditions in the Gulf of Riga (Baltic Sea). *Submitted manuscript.*

VI  Lehtonen K.K. & Andersin A.-B. Population dynamics, response to sedimentation and role in benthic metabolism of the amphipod *Monoporeia affinis* in an open-sea area of the northern Baltic Sea. *Submitted manuscript.*

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Bottoms up!
Abstract

Seasonal and spatial variations in the physiological condition of two benthic, deposit-feeding amphipods Monoporeia affinis Lindström and Pontoporeia femorata Kroyer from different areas of the northern Baltic Sea were investigated by examining their biochemical composition (mainly lipids) and metabolism (mainly ammonia excretion). In addition, by combining the metabolic and population data, the potential of the amphipod populations to mineralize carbon and nitrogen was estimated.

The main part of the thesis consists of an extensive seasonal study on M. affinis at a deep, open-sea station in the Bothnian Sea (1991-1993). A seasonal study was also carried out in the Gulf of Riga (1994-1995) at two shallower stations characterized by different environmental conditions. To acquire a broader view of spatial variations, in May-June 1993 a "snap-shot" study was carried out at 12 open-sea stations that covered the Bothnian Bay, Bothnian Sea and Gulf of Finland. Prior to all of these, an experimental study focusing on the effects of starvation on the metabolism of M. affinis was made to form an understanding of the impact of nutritional conditions.

The results of these studies show distinct physiological and biochemical responses to changes in environmental conditions by the amphipods, with sedimentation of the spring bloom triggering most of the changes observed. The physiological parameters studied were observed to vary significantly both seasonally and spatially, indicating variability in the bioenergetic strategy of amphipods inhabiting environmentally dissimilar areas, nutrition being the most important regulatory factor. The results from the Bothnian Sea implied a tight pelagial-benthos coupling, i.e. production and sedimentation of organic particulate matter and utilization by amphipods. Nutrition-related density-dependency is regarded as being the prime cause of the long-term oscillations in amphipod populations observed in earlier studies. The role of benthic amphipods in the mineralization of organic matter was shown to be marked especially in open-sea areas with low-to-moderate sedimentation rates and high amphipod densities.

Key words: Baltic Sea, benthic amphipods, biochemical composition, bioenergetics, lipids, metabolism, mineralization, Monoporeia affinis, Pontoporeia femorata, population dynamics, seasonal variation.
1 Background

Throughout the history of Baltic Sea ecosystem research, scientists have found themselves wandering too often in alleys of speculation over the physiological characteristics of the studied organisms, seeking explanations for their findings at higher levels of biological organization. Although an abundant number of basic ecological studies — although often simply monitoring of the biomass and abundance of organisms — has been carried out in this area interest in examining the physiological characteristics of organisms living in this exceptional environment has been disappointingly low.

Since physiological functions are the ones that really show us whether an organism is dead or alive, its level of activity, health, prospects of reproducing successfully, and potential gain of and effect on its environment, it is obviously of utmost importance to have basic physiological knowledge particularly of species that form the main components of the ecosystems. Moreover, especially in connection with environmental monitoring, physiological and biochemical parameters often come in handy as indicators of the effects of changes in environmental conditions, provided they are interpreted in a sensible way.

In the Baltic Sea, low species diversity is a characteristic phenomenon, caused mainly by constantly low salinity (classically shown by Remane and Schlieper 1971). Due to this and other abiotic and biotic characteristics of the area, many researchers share a view of the Baltic Sea as a huge, unique pool for scientific research. Certainly the physiological characteristics of organisms adapted to these conditions tend to be rather special; this leads one to suspect that knowledge on even closely-related species inhabiting true marine or limnic environments is not necessarily applicable to the organisms inhabiting the constantly brackish-water Baltic Sea.

For practical reasons, the lack of physiological studies, especially with regard to the benthos, is most evident in the open-sea areas. However, interesting phenomena that have not been explained by standard population analyses occur in these areas. Low diversity in the Baltic Sea simplifies food-web analysis and the study of many other biological interactions. Under such conditions, knowledge of the physiology of a dominant species in a study area can be very useful, especially in open-sea areas, because it can often be applied to large geographical areas, not only to local communities.

In short, investigations of the ecological physiology of certain, highly dominant species provides valuable information about the functioning of the ecosystem in large geographical areas, as in the case of this study, the northern Baltic Sea. I was given an excellent opportunity to study the physiology of two amphipod species that dominate most open-sea soft bottoms of the northern Baltic Sea. I have tried not to waste this opportunity; the results and conclusions of my work are presented in this thesis.

2 Introduction

2.1 The species investigated: general biology

The amphipods *Monoporeia affinis* (Lindström) (formerly named *Pontoporeia affinis*; see Bousfield 1989) and *Pontoporeia femorata* Krøyer are dominant members of the soft-bottom macrobenthic communities of the northern Baltic Sea (e.g. Segerstråle 1937, Ankar and Elmgren 1975, Elmgren 1978, Andersin et al. 1978, 1984). *M. affinis* is usually the dominant macrobenthic species, with densities reaching 10,000 ind m⁻² and more. Originally limnic, *M. affinis* survives in brackish water up to 7-8 % S. while the marine *P. femorata* is found in significant abundance only in >7% S. The two species coexist in areas where the salinity is suitable to both. Because of their high abundance and specific biological characteristics, the amphipods form a most important link between the pelagic and benthic communities of the northern Baltic Sea, especially in open-sea areas.

The amphipods feed mainly on organic detritus present in the surface layer of the sediment and on phytoplankton that reaches the bottom via sedimentation. Both species are night-active, with *M. affinis* showing a higher swimming and metabolic activity than *P. femorata* (Lopez and Elmgren 1989). *M. affinis* also lives closer to the sediment surface (Hill and Elmgren 1987) and has a faster feeding rate than *P. femorata* (Lopez and Elmgren 1989). Both species are semelparous, usually reproducing in early spring. The life-cycle of *M. affinis* has been shown to vary markedly between locations and ranges from 1 to 4 years (e.g. Segerstråle 1937, Andersin et al. 1984, Leonardsson et al. 1988).

The population densities and biomasses of both species show substantial spatial, seasonal and interannual variations (e.g. Andersin et al. 1978, 1984, Sarvala 1986, Uitto and Sarvala 1991, Maximov 1997). Lake studies have revealed strong evidence of
pelagic-benthic coupling, i.e. an interaction between the quantity and quality of algal blooms and the success of benthic amphipod populations (Johnson and Wiederholm 1992, Fitzgerald and Gardner 1993); also, studies performed in shallow, coastal areas of the Baltic Sea show similar indications (Cederwall 1977, Elmgren 1978).

Although comprehensive studies on the general biology of these amphipod species exist, their metabolic and biochemical characteristics have received considerably less attention, with the exception of studies by Cederwall (1979) and Hill et al. (1992). Studies are available, however, on the metabolism of Diporeia spp. (formerly Pontoporeia hoyi [Bousfield 1989]), the North American freshwater relative of M. affinis (Johnson and Brinkhurst 1971, Nalepa et al. 1983, Gardner et al. 1987, Gauvin et al. 1989). A typical feature for all the three amphipod species is their exceptionally high lipid content (e.g. Green 1971, Gardner et al. 1985a, b, Quigley et al. 1989, Hill et al. 1992). Since M. affinis and P. femorata are key components of the Baltic Sea benthos, further knowledge of their physiology is essential to our understanding of their role in the ecosystem.

2.2 The species in relation to their environment

2.2.1 Nutritional conditions

In open-sea areas, the nourishment of benthic deposit-feeders is largely dependent on autochthonous food sources. In contrast, in many coastal areas, the importance of allochthonous material may be significant, but material that reaches the benthos in this way is usually of low quality (e.g. low nitrogen content, refractory substances; e.g. Parsons et al. 1977) and not ideal food. As a result, the growth and overall bioenergetic strategy of benthic organisms in different sea areas are strongly influenced by geographically varying nutritional conditions.

The nutritional quality of the upper sediment layer is governed by both the quantity and quality of sedimentation input. In sub-boreal temperate waters, like the Baltic Sea, the major part of the annual sedimentation occurs during and slightly after the spring phytoplankton bloom, in open-sea areas within 5-6 weeks (e.g. Smetacek et al. 1978, Kapparinen et al. 1984, Leppänen 1988). During the remainder of the year the input is small (e.g. Jansson 1978, Andersson 1996). This pattern of sedimentation generates strong seasonal variability with respect to the availability of good-quality nutrition for benthic organisms, especially in areas where populations are dense and food resources become rapidly depleted. Furthermore, food availability is often strongly affected by inter- and intraspecific competition.

Benthic organisms may confront periods comparable to starvation due to the gradual depletion of food resources and deterioration of food quality. Capability to withstand nutritional stress is of crucial importance. Energy storage during food abundance and metabolic energy-saving adjustments triggered by food deficiency are mechanisms common to most organisms. Although immediate effects of poor nutrition are sometimes hard to recognize, the reproductive potential of animals may become reduced and, eventually, the effects will be manifested at population level through a smaller amount of offspring and/or survival capacity of the young.

2.2.2 Role in benthic mineralization processes

The fact that benthos plays an important role in the mineralization of organic particulate matter and in benthic nutrient dynamics has been acknowledged for a long time. As the dominant species of soft-bottoms in the northern Baltic Sea, M. affinis and P. femorata may have a significant influence on these processes, especially in areas of high population density. Besides the direct mineralization of organic matter that results in the release of CO₂ and nutrients, the strong bioturbation activities of benthic amphipods change the texture and chemical environment of the top sediment layer, resulting in e.g. increased bacterial production (e.g. van de Bund et al. 1994). In this way amphipods may affect various benthic processes, e.g. the rates of nitrification and denitrification (e.g. Pelegrí and Blackburn 1994, Pelegrí et al. 1994).

2.3 The study objectives

2.3.1 Metabolism

Oxygen uptake rate (\(\dot{V}O_2\)) is a general measure of metabolic activity, while the ammonia excretion rate (\(\dot{V}NH_3\)) implies protein catabolism; using their atomic equivalents, an index of physiological condition, the atomic O:N ratio can be obtained. At steady-state, the O:N ratio indicates the relative proportion of protein used for energy production compared to other main energy-yielding substrates, lipid and carbohydrate (e.g. Conover and Corner 1968,
review by Mayzaud and Conover 1988), and has been used for determining the physiological condition of various marine invertebrate groups, including amphipods (e.g. Pederson and Capuzzo 1984, Aarset and Aunaas 1990), mesozooplankton (e.g. Conover and Corner 1968, Mayzaud 1973, 1976) and bivalves (e.g. Bayne et al. 1985, Widdows 1978). In addition, metabolic rates can be used to estimate the potential of animal populations to mineralize organic matter.

2.3.2 Biochemical composition

Gross biochemical composition (lipid, protein and carbohydrate), lipid class composition, and, more roughly, elemental composition (carbon and nitrogen) indicate the nutritional state, and the reproductive and survival potential of organisms. Spatially and seasonally differing environmental nutritional conditions are reflected in the body composition of animals, which must adjust their bioenergetic strategy to short- and long-term variations in food supply.

Lipid accumulation is the most widespread long-term energy storage strategy in aquatic crustaceans. Lipid — mainly triacylglycerols (TAG) — has been shown to be the major energy storage component in M. affinis and P. femorata (Hill et al. 1992), and also in Diporeia spp. (e.g. Gardner et al. 1985a,b, Gauvin et al. 1989, Quigley et al. 1989). Moreover, reproductive potential is largely dictated by lipid content since lipid is commonly used to the build-up of reproductive tissue and the formation of sexual products (e.g. review by Sargent and Henderson 1986, Gatten et al. 1980).

2.4 The study areas

2.4.1 Deep, open-sea area: Bothnian Sea

The main part of this study was performed at a deep (125 m), open-sea station (Baltic Monitoring Programme Station SR5) in the Bothnian Sea (Gulf of Bothnia) (Fig. 1). The area is characterized by a seasonally constant near-bottom temperature range (2-5°C) and moderate rates of primary production and sedimentation, concentrated in the late spring - early summer period (VI). The metabolism (IV) and the gross biochemical and lipid class composition (III) of M. affinis were investigated to determine the effects of seasonal and interannual variations in food availability on their physiology and population dynamics. The contribution of the population to carbon and nitrogen mineralization in the benthic environment was estimated by combining the metabolic measurements with population data (VI). Prior to these studies, an experiment was designed to study the effects of a short-term starvation period on the metabolism of M. affinis, in order to understand the responses of the amphipods to changes in food availability (I).
2.4.2 Eutrophied, coastal area: Gulf of Riga

A seasonal study to determine changes in the lipid content and $\text{NH}_4^+$ of both *M. affinis* and *P. femorata* was carried out in the Gulf of Riga, a semi-enclosed subregion of the Baltic Sea (Fig. 1) (V). The gulf is heavily influenced by riverine input, the river Daugava being the main source of nutrients and particulate matter. A gradual eutrophication of the gulf during the past decades has been observed (reviewed in Ojaveer 1995), characterized by high levels of nutrients (Yurkovskis et al. 1993, Kouts and Håkansson 1995), primary production (Andrusaitis et al. 1992, Tenson 1995) and changes in the zoobenthic community (Lagzdins et al. 1987). Both the nearshore (GR1: depth 28 m) and the offshore (GR5: 44 m) study stations exhibited seasonal fluctuations in near-bottom temperature (GR1: 0.3-12.0°C, GR5: 0.3-9.0°C) and oxygen conditions (GR1: 3.7-12.6 mg O$_2$ l$^{-1}$, GR5: 2.9-12.2 mg O$_2$ l$^{-1}$). Parallel population data by Yermakovs and Cederwall (in prep.) were used to estimate the contribution of the amphipod populations to benthic carbon and nitrogen mineralization.

2.4.3 Deep, open-sea areas: post-bloom study

Soon after the sedimentation of the spring bloom, a "snap-shot" study was made to examine the lipid content and $\text{NH}_4^+$ of 9 *M. affinis* and 3 *P. femorata* populations from different open-sea regions of the northern Baltic Sea, the Bothnian Bay, Bothnian Sea and Gulf of Finland (Fig. 1) (II). The stations studied exhibited differing environmental characteristics, with depth ranging between 51 and 212 m, temperature between -0.1 and 4.2°C, and salinity between 3.4 and 8.0 °C (at the time of sampling). The three main subregions show marked differences in primary production (e.g. Lassig et al. 1978, reviews by Elmgren 1978, 1984) and probably also in sedimentation rates. The results obtained from the $\text{NH}_4^+$ measurements were combined with population data to be able to estimate the contribution of the amphipod populations to benthic nitrogen mineralization at the time of sampling.

3 Material and methods

3.1 Sampling

Sampling and measurements of metabolic rates were carried out aboard the *Aranda* of the Finnish Institute of Marine Research (FIMR), following, usually, the same procedure. van Veen grab samples were rinsed with cooled sea water and the amphipods were sieved gently upon a 0.5 mm mesh. The amphipods were transferred rapidly into the cold room, where they were kept in 15 l aquaria containing aerated, filtered sea water and a 1.5 cm layer of fine, cleansed sand. The amphipods were kept in the dark at the experimental temperature (usually 4°C) for 1-3 days prior to metabolic measurements. The subsequent biochemical analyses were performed in FIMR laboratories. Sampling for the different studies was made as follows:

- I: Samples of *M. affinis* for the starvation experiments were collected from the Bothnian Sea open-sea station SR5 in March and June 1992.

- II: 12 stations in the Gulf of Finland, Bothnian Sea and Bothnian Bay were sampled for *M. affinis* and *P. femorata* during May-June 1993.

- III, IV, VI: seasonal samples of *M. affinis* were collected from the Bothnian Sea open-sea station SR5 on 17 occasions between January 1991-July 1993.

- V: seasonal samples of *M. affinis* (station GR1) and *P. femorata* (station GR5) were collected between April 1994-May 1995. For studying the effects of temperature on the $\text{NH}_4^+$, additional samples of both species were taken at 3 open-sea stations in the Gulf of Finland and one in the Bothnian Sea (SR5) between May 1995-September 1996. In the Gulf of Riga, the Latvian vessels "GeoFizikis" and "Antonija" were also used for sampling.

3.2 Measurement techniques

The techniques used are here described very briefly. Detailed descriptions of the methods are found in the papers indicated by Roman numerals.
3.2.1 Determination of metabolic rates

After an acclimatization period of not less than 24 h, the amphipods were incubated for 12-24 h in 300-ml erlenmeyer flasks ($V_{O_2}$, $V_{NH_3}$) (I, IV) or 25-ml liquid scintillation vials ($V_{NH_3}$) (I, II, V). Changes in oxygen and ammonia concentrations were determined using a modified Winkler method and the phenol-hypochlorite method of Solórzano (1968), respectively. Weight-specific metabolic rates were calculated after the lyophilization and weighing of the experimental specimens.

3.2.2 Biochemical measurements

The lyophilized individuals were homogenized and analyzed for total lipid using the method of Gardner et al. (1985a). Lipid classes were determined using TLC-FID (l中国市场 analyzer) (II, III, V). In the Bothnian Sea study, protein (Bradford 1976), and carbon and nitrogen (Heraeus CHN analyzer) were also determined (III).

3.2.3 Population data

Population studies were carried out simultaneously with the determination of metabolic rates and biochemical composition. The population samples (usually 5 Box Cores) were stored in 5% hexamin-buffered formalin for 3 months prior to analysis. After counting, the body length and the wet and dry weights of the individuals were recorded (II, V, VI).

3.2.4 Bioenergetic calculations

In the Bothnian Sea study (III, IV), metabolic and biochemical parameters were converted to energy equivalents (Gnaiger 1983, Elliott and Davison 1975, Winberg 1971). Daily energy consumption/accumulation rates were determined for a mean-size individual from each annual cohort. Changes in these rates, due to growth and seasonal variability of the parameters in the equations describing metabolic rates (IV), were taken into account by applying linear interpolations of each parameter between each sampling date. Daily growth rates and the subsequent changes in the content of specific biochemical components (accumulation and depletion rates) were obtained in a similar way.

3.2.5 Mineralization of carbon and nitrogen

Weight-specific excretion and respiration rates, determined for individuals representing 1-mm length classes, were multiplied by the number of the individuals in each respective length class (II, V, VI). The metabolism of the whole population was calculated by summing-up the values of all length classes. Daily mineralization rates of the amphipod population were obtained by linear interpolation between the metabolic rates measured at each sampling date; periodic (monthly, annual) values were obtained by summing daily values for the interval desired.

3.2.6 Bothnian Sea: sedimentation

In the Bothnian Sea, sedimentation during 1991 and 1993 was measured by using an automated, funnel-shaped multisample trap, moored at sampling station SR5 at the depth of 80 m (VI). The data obtained were used in the estimation of the proportion of deposited carbon and nitrogen assimilated by the local $M. affinis$ population. The measured sedimentation rates, as well as parallel data on primary production at the study station in 1991 (Andersson et al. 1996), were interpolated linearly over the annual study periods, and periodical totals of production and sedimentation (annual, monthly) were obtained from the daily rates.

4 Compilation of main results

The results of the studies are presented here as a brief compilation only. An excessive use of numerical values has been avoided; for greater details, please consult the respective papers indicated by Roman numerals.

4.1 Metabolism

4.1.1 Effects of short-term starvation

During the course of the 8-d experiments $M. affinis$ showed a relatively small decrease in $V_{O_2}$ compared to the reduction in $V_{NH_3}$ (I). Compared to the June experiment, the amphipods in the March experiment showed low $V_{NH_3}$ already at the start of the experiment. In both of these experiments, the
changes observed in metabolic rates resulted in elevations in the O:N ratio, indicating a shift into more lipid-based metabolism as starvation progressed.

Handling stress had a significant effect on the \( \text{NH}_4^+ \), which was always highest immediately after sampling. In the Gulf of Finland population (LL4a; Fig. 1), the excretion rate measured directly after sampling was about twice higher than that recorded after keeping the amphipods for 4 h in the laboratory, and the rate remained stable after 24 h. However, following stabilization, the \( \text{NH}_4^+ \) remained strikingly lower in amphipods collected from the Bothnian Sea station (SR5) compared to those collected from the Gulf of Finland and Bothnian Bay (CVI). The estimated O:N ratios indicated lipid-dominated energy metabolism in the Bothnian Sea population, while the catabolism of protein was more marked in the animals from the Gulf of Finland; in the Bothnian Bay animals, the O:N ratios were intermediate.

4.1.2 Effects of temperature on ammonia excretion

The magnitude of the effect of temperature elevation (from 4°C to 12°C) on the \( \text{NH}_4^+ \) of the amphipods appeared to depend on the level of excretion at 4°C (V). For \textit{P. femorata} the lowest temperature coefficient \( Q_{10} \) (1.15) was recorded at station GF2 (Gulf of Finland) at a time of very high \( \text{NH}_4^+ \) at 4°C, while the highest coefficient (2.80) was recorded at station GR5 (Gulf of Riga), the \( \text{NH}_4^+ \) at 4°C being half that recorded at station GF2. For \textit{M. affinis}, the highest coefficient (3.93) was found at station JML (Gulf of Finland) during low "ambient" \( \text{NH}_4^+ \), and the lowest (2.21) at the same station during a high-excretion period.

4.1.3 Seasonal and spatial variations

4.1.3.1 Bothnian Sea

For the early-summer period, in \textit{M. affinis} an overall increase in \( \text{VO}_2 \) of 22% was observed, but overshadowed by dramatic increase in \( \text{NH}_4^+ \), 5-8 times higher than for the winter-spring period (Fig. 2) (IV). During each of the three study years, the peak of \( \text{NH}_4^+ \) occurred in the early summer, while in winter and spring the rate was extremely low. Due to this high variability, combined seasonal \( \text{NH}_4^+ \) vs. dry weight data showed poor correlation. In general, the gravid females showed a significantly higher weight-specific \( \text{NH}_4^+ \) compared to juveniles (=non-mature individuals). The O:N ratios indicated that \textit{M. affinis} relied heavily on lipid for metabolic energy production during most of the year, except in early summer when the utilization of lipid and protein was almost equal. Furthermore, the results indicate the existence of a time-lag between the sedimentation of the phytoplankton bloom and the metabolic response of the amphipods.

To examine the potentially biasing effect of seasonal changes in body composition on weight-specific metabolic rates, biochemical data (III) were employed to scale the \( \text{VO}_2 \) against the amount of specific body constituents (protein, nitrogen, "non-lipid dry weight"). In most cases, elevations in the slope (b) of the allometric respiration (R) equations \( R = a \cdot \text{weight}^b \) were observed, indicating a shift to more size-independent metabolic rates (IV). Compared to the winter-spring period, however, the higher level of \( \text{VO}_2 \) observed during the May-September period was evident irrespective of the weight parameter used. The use of different weight parameters did not improve the poor \( \text{NH}_4^+ \) vs. weight correlations.
4.1.3.2 Gulf of Riga

At the nearshore station GR1, the $\dot{VNH}_4^+$ of M. affinis was slightly elevated in early May after the spring bloom, while at the offshore station GR5 seasonal variation in the $\dot{VNH}_4^+$ of P. femorata was not significant (Fig. 2) (V). Compared to M. affinis at station GR1, P. femorata at station GR5 had constantly a significantly higher $\dot{VNH}_4^+$. The gravid females of both species, as well as male P. femorata caught at station GR5 showed a significantly higher $\dot{VNH}_4^+$ compared to juveniles. Dry weight vs. $\dot{VNH}_4^+$ regressions proved to be non-significant for M. affinis, but data on P. femorata indicated that $\dot{VNH}_4^+$ is weight-dependent although the correlation was not strong.

4.1.3.3 Other areas: post-bloom study

Substantial variability in the excretion rates of the amphipods was observed to exist between the study regions. In the M. affinis populations of the Bothnian Sea the $\dot{VNH}_4^+$ was virtually identical at the 4 stations studied (II). In the eastern Gulf of Finland and the Bothnian Bay the $\dot{VNH}_4^+$ was almost twice that found in the Bothnian Sea. Regression analyses showed that the weight-specific $\dot{VNH}_4^+$ of M. affinis was not dependent on spatial differences in dry weight, lipid level or neutral-to-polar lipid (NL:PL) ratio. At the Gulf of Finland stations LL6a and LL11, P. femorata populations exhibited excretion rates close to those measured for M. affinis in the
eastern Gulf of Finland and Bothnian Bay; however, the population at station LL9 showed a significantly lower rate.

4.2 Body composition

4.2.1 Seasonal and spatial variations

4.2.1.1 Bothnian Sea

Seasonal changes in the biochemical composition of *M. affinis* at station SR5 (III) were closely coupled with the growth dynamics of the species at this location (see below) (VI). During 1991-93, the lipid level (% dry wt) of the amphipods varied between 15-45% and showed both seasonal and interannual variation (Fig. 3). The lowest lipid levels always occurred in March-April, while rapid accumulation was recorded between late May and mid-June, with levels peaking in August-September. Accumulation rates of lipid were generally high in June-August, but the “net lipid balance” (accumulation minus depletion) turned negative towards the late autumn-winter period. Gravid females had characteristically lower lipid levels (15-20%) compared to juveniles.

Triacylglycerols (TAG) were always the major lipid class (67-95% of total lipids), their levels correlating significantly with the levels of total lipid and carbon. The phospholipid fraction comprised between 4-23% of the total lipid measured and each of the other lipid classes (free fatty acids, sterols/diacylglycerols and acetone-mobile polar lipids [mostly pigments and glycolipids]) less than 7%. The NL:PL ratio was low in the spring and early summer, peaking between late summer and early autumn. The ratio was invariably higher in the 2+ year-olds compared to the 1+ year-olds, while, in general, the gravid females had a low NL:PL ratio.

Protein comprised 17-29% of body dry weight, varying mainly according to season but also because of interannual variability in body size. Carbon (33-56%) and nitrogen (5-9%) levels closely followed the seasonal patterns of the lipid and protein levels, respectively. The molar C:N ratio peaked in August-September; the ratio was lowest in April 1991, while in March-May 1992 and 1993 it was markedly higher, coinciding with higher lipid levels. As expected, the C:N ratio correlated significantly with the lipid:protein ratio. The gravid females showed a lower C:N ratio in comparison with the juveniles.

Development of the energy content (J ind⁻¹) in

![Fig. 3. Monoporeia affinis and Pontoporeia femorata. Seasonal and spatial variations in lipid levels in individuals representing the reproducing generation in each study location. The data from the Bothnian Sea station SR5 comprises measurements from 3 years (January 1991-July 1993). The Gulf of Riga stations (GR1 & GR5) were studied between January 1994-May 1995; measurements performed in May 1995 have been incorporated to the curve between April and July 1994. G=gravid females. Adapted from papers III and V.](image-url)
mean-size individuals representing the different annual cohorts showed similar seasonal patterns; interannual variations were due to the differences in the size of the individuals (VI). As might be expected when examining the observed changes in lipid levels, the energy value (J mg\(^{-1}\)) of the body matter showed seasonal and also interannual fluctuations, with the highest values in late summer (28.2 J mg\(^{-1}\)) and lowest in spring (22.5 J mg\(^{-1}\)). The energy value of the 1+ year-olds was invariably lower compared to the 2+ year-olds, until the latter entered the reproductive phase. Bioenergetic calculations based on metabolic rates and changes in body composition showed that, during the winter-spring period, a substantial amount of metabolic energy is obtained by the combustion of body matter, mainly lipid.

4.2.1.2 Gulf of Riga

In 1994, the maximum lipid level (36%) attained by _M. affinis_ at the nearshore station GR1 in summer significantly reduced by November (21%) (Fig. 3) (V). Lipid balance calculations confirmed that the amphipods at station GR1 did not accumulate lipid during that period. Ovigerous or gravid females continued to deplete lipid at a high rate, exhibiting extremely low lipid levels in March 1995 (9%). The population exhibited a 2-year life-cycle; after the spring bloom, the lipid level of the forthcoming reproducing generation (cohort born in 1994) was already greatly elevated in early May 1995 (37%).

In _P. femorata_ at offshore station GR5, the decline in the mean lipid level between July and November 1994 was considerably less (from 37 to 30%, Fig. 3). The lipid balance was positive throughout the autumn, only turning negative between gravity and the release of offspring. The forthcoming reproducing generation (also having a 2-year life-cycle) showed moderate lipid levels in January and March 1995 (27%), but a sharp increase after the spring bloom in early May (37%).

The levels of TAG were constantly higher in _P. femorata_ at station GR5 (seasonal range: 63-81%) compared to _M. affinis_ at station GR1 (44-73%), while the proportions of phospholipids were 11-22% and 18-38%, respectively.

4.2.1.3 Other areas: post-bloom study

In _M. affinis_ the lowest total lipid levels were recorded for both Bothnian Bay populations (mean 15%) (II). Individuals at the four Bothnian Sea stations showed higher levels (34%) than the three Gulf of Finland populations (24%). In the Gulf of Finland, _P. femorata_ at station LL6a, despite being very large, had a lower lipid level (23%) than individuals from stations LL9 and LL11 (29%).

The highest TAG levels were recorded in _M. affinis_ at stations SR5 (Bothnian Sea) and F42 (Gulf of Finland) (mean 85%), while the amphipods at both Bothnian Bay stations had the lowest levels (54%). The NL:PL ratio was significantly dependent on the lipid level and dry weight of the individuals. In _P. femorata_ the lipid class composition was similar at the three Gulf of Finland stations studied, with lower TAG levels (76%) compared to _M. affinis_ (except for _M. affinis_ collected from the Bothnian Bay).

4.3 Observations at population level

4.3.1 Mineralization of carbon and nitrogen

At the Bothnian Sea station SR5 the annual carbon mineralization potential of the amphipod population was 5-10 times higher than at the Gulf of Riga stations GR1 and GR5 (Table 1) (V, VI). With regard to nitrogen the release rates between the two subregions were more similar, although the difference between 1991 and 1992 at station SR5 was about 2-fold. In the post-bloom study, highly variable daily rates were recorded in the different study areas (II).
Table 1. *Monoporela affinis* and *Pontoporeia femorata*. Mineralization potential of different amphipod populations. $R_{\text{min}}$ and $R_{\text{max}}$ = minimum and maximum daily mineralization rates during the year. Adapted from papers V and VI.

<table>
<thead>
<tr>
<th></th>
<th>Carbon</th>
<th>Nitrogen</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Daily rate</td>
<td>Annual total</td>
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<tr>
<td></td>
<td>mg C m(^{-2})</td>
<td>g C m(^{-2})</td>
</tr>
<tr>
<td>$R_{\text{min}}$</td>
<td>$R_{\text{max}}$</td>
<td></td>
</tr>
<tr>
<td><em>M. affinis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SR5 1991*</td>
<td>18.8</td>
<td>72.2</td>
</tr>
<tr>
<td>SR5 1992*</td>
<td>27.1</td>
<td>50.1</td>
</tr>
<tr>
<td>SR5 1993**</td>
<td>19.7</td>
<td>39.9</td>
</tr>
<tr>
<td>GR1 1994***</td>
<td>3.9</td>
<td>15.0</td>
</tr>
<tr>
<td><em>P. femorata</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GR5 1994***</td>
<td>0.7</td>
<td>9.9</td>
</tr>
</tbody>
</table>

* Jan 15 - Jan 14 next year  
** Jan 15 1993 - Jul 28 1993  
*** Dec 15 1993 - Jan 5 1995

4.3.2 Bothnian Sea: pelagic-benthic coupling

4.3.2.1 Seasonal and interannual variations in population dynamics

During each study year the period of rapid growth commenced some weeks after the start of the spring bloom sedimentation and continued until autumn (VI). From late autumn to spring the growth of individuals ceased completely. Interannual differences between cohorts born in different years were observed. The most marked differences in individual mean weight were observed in the gravid ca. 3-year-olds and 2+ year-olds collected in winter-spring of 1991 and the corresponding year-classes sampled in 1992 and 1993, which were twice the weight. The highest biomass values of the population occurred always in autumn and the lowest in spring. Furthermore, the abundance and biomass of the population showed a clear decreasing trend between 1991-1993.

4.3.2.2 Carbon requirements of the amphipod population in relation to primary production and sedimentation

At the Bothnian Sea station SR5 in 1991, the intensive period of primary production occurred in April-May (Andersson et al. 1996), while sedimentation peaked slightly after, by early June about 90% of the annual carbon sedimentation had reached the bottom (VI). A gradual reduction in the nutritional quality of the settling material was observed towards autumn. Of the annual primary production (105 g C m\(^{-2}\)), an amount of carbon corresponding 17.5% was found sedimented in the 80 m trap. During the "active period" of sedimentation and amphipod growth (April 15-July 14), 20.5% sedimentation of the carbon produced occurred. In 1993, during the "active period", the organic material deposited was ca. 50% less than in 1991.

Using the data on primary production in 1991, the *M. affinis* population was calculated to have assimilated 17.5% of the pelagially produced carbon. With specific regard to the "active period" (April 15-July 14), a proportion of 10.2% was calculated. In both 1991 and 1993, during the "active period", about 50% of the sedimented carbon was calculated to have been assimilated by amphipods. The production-to-respiration ratio (as carbon equivalents) during this period was significantly higher in 1991 (1.23) compared to 1992 (0.46) and 1993 (0.58), indicating a significant allocation of food energy to growth in 1991.

5 Discussion

Depending on area, season and even the year of sampling, the two amphipod species studied exhibit distinct variability in their metabolic rates and body composition. In the following sections these results
are discussed in view of metabolic physiology, energy allocation, effect of environmental conditions and, ultimately, the population dynamics of the species especially with respect to previous observations on the long-term oscillations in the populations *M. affinis* from the Bothnian Sea.

Since the Bothnian Sea *M. affinis* population at station SR5 was studied more intensively than the others, with more information available on local environmental nutritional factors, the emphasis of the discussion is on the biology of this population. However, the studies performed in other areas, especially in the Gulf of Riga, provide excellent possibilities to compare amphipod populations inhabiting areas characterized by different environmental conditions.

### 5.1 Specific physiological characteristics of the species studied

#### 5.1.1 Metabolism

The starvation experiments indicated that, after sampling stress has been overcome, food deprivation causes *M. affinis* to rapidly shift its metabolic balance towards lipid utilization, observed as marked elevations in the O:N ratio during starvation due to a decline in the \( \hat{\text{VNH}}_4 \) (I). Under low-nitrogen food conditions, a similar nitrogen-conserving metabolic strategy has been observed in the amphipod *Calliope laeviusculus* (Pederson and Capuzzo 1984). Nitrogen release rate appears to coupled with the nutritional state of the amphipods; this is a point of great interest in regard to the objectives of the whole study.

Immediately after or some hours following collection, *M. affinis* expressed a high \( \hat{\text{VNH}}_4 \); a similar phenomenon is common in a number of invertebrates with different ecological niches and life strategies, including bivalves (Bayne and Sculbard 1977), ctenophores (Kremer 1982), copepods (Le Borgne 1979), chaetognaths (Szyper 1981) and burrowing amphipods (Hawkins and Keizer 1982). The high excretion rates observed are probably caused by the nutritional state of the amphipods; this is a point of great interest in regard to the objectives of the whole study.

In conclusion, the observed "station-and-season-specific" levels of \( \hat{\text{VNH}}_4 \) (I, II, IV, V) must derive from differences in the amount of body energy reserves and/or (2) recent feeding history.

In general, the excretion rates measured for *M. affinis* and *P. femorata* (I, II, IV, V) were lower than those measured for other benthic (e.g. *Crangon* sp.; Nelson et al. 1979, Regnault 1984, 1986, review in Regnault 1987) and pelagic (e.g. Conover and Cornor 1968, Mayzaud 1973, 1976, Ikeda 1977) crustaceans. The O:N ratio of *M. affinis* is strikingly high during most of the year compared to other benthic crustaceans (e.g. Pederson and Capuzzo 1984, Chapelle et al. 1994), indicating extensive use of substrates other than protein for energy production. The results imply, however, that *P. femorata* has a higher excretion rate than *M. affinis* (II, V); furthermore, the excretion rate of *P. femorata* seems to be less affected by changes in nutritional and temperature conditions (V). Despite these interspecific differences, the catabolism of body protein seems to play a secondary role in the production of metabolic energy in both species, although seasonal variation in the \( \hat{\text{VNH}}_4 \) can be very marked (IV). It is interesting to note that carnivorous feeding in aquatic crustaceans is usually associated with a high \( \hat{\text{VNH}}_4 \) (Ikeda 1977, Blažka et al. 1982, Gaudy and Boucher 1983, Pederson and Capuzzo 1984). The low \( \hat{\text{VNH}}_4 \) observed in *M. affinis* and *P. femorata* may signify that these amphipods are feeding mainly on material of plant origin.

Controversy has surrounded the question of whether the \( \hat{\text{VNH}}_4 \) of crustaceans depends on the availability of food (Conover and Corner 1968, Takahashi and Ikeda 1975, Ikeda 1977) or not (Gardner and Paffenholzer 1982, Miller and Landry 1984). Some experimental studies have indicated that the excretion rate of benthic invertebrates is regulated predominantly by endogenous processes rather than by the quantity or quality of food (Hawkins and Keizer 1982, Gardner et al. 1983). In the present study cessation of feeding was not examined, but it is unlikely to be the cause of the reduced \( \hat{\text{VNH}}_4 \) observed in juvenile *M. affinis* during the autumn-winter period (IV). A more likely explanation is in the quality or source of food, combined with increased utilization of reserve lipid for metabolic needs. It is evident that differences in existing body energy reserves by themselves can invoke different physiological responses to varying feeding conditions, e.g. when lipid reserves fall below a certain threshold, protein catabolism will intensify.

It has been claimed that sexually maturing *Diporeia* spp. stop feeding (Moore 1979, Quigley 1988, Quigley et al. 1989). Current bioenergetic studies do not, however, support this view with re-
femorata lives at the very limits of its salinity toler

ance and its excretion rates may be affected by sa

nalinity stress.

At the deep Bothnian Sea station SR5, the tem

erature remained practically at steady-state throu

ghout the year (IV), and could not possibly be

the cause of the observed metabolic changes in M.

affinis. In the other deep areas studied, despite co

siderable differences in depth, the ambient tempera

tures were low at all stations at the time of sampl

ing, with no logical correlation with the variable e

cretion rates observed (II). Furthermore, at the Gulf

of Riga station GR1, an increased $\text{NH}_4^+$ in M.

affinis was recorded in May, at a time of low tempe

rature (2.9°C) (V). In conclusion, seasonal changes in te

mperature do not provide an explanation for the ob

served metabolic changes.

In view of the above discussion on the potential abiotic factors, it is clear that the metabolic changes observed are a manifestation of increased feeding, activity and growth of the amphipods in response to the sedimentation pulse which reaches the bottom in late spring (IV, V). An elevation in $\text{O}_2$ in response to food availability has been observed in crustaceans (e. g. Pederson and Capuzzo 1984, Torres et al. 1994) and is very likely caused by the so-called specific dynamic action (Kristo et al. 1985). How

ever, regarding the nitrogen excretion of M. affinis, seasonal variations in rates were less marked in the Gulf of Riga than in the Bothnian Sea (IV, V). Interes

singly, Gardner et al. (1987) did not register any effects of the sedimentation of the spring bloom on the $\text{NH}_4^+$ of Diporeia spp. in Lake Michigan. These geographical dissimilarities between populations strongly suggest that it is environmental nutritional conditions that regulate the metabolic rates of these benthic amphipods; however, a straightforward inter

pretation is bound to be invalid without a detailed examination of the prevailing nutritional conditions.

Differences in the feeding history of the am

phipods appears to regulate also the magnitude of

the effect of elevated temperature on $\text{NH}_4^+$ (V).

Furthermore, the effect of temperature on $\text{NH}_4^+$

was, in general, more pronounced for M. affinis than

for P. femorata, suggesting that the latter species is more capable of regulating its excretion rate as tempe

rature rises. The level of excretion by P. femorata

at 4°C is usually higher than that of M. affinis (II, V).

The advantages of this kind of metabolic strat

ey with respect to adaptation are difficult to evalu

ate without more detailed experimentation, but are probably linked to the earlier observations of behav

ioral and physiological differences between the two species (e. g. Cederwall 1979, Lopez and Elmgren 1989).

Assuming that $Q_{10}$ for $\text{O}_2$ would remain close to 2.0, the practically temperature-independent $\text{NH}_4^+$ ($Q_{10}=1.15$, V) recorded for P. femorata dur

ing a high-excretion period would result in an ele

vated $\text{O}:\text{N}$ ratio following a temperature increase, indicating a shift into a more lipid-based energy metabolism. For M. affinis the $Q_{10}$ for $\text{NH}_4^+$ ranged between 2.2 and 3.9 (V), indicating that a tempera

ture elevation increases the immediate use of protein for metabolic energy. Apparently, the two am

phipods species have different capabilities for modified their bioenergetic strategy, and, subsequent

ly, differing modes of adaptation to varying temperature and nutritional conditions.

To sum up the metabolic studies, the effects of nutritive factors on the metabolic rates and the quali

tative utilization of body reserves are evident. Since the $\text{NH}_4^+$ of the amphipods indicates the more-or-less recent feeding history of the individu

als, it reflects the nutritional conditions prevailing in the benthic environment. Thus the recorded changes, especially in the $\text{NH}_4^+$, are useful indicators of both abundance and lack of good-quality food.
5.1.2 Body composition

As stated earlier, a high lipid level is the striking biochemical feature in *M. affinis*, *P. femorata* and *Diporeia* spp. Over all the other body constituents measured here, the accumulation of lipid deserves most attention, since it clearly reflects the nutritional condition of the amphipods and plays a vital role in reproduction.

The seasonal range in the lipid levels (17-45% including gravid) of the reproducing 2+ year-olds of the Bothnian Sea open-sea *M. affinis* population (III) was different from that recorded for the species at the Gulf of Riga nearshore station GR1 (9-36%) (V). Also, both ranges were considerably wider than that reported by Hill et al. (1992) from a coastal population in the Askö area. The maximum levels equal levels measured in Lake Michigan for *Diporeia* spp. (Gardner et al. 1985a,b, Gauvin et al. 1989). In contrast, in the Bothnian Bay, very low lipid levels (15%) were recorded in early June (II). Regarding lipid class composition, a similar kind of spatial variability was observed in the proportions of different lipids (II, III, V). In the Bothnian Sea, TAG levels were always >70% of total lipids, but at the Gulf of Riga nearshore station GR1, TAG levels were 45-73%. In a coastal Askö area, Hill et al. (1992) recorded almost equal proportions of TAG and phospholipids in *M. affinis* in the spring. Evidently, substantial spatial and seasonal variation in the lipid dynamics of the species exist; these differences are likely to be caused by varying nutritional conditions and have, most likely, a direct effect on the bioenergetic strategy and reproductive potential of the species.

The high O:N ratio (>200) observed in *M. affinis* in winter-spring indicates an almost exclusive utilization of lipids for energy production during the period (I, III). Bioenergetic calculations (III) demonstrated that, although growth had completely ceased (VI), *M. affinis* obtained energy from the environment also during the winter-spring period. In the open-sea area of the Bothnian Sea, high lipid (and especially TAG) level is serving as a means for surviving long-lasting poor food conditions. The fecundity of the individuals was observed to be lower than in coastal areas (VI; Cederwall 1977, Sarvala 1986); clearly, a trade-off between survival during unfavourable periods and high reproductive potential seems to be in effect in this strongly food-limited area (VI).

The maximum lipid levels (37%) in *P. femorata* at the Gulf of Riga offshore station GR5 were significantly higher than those recorded previously for this species (II; Paradis and Ackman 1976, Hill et al. 1992). Furthermore, excluding the gravid females, the seasonal range in the lipid levels was rather narrow (27-37%). The lower lipid levels recorded for *P. femorata* suggest that the species has a different bioenergetic strategy by comparison to *M. affinis* (Hill et al. 1992, III). This is corroborated by observations on some other biological characteristics (e.g. Cederwall 1979, Lopez and Elmgren 1989). The Gulf of Riga study, however, shows that, under advantageous food conditions, *P. femorata* is capable of attaining high lipid and TAG levels, i.e. close to those recorded for *M. affinis*. The positive lipid balance recorded at station GR5 between July and November is even more distinct than that recorded for *M. affinis* at the Bothnian Sea, and dramatically different from the zero-or-negative lipid balance of *M. affinis* at station GR1 (III, V). This shows that food availability plays a crucial role in determining the physiological condition of both species. The potentially significant role of inter- and intraspecific competition for food is discussed later.

In most aquatic crustaceans the production of eggs is related to the lipid content of individuals (e.g. Clarke et al. 1985); in some cases, the relation between lipid mass and body size ("target size" of reproduction) is a triggering factor for the onset of the reproductive phase. In Bothnian Sea *M. affinis*, the lipid and TAG levels of the non-reproducing 1+ year-olds were always only slightly lower than that of the 2+ year-olds entering the reproductive phase (III). This implies that a high lipid level in *M. affinis* does not necessarily lead to the onset of reproduction, as the juveniles accumulate lipid merely for overwintering. A similar life-strategy has been demonstrated for juveniles of the deep-water prawn *Pandalus borealis* (Hopkins et al. 1993). It is possible that the main reason why the 1+ year-olds at the Bothnian Sea study station do not reproduce despite a high lipid level is because allocation of lipid for development of reproductive tissue and eggs would result in serious starvation before brood release, which normally occurs some 8 months after the major — and practically only — period of sedimentation of good-quality food. In addition, a low lipid content may reduce the viability of offspring (Ouellet et al. 1992), and may be contributing to the observed interannual variations in the recruitment success of the cohort (VI).

In the Bothnian Sea (III), as well as in the Gulf of Riga (V), the lipid level of the reproducing generation of both *M. affinis* and *P. femorata* decreased in late autumn; especially at station GR1 the decrease was extensive in gravid *M. affinis*. Also Hill et al. (1992) noted a decrease in the lipid levels of males and females in October. Apparently, the significantly reduced lipid and TAG levels in gravid females are characteristic for both species. Alloca-
tion of lipids and especially TAG to the elaboration of reproductive tissue has also been shown in krill (Falk-Petersen et al. 1981). Moreover, if feeding is reduced during and after maturation, the depletion of body lipid for maintenance metabolism is further accelerated. After fertilization the progressively increasing metabolism of the developing embryos further reduces the total lipid and TAG contents of the "mother-brood -complex". Thus it is evident that the reduced lipid levels are causing the increased protein catabolism observed in gravid females (IV, V). In conclusion, the balance in the allocation of lipid between metabolism and reproduction is a key feature in the adjustment of the bioenergetic strategy of amphipods facing different environmental regimes, and is intimately linked to the life-cycle of the species.

5.2 Effects of environmental nutritional conditions on the physiological condition of the amphipods

In the section above, the seasonal and spatial variability in the metabolic and biochemical characteristics of the amphipod species studied have been discussed, and it is apparent that differing environmental conditions, especially those related to nutrition, have a strong influence on the physiological condition of the animals. Pelagic processes, mainly primary production and sedimentation, have an essential role, since they control the quantity and quality of food available in the benthic environment. In addition, other biotic (e.g. intra- and interspecific competition) and abiotic (e.g. temperature, re-deposition of sedimented matter by near-bottom currents) factors can have a significant role.

To gain insight into the role of primary production and sedimentation in controlling the dynamics of benthic amphipod populations, it is necessary to examine the main features of these processes in the Baltic Sea.

5.2.1 Primary production and sedimentation in the Baltic Sea

In the northern Baltic Sea, trophic conditions vary considerably between sea areas (e.g. Lassig et al. 1978, review by Elmgren 1984). The data on primary production and sedimentation at the Bothnian Sea station SR5 (Andersson et al. 1996, VI) are in accord with earlier research (e.g. Lassig et al. 1978, Kuparinen et al. 1984, Leppänen 1988, Andersson and Rudehäll 1993, Heiskanen and Kononen 1994). Therefore, according to existing information about pelagic productivity, the subareas studied can be classified, roughly, as follows: Gulf of Finland and Gulf of Riga – "eutrophic", Bothnian Sea – "mesotrophic", and Bothnian Bay – "oligotrophic". In acknowledging the typical relationship between primary production and sedimentation, it is evident that the benthos in the Gulf of Finland and the Gulf of Riga receives more organic particulate material during the growing season than the Bothnian Sea or the Bothnian Bay.

In the Baltic Sea during the spring bloom, the downward flux of algae through the water column occurs within a few days, even in deeper areas (e.g. Smetacek et al. 1978, Smetacek 1985 and citations within). Since zooplankton grazers are generally of low abundance at the start of the spring bloom (e.g. Viitasalo 1994), large quantities of relatively unprocessed, high-quality material are likely to reach the benthos in relation to primary production. However, lateral transport processes (e.g. Graf et al. 1982, Leppänen 1988), resuspension and focusing of particulates in temporary or permanent sedimentation sinks may effect sedimentation patterns, thus creating serious problems in the reliability of gross deposition rates, especially in areas characterized by complex hydrodynamics. As a result, sedimentation can seldom be measured with sufficient reliability to create accurate carbon budgets for pelagic-benthic coupling.

Although primary production during the spring bloom in the open-sea areas of the northern Baltic Sea does not show particularly striking interannual variation (reviews by Elmgren 1978, 1984, Lassig et al. 1978, Larsson and Hagstrom 1982, Andersson et al. 1996), local variation in sedimentation rates may well occur due to interannual differences in the succession and composition of the spring bloom phytoplankton assemblage. Diatoms are known to sink fast during the blooms (e.g. Smetacek 1985), while dinoflagellates mostly disintegrate in the water column (e.g. Heiskanen and Kononen 1994). Thus, interannual variations in the respective proportions of dominating phytoplankton species may explain the changes in the quantity and quality of sedimented matter (VI), both of which are crucial to the benthos. Although still somewhat speculative, this is another potential factor corroborating the theory that changes in the dynamics of the pelagic component of the marine ecosystem have a direct effect on the benthos.
5.2.2 Spatial variability in the condition of
the amphipods in relation to environmental
nutritional conditions

The present study shows that spatial variability in
trophic characteristics between different subregions
of the Baltic Sea is reflected as differences in the
physiological condition and bioenergetic strategy of
the amphipods. To proceed with the discussion, a
hypothesis on the relationship between the nutritional
conditions prevailing in different Baltic Sea
subregions and the ensuing physiological adaptations
observed in the amphipods is presented.

(1) Bothnian Sea. The observed high lipid levels
imply that the amphipods in this sea region have
adopted an energy storage strategy which ensures a
maximum benefit from the short-but-intensive pe-
riod of spring phytoplankton sedimentation (II, III,
VI). A very low \(\text{NH}_3\) (except in summer) indicates
a low-quality diet and/or extensive utilization of
lipid for energy production in order to save amino
groups (II, IV).

(2) Gulf of Riga (inshore vs. offshore areas). Primary
production and nutrient levels in the Gulf of
Riga are among the highest in the Baltic Sea, leading
to a large deposition of organic particulate matter. In
addition, although allochthonous riverine input in
nearshore regions is high, the material is low in nu-
tritional quality. The nearshore station GR1 con-
sisted of sandy mud with a low organic content,
while the offshore station GR5 was characterized by
organic-rich mud (Carman et al. 1996). It is con-
ceivable that resuspended fine particulate material is
effectively transported from basin margins and re-
deposited at central-basin accumulation areas, es-
specially after the breakdown of the thermocline in
autumn. This material, together with the sedimenta-
tion of the potentially important late-summer phy-
toplankton bloom, offers a "new" food source for
benthic organisms inhabiting the offshore areas.
Consequently, the substantial lateral transport of
material is likely to reduce food availability of ben-
thos in nearshore areas. Despite clear differences in
the condition of nearshore and offshore amphipod
populations—which may be caused partly by inter-
specific differences—the higher and more constant
\(\text{NH}_3\), despite a relatively high lipid level, indicate
adaptation of the amphipods to more stable nutri-
tional conditions compared to the Bothnian Sea and
Bothnian Bay. Implications of similar adaptations
have been recorded also for the amphipods inhabiting
the eutrophic Gulf of Finland (II, Lehtonen unpublished data).

(3) Bothnian Bay. The spring bloom peaks later
than in the more southern areas, and is remarkably
lower in intensity; the "peak" is distributed more
evenly over time or may be missing altogether
(Lassig et al. 1978). In addition, high concentrations
of allochthonous humic substances of refractory na-
ture in the sediment are characteristic for this area
(Gripenberg 1934). These factors are likely to cause
the observed slow growth in the population (low
production:biomass ratio) in the area (Andersin et al.
1984). Physiologically, poor nutritional conditions
manifest as high \(\text{NH}_3\), in this case as a sign of an
increased catabolism of body protein triggered by a
low lipid level (I, II), but more information is
needed on seasonal changes in the metabolism and
biochemical composition of the amphipods from this
specific area.

5.2.3 Bothnian Sea: the time-lag

At the Bothnian Sea station SR5, a time lag between
the sedimentation of the spring bloom and the
physiological response (III, IV) and growth (VI) of
the \(M. \text{affinis}\) population was observed. Previously,
Uitto and Sarvala (1991) noted a time-lag between
sedimentation and the growth of both \(M. \text{affinis}\)
and \(P. \text{femorata}\) in Tvarminne coastal area, attributing
it mainly to progressive increase in temperature during
the summer. However, a similar lag exists in the
present study area, which is characterized by a con-
stant seasonal temperature regime.

In the Baltic Sea, the physiological response of
benthic macrofauna to sedimentation input has been
studied only in shallow areas (Graf et al. 1982, 1983,
Christensen and Kanneworff 1985; measured as bio-
chemical changes). In these studies, the response
was shown to be immediate or delayed; interspecific
differences in feeding behaviour, feeding niche and
the principal source of nutrition are usually consid-
ered the main reasons for the varying speed of re-
spone. Possibly, the fresh algal material must be
partially processed by other benthic consumers
(bacteria, meiofauna) before becoming optimally
available to amphipods. Some microalgae show no
signs of decomposition even after several weeks of
exposure (Gunnison and Alexander 1975); further-
more, low temperature delays the decomposition
process. From a physiological perspective, the long
period of poor nutritive conditions during the winter
may decrease the ability of the amphipods to assim-
late food efficiently because of reduced levels of key
digestive enzymes, as observed in the copepod Cal-
anus hyperboreus (Head and Conover 1983). Thus,
the observed time-lag is possibly a result of both
temporarily impaired assimilation ability of the am-

phipods and the suboptimal palatability of the fresh food.

5.3 Utilization of organic matter by the amphipods: a system-wide view

5.3.1 Bothnian Sea: requirements in relation to input

Several studies at various locations have indicated that a large portion of the pelagial material produced is utilized by the benthos (e.g. Riley 1956, Ankar 1977, Elmgren 1978, Wassmann 1984, Bergström and Sarvala 1986). Apart from the macrozoobenthos, the meiofauna and bacteria have a very significant, and usually considered, predominant role in the utilization of deposited organic matter. In the Bothnian Sea study area, the respiration of M. affinis comprises about 30% (seasonal average) of total benthic community respiration (Karjala et al. in preparation); combined with the allocation of carbon for growth (VI), it is apparent that a highly significant portion of the sedimented organic matter at the location is consumed by amphipods.

With regard to the utilization of the pelagially produced organic matter, taking into account the action of other consumers in both the pelagial and benthic food webs, annual carbon and nitrogen requirements of the M. affinis population are high (VI). With regard to sedimentation, due to the difficulties in measuring the actual amount of material deposited at the study site, the 50% assimilation rate by the amphipod population, calculated for the "active period" in 1991 and 1993, may be an overestimation. However, even if the actual deposition rates were, say, 2-3 times higher than those recorded here, the carbon (and nitrogen) demand of the amphipods would still underline that the population is strongly limited by food, considering the utilization of food by other components of the benthic system.

5.3.2 Mineralization of carbon and nitrogen

The importance of benthic fauna in nitrogen mineralization processes, either by direct metabolism or by enhancing bacterial activity via bioturbation is well known. Gardner et al. (1987) estimated the excretion of an abundant Diporeia spp. population to be responsible for up to 42% of total benthic nitrogen release in Lake Michigan. Henriksen et al. (1983) showed that excretion by the amphipod Corophium volutator could account for 80% of the net $\text{NH}_4^+$ flux from the sediment and provide nitrifying bacteria with a potentially significant source of $\text{NH}_4^+$. Moreover, bioturbation by C. volutator has been shown to enhance also benthic denitrification rates (Pelegrí and Blackburn 1994, Pelegrí et al. 1994).

Since the excretion rate of amphipods is greatly determined by the availability of good-quality food (IV), the estimated $\text{NH}_4^+$ release by the populations showed more variability than the rates of carbon mineralization, both seasonally and between the different sea areas (II, V, VI). The "post-bloom study", which provided information on $\text{NH}_4^+$ close to their annual maxima, showed clearly that the highest daily $\text{NH}_4^+$ release rate recorded at the Bothnian Sea M. affinis station US6b was due to the high population density (over 10,000 ind m$^{-2}$) (II). The moderately abundant P. femorata population at the Gulf of Finland station LL6a had an almost equal rate of $\text{NH}_4^+$ release, but this was attributed to the high weight-specific excretion rates and the large size of the amphipods (II). Another distinct case is the Bothnian Bay, where the small size of M. affinis resulted in a very low total release of $\text{NH}_4^+$ despite a high weight-specific excretion and relatively abundant populations. These examples illustrate exquisitely that several factors — abundance, size and metabolic activity of individuals — are responsible for the observed high variability in the rates of $\text{NH}_4^+$ release by amphipod populations.

By considering the scheme above, the observed differences in the annual mineralization rates of the amphipod populations of the Bothnian Sea and Gulf of Riga stations can be rationalized. In the Gulf of Riga the estimated annual total respiration rates (1.7 and 3.0 g C m$^{-2}$ yr$^{-1}$) (V) recorded were considerably less than that recorded by Bergström and Sarvala (1986) for a coastal M. affinis population (11.9 g C m$^{-2}$ yr$^{-1}$) in an area where summer temperatures up to 18°C were recorded; however, this was clearly due to higher abundance in the latter area. In the Bothnian Sea, despite a constantly low temperature, the annual respiration of the M. affinis population was even higher (14-17 g C m$^{-2}$ yr$^{-1}$) (VI). Considering the higher primary productivity of the Gulf of Riga discussed earlier, mineralization by the amphipods in the area probably plays only a minor role. Conversely, in the "mesotrophic" Bothnian Sea, metabolism by the abundant M. affinis populations is likely to be an exceedingly important component in benthic mineralization process.
5.4 Population dynamics: observations and hypotheses

5.4.1 Factors affecting the life-cycle

The longevity of the amphipods has been associated with depth and temperature (Segerstråle 1937, Moore 1979, Leonardsson et al. 1988) and trophic conditions (Siegfried 1985). Reduced metabolic rates caused by constantly low temperatures are commonly considered to result in longer life-cycles. Metabolic rates may also be lower during adverse food conditions (IV). As discussed, the growth of *M. affinis* cannot be temperature-regulated in deep, open-sea areas (VI). Depth per se does not seem to be the decisive factor determining the condition of the amphipods, since high lipid levels were recorded both at deep and shallow stations (II, III, V). However, deep areas and depressions of the seabed often function as sedimentation sinks, creating favourable conditions for benthic life with regard to food availability. Considering these factors, in the shallower coastal areas where strong seasonal oscillations in temperature and more stable food conditions may have considerable effects on metabolism, the long-term bioenergetic strategy, life-cycle and population dynamics of the amphipods are likely to be different in comparison to deep, open-sea areas.

5.4.2 Interspecific interactions

In addition to spatial differences in the direct input of food, the growth and condition of the amphipod populations may be strongly affected by interactions between species. In the Bothnian Sea and the other open-sea areas studied, amphipods are, overwhelmingly, the dominant macrozoobenthic organisms (II, V, VI); thus, in these areas, interspecific competition for food (at macrozoobenthic level) as a factor regulating the condition of individuals and the population dynamics can be disregarded. This was not the case at the Gulf of Riga nearshore station GR1, where other organisms (e.g. the polychaete *Marenzelleria viridis*, *C. volutator* and the bivalve *Macoma balthica*; Yermakovs and Cederwall in prep.) comprised by far the greatest part of the benthic biomass and are certain to compete intensively for nourishment with *M. affinis*.

Interspecific interactions also include the potential role of bacteria and meiofauna as a food source for the amphipods (e.g. Ankar 1977). Although not comparable with the algal sedimentation in terms of biomass, benthic bacteria are a more predictable and stable food source (Johnson et al. 1989). However, bacteria have been shown to provide only 24-32% of the annual carbon requirements of a *M. affinis* population (Uitto and Sarvala 1991) and only 6% of the needs of the young-of-the-year (Goedkoop and Johnson 1994). Implications of predation on some meiofaunal taxa by *M. affinis* have been observed (Elmgren et al. 1986, Olafsson and Elmgren 1991, Sundelin and Elmgren 1991). Active predation, however, can be questioned, but it is highly probable that the amphipods, at least when they have reached an adequate size, passively ingest meiofauna while processing the sediment. However, as discussed earlier, the generally low N:NH₄ does not support the idea of meiofauna being a significant food source for *M. affinis*.

5.4.3 Intraspecific interactions

In food-limited areas, the growth of the population leads to faster depletion of the annual quality-food resources, resulting in reduced growth and less accumulation of energy reserves. Following a simple model, since the fecundity of amphipods is size-dependent (VI, Cederwall 1977), reduced growth in the reproducing generation due to poor food availability results in a smaller number of offspring and, subsequently, a decline in population size. However, a deeper examination reveals that the mechanisms regulating population size are far more perplexing. Variability in the recruitment success of the young-of-the-year has a potential role in the observed long-term variations in population size (ca. 7-year cycle, Andersin et al. 1978, 1984). Theoretically, even a minor increase in the proportion of offspring that survive the high-mortality "babyhood" period results in a distinctly more abundant cohort (e.g. Valiela 1984, review by Gosselin and Qian 1997). In spring 1991, the estimated number of offspring in the Bothnian Sea of *M. affinis* population was high, occurring during a period of very high population density (VI). Recruitment success was very significant (56%) despite the high density. Experiments have indicated that high density together with the presence of older generations has a negative effect on the growth and survival of the young-of-the-year *M. affinis* (Hill 1992). However, during a year of good food availability, competition between the young-of-the-year and the older cohorts is alleviated, and the prospect of the young passing the bottleneck of recruitment is increased. In 1992, the survival rate was poor (12%), despite a somewhat reduced population size; this suggests that the input of food (not measured) had been smaller in 1992.
Finally, in 1993, the survival of the offspring increased markedly (38%), although sedimentation was about 50% lower than in 1991; by this time, the abundance of the population had reduced to half of that recorded in 1991, with the result that competition pressure was greatly relieved.

A complex relationship between the amount of food input, population density and the relative portions of individuals representing different annual cohorts seems to exist. However, a tentative mechanism for explaining the interannual variability and even long-term oscillations in the Bothnian Sea amphipod populations can be formulated.

First, we assume that the variability in the amount of the annual input of food is small. Thus, during the phase of annually rising population density, the mean size of the individuals gradually decreases, since progressively less food is available per capita. Once the density of the population has exceeded the "carrying capacity" of the environment, the recruitment success of the young-of-the-year decreases markedly, or may even collapse, due to intraspecific competition for food. A key point to be observed here is that, since this study population exhibits a 3-year life cycle, the consequences of recruitment failure are only manifested in a significant way after 3 years, when the poorly-recruited cohort reproduces. Meanwhile, the small contribution of this cohort to the population actually increases the survival prospects of the others, especially the two following annual cohorts.

Second, it is suggested that the depth of the ebb in the curve describing the long-term fluctuations in the abundance and biomass of the population should be determined by food conditions. If the two cohorts that follow the cohort that failed encounter years characterized by abnormally low sedimentation (that affects negatively their recruitment, survival or reproduction), the collapse in the population will be severe, despite the fact that intraspecific competition is constantly alleviated by a lowered density. However, if the following years are 'normal' regarding nutritional conditions, the next two cohorts will thrive and yield a successful offspring when their turn to reproduce is at hand; in this case, the ebb in the curve will be only moderate. Conclusively, the effects of irregularities occurring in annual sedimentation rates on the amphipod population are dependent on the density and structure of the population.

Most of the observed variations in the biochemical characteristics of the amphipods coincide with the changes recorded in environmental and population parameters. In the Bothnian Sea M. affinis collected in winter and spring 1991 were significantly smaller than at corresponding times in 1992 and 1993 (VI). However, the lipid level of the amphipods was high in late summer during all study years (III), regardless of the observed variations in the secondary productivity of the population (VI). And yet this is not surprising since the abundance and biomass of the population showed a decreasing trend during the study years, leaving more food available for a smaller population to exploit. Connected with the exceptional biochemical characteristics of amphipods, a lipid-related "buffering capacity" may be in use, i.e. the energy reserves attained during the previous year help to withstand a year of low sedimentation input. In the Gulf of Riga, the low-density population of P. femorata at station GR5 sustained unusually high lipid levels until late autumn, while M. affinis, occurring at station GR1 in a considerably higher density, facing also a strenuous interspecific competition (see above) showed rapid depletion of lipid deposits during the autumn (V). These characteristics are evidently connected not only to differences in the amount of food arriving at the bottom, but its ultimate availability to individual amphipods.

As a concluding remark regarding competitive interactions within and between species, the present studies show that both the role of density-dependent regulation and, especially in coastal regions, interspecific competition for available food resources can be important biological factors affecting the population dynamics of the amphipods in the northern Baltic Sea. However, these mechanisms are strictly coupled with an exogenic regulating factor that emerges as the primary variable: the quantity and quality of available food.

6 Conclusions

In what way does this work contribute to our knowledge of the two amphipod species and their relation to the environment? The general conclusions acquired in this thesis are presented below.

1 Although M. affinis and P. femorata differ in their behavioural and physiological characteristics, the present study emphasizes the importance of nutritional conditions in regulating the bioenergetic strategy of both species.

2 Variability in metabolism, particularly in ammonia excretion, reflects changes in the availability and abundance of good quality food. Poor nutritional conditions shift the metabolic balance
of the amphipods progressively towards the utilization of reserve lipid, which is observed as a decreased ammonia excretion rate. Since the effect on the oxygen consumption rate is considerably smaller, the ammonia excretion rate can be successfully used as an indicator of benthic nutritional conditions, providing that the amphipods are properly acclimatized (avoiding handling stress and also starvation conditions) and not extremely lipid-poor (intensified catabolism of body protein resulting in increased ammonia excretion).

3 Due to the functional anomalies related to their life-stage, adult individuals (males and gravid females) exhibit significantly different bioenergetic characteristics compared to juveniles.

4 The magnitude of the effect of temperature rise on the ammonia excretion rate of amphipods seems to be associated with these rates measured at "ambient" near-bottom temperature (4°C) and, thus, with their recent feeding history. Of the two species, P. femorata seems more capable of regulating its nitrogen release when the temperature elevates, which may denote a shift into a more lipid-dominated metabolism at higher temperatures.

5 Environmental food conditions strictly control the lipid dynamics of both amphipod species. Under a highly-concentrated seasonal sedimentation pattern, the bioenergetic strategy of the amphipods includes a rapid accumulation of lipid (mainly triacylglycerols) after the spring bloom. The lipid is utilized for metabolic fuel under poor nutritional conditions, or reproduction; thus, its levels directly regulate the survival and reproductive capacity of the individuals.

6 When abundant, the amphipods have a significant effect on benthic mineralization processes especially in areas where annual sedimentation of organic matter is low or moderate. Besides abundance and temperature, the mineralization rates (especially of nitrogen) are determined by the degree of input of organic matter to the benthic system, which is itself reflected as changes in the metabolic rates of individuals.

7 The coupling between sedimentation input and growth and condition of the amphipod populations is close, especially in food-limited open-sea areas. Interannual variability in the quantity and quality of sedimenting matter may result in differences in growth, lipid accumulation, fecundity and the survival potential of the offspring. However, since interannual variations in the rates of primary production and sedimentation within specific locations do not seem to be dramatic and are likely to be non-cyclic, intraspecific competition for available food has probably a key position in the explanation of the previously recorded long-term oscillations in the population size of amphipods in open-sea areas.

7 Acknowledgements

This kind of work cannot be done single-handedly (although I stubbornly thought so!). Numerous people have contributed to the process that led to the initiation and completion of this thesis, by lending a helping hand during the physical part or boosting my morale during the desperate periods. However, space (in this case) is limited: if I tried to recall everyone who has handed me a benthos sample or a much-needed beer during these important years, I would remain in square one.

Starting from the cradle of my studies, the Division of Animal Physiology, University of Helsinki: in the dark, cigarette-smelling second-floor corridor wandered an unorthodox duo, Professor Rolf Kristoffersson and "The Mussel Girl" Inke Sunila. Both were instrumental in my choosing to attempt the strange art of the physiology of marine benthic organisms. With Inke, I spent some unforgettable (and some completely forgotten) moments in numerous Helsinki watering holes, looking for ideas and inspiration!

Tvärminne Zoological Station was my next destination, although only for an unfortunately brief period. I worked under a number of financiers and, under the star-studded late-autumn sky of Tvärminne-by-the-sea, I came to understand the needs and art of independency (mind you, I still intend to publish my Mytilus works some day!).

Next step was the crucial one, with Professor Paavo Tulkki calling me to duty para patria to master the art of being a gentleman instead of even a naval officer. The Department of Biological Oceanography, at the Finnish Institute of Marine Research, has become my "temporary" home since 1990. Ami Andersin (rumoured to have been born on the 1.0 mm sieve) taught me the secrets of benthic amphipods, and as a dear friend and colleague puts up reasonably well with my sometimes explosive temper. Forgetting nobody: hats off to the rest of the
Cruises aboard RV “Aranda” became everyday stuff during this assignment. A total of eleven months at sea did certainly not go without incidents, many of them memorably hilarious. The crew of the vessel is appreciated for making me feel safe even in rough weather, and the kitchen personnel for stuffing us with Argentinian beef prior to heavy sampling. The “Boys” from the Technical Department of FIMR always lent a helping hand (occasionally extended with a scary wrench), launching a couple of affectionate five-letter words not to be printed here.

Since marine biology is a science that is highly international by nature, during the years I have had the pleasure of meeting a great number of colleagues from different countries, and shared valuable conversations which have contributed greatly to my limited understanding of the secrets of the Big Blue.

The Gulf of Riga project, financed by the Nordic Council of Ministers, saved my buttocks for many years (although I guess nobody really knew what I was up to in the whole project...). Anyway, Hasse Cederwall (University of Stockholm) somehow kept faith in me, providing me also with the occasional shot of Irish. Other people within the Benthos Group that kept me good company during this personally important project were Bertil Widbom (University of Stockholm), Leva Upeniece, Parsla Pallo, Juris Aigars, Vadims Yermakovs (Institute of Aquatic Ecology, University of Latvia), Oskars Stiebrins (Latvian Hydrometeorological Agency) and Birger Larsen (Danish Geological Survey).

Technical assistance in putting up this final version was kindly provided by Mrs. Leena Parkkonen and Ms. Leena Rome, not forgetting the spirited-as-usual language check by Mr. Richard Thompson Coon (Gulf of Finland Environment Society).

The existence of the (in)famous Zuliman Child (Slight Return) heavy blues outfit (consisting traditionally of biologists only) parallels exactly my time spent with the amphipods. I warmly thank all you guys for dragging me down from the clouds every now and then by cracking a devastating basist joke or two. Without the band, a private place in the funny farm would have been guaranteed ages ago.

For the more private part of my life, I want to thank my long-time companion, my friend Anneli for love and putting up with me during this crucial time; our lovely (and wild!) daughter Eeva has always made me smile (although now I had to seek refuge to be able to complete this job!).

I give my humblest thanks to my late father Keijo K. Lehtonen and my mother Seija: without your guidance and attitude towards life I would probably have become an economist or even worse. Thanks for giving me this life.

The Doobie Brothers are given credits for the song "Takin’ it to the streets" - that goes as a thanks to my brother Janne for sharing the football fanaticism with me.

É a vida é.
Praia da Rocha, Portugal
April 1997

8 References


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