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Seasonal changes in lipid content and composition in the benthic amphipods *Monoporeia affinis* and *Pontoporeia femorata*

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Abstract

Seasonal variation in lipid content and composition was studied in deposit-feeding amphipods from a Baltic archipelago. In *Monoporeia affinis,* which is more active and has a higher respiration rate, lipid levels were low in winter and early spring, rose to 27% of the dry mass in late summer, then declined in autumn. In *Pontoporeia femorata,* which regulates its oxygen consumption, lipid levels were 20–23% of the dry mass. In October, maturing male *P. femorata* had a significantly lower lipid content than females. Triacylglycerol and phospholipid accounted for ~90% of lipids. Phospholipid dominated in *M. affinis* in March, but triacylglycerol accumulated and became the main lipid after the spring bloom. Triacylglycerol was always the main lipid in *P. femorata,* but also accumulated after the spring diatom bloom. Both species seem to assimilate and store food resources from the diatom bloom. The higher feeding rate of *M. affinis* may explain its greater accumulation of lipid. Lower metabolic costs in *P. femorata* may allow it to maintain steady lipid levels for most of the year.

Lipids are often stored by animals to provide energy during periods when food supplies are low or metabolic demands are relatively high, as they provide twice as much energy per unit mass as carbohydrates or protein (Hadley 1985). Marine invertebrates also store lipids for reproduction, to regulate buoyancy, or as a response to physical factors such as oxygen levels and temperature (Lawrence 1976).

Triacylglycerol is the main storage lipid in benthic amphipods (Clarke et al. 1985). The deposit-feeding benthic amphipods that were previously classified in the genus *Pontoporeia* (*see* Bousfield 1989) accumulate lipid. Oil droplets have been observed in the body of *Monoporeia affinis* (Lindström) from the Baltic Sea, *Diporeia hoyi* (Smith) from North American lakes and *Pontoporeia femorata* Krøyer from the coast of Nova Scotia (Segerstråle 1937; Green 1971; Paradis and Ackman 1976). In *D. hoyi* from Cayuga Lake, lipid levels were 33% of the dry mass (Green 1971). In the same species from Lake Michigan, lipids constituted up to 54% of the ash-free dry mass, and triacylglycerol constituted >60% of the lipids (Gardner et al. 1985*b*).

In Lake Michigan, the lipid content of *D. hoyi* varied during the year and increased following the spring phytoplankton bloom (Gardner et al. 1985*b*). Amphipods that were deprived of food mobilized lipids during starvation, which supports the theory that this species accumulates lipids as an energy store after the spring bloom (Gardner et al. 1985*b*; Gauvin et al. 1989).

In the brackish Baltic Sea, *M. affinis* and *P. femorata* co-occur in deep-water muddy sediments, where they often account for most of the macrofaunal abundance and biomass (Elmgren 1978). They occur mainly in the top 5 cm of the sediment, but swim at night (Segerstråle 1950; Hill and Elmgren 1987). Their main period of growth is during the spring phytoplankton bloom and a few months thereafter (Cederwall 1977;

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Sarvala 1986; Uitto and Sarvala 1991), and food is in short supply during the rest of the year (Elmgren 1978). These amphipods may therefore store lipids in connection with the spring bloom, as does *D. hoyi.*

Monoporeia affinis and *P. femorata* are semelparous and their life cycle lasts from 1 to 3 yr in the northern Baltic proper (Segerstråle 1950). The young normally hatch in March–April, and the adults reach sexual maturity in autumn. From about October onward, males undergo a metamorphosis that adapts them for pelagic life, stop feeding, mate with females in the water column, and then die. The females die after releasing the young the following spring (Segerstråle 1950). *M. affinis* is more fecund, is a more active swimmer, and has a higher respiration rate (Cederwall 1977, 1979). It is found closer to the sediment surface and feeds more rapidly than *P. femorata* (Hill and Elmgren 1987; Lopez and Elmgren 1989). These differences in activity and feeding suggest that the two species may differ in the way that they store and use lipids for basic metabolic needs and reproduction.

The aims of this study were to follow lipid levels in sympatric populations of *M. affinis* and *P. femorata* for a year and to examine the lipid composition in relation to the spring phytoplankton bloom.

Materials and methods

Collection of animals—Sediment and animals were collected monthly from October 1988 to October 1989 with a benthic dredge at a depth of 30–40 m, close to a permanent benthic station. No samples were taken in November 1988. The collection site was in Hållsfjärden Bay, off the Baltic field station of Stockholm University (Askö Laboratory: 58°49′N, 17°38′E). In this area and depth range, *M. affinis* is more abundant than *P. femorata* and both species have a 2-yr life cycle, although some animals may live for 3 yr (Cederwall 1977).

Amphipods were sieved from the sediment and kept in cooled brackish water overnight to allow them to empty their guts. About 50 animals of each species from the same age class were picked and then randomly sorted into batches of five.

Determination of lipid content—Animals were rinsed in distilled water, dried in batches of 5 or 10 at 60°C for 1–5 d, then stored in a desiccator. Replicate samples of 10–20 animals were preserved in 4% buffered formaldehyde. The dried samples were analyzed at the Great Lakes Environmental Research Laboratory in 1990. Individual animals were weighed, and total lipid mass was determined with the gravimetric method described by Gardner et al. (1985*a*). Seven to ten animals from an age class were analyzed individually each month, except August 1989, when the small young of the year were analyzed in pairs. In September 1989, few *P. femorata* were found, so the values for total lipid content are from the animals collected for analysis of lipid composition (*see below*). In October 1989, sexually mature amphipods were divided into males and females. The term lipid content refers to the mass of lipid, while the term lipid level refers to the percentage of lipid in relation to dry mass.

Determination of lipid composition—Animals were flown live to the U.S. in brackish water in cooled containers on three occasions in 1989: in March before the spring bloom, in June after the spring bloom, and in September. In September, at least half of the amphipods of both species seemed to be maturing females, as the gonads were opaque. The total body length was measured with a digitizer (Quigley and Lang 1989). The amphipods were then rinsed in distilled water, blotted dry, and placed in individual preweighed glass microcentrifuge tubes. They were dried in a desiccator at 50°C for 48 h under a slow flow of nitrogen. This technique maintains the integrity of all lipid classes. Relative proportions of the main lipid classes were determined from the final lipid extracts by means of thin-layer chromatography with flame ionization detection (TLC-FID) (Parrish 1986, 1987; Parrish et al. 1988). These lipid extracts were stored under N_2 and then frozen until the lipid-class analyses were carried out. Degradation of lipids during drying, extraction, and storage seemed to be minimal, as, except for two cases, $<5\%$ of the observed lipids occurred as free fatty acids. Lipid-class analyses were done on 11–16

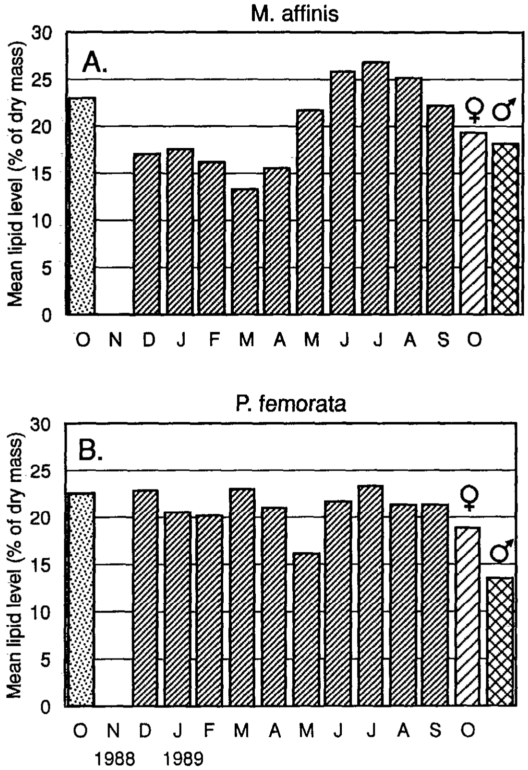

Fig. 1. Mean lipid levels in adult *Monoporeia affinis* and *Pontoporeia femorata*. The hatched bars show the generation born in 1988, 1-yr old at the beginning of 1989. Maturing males and females were analyzed separately in October 1989. The stippled bars show sexually maturing animals (the year class born 1987 or before) in October 1988.

amphipods of each species each month. Lipid classes were separated by sequentially developing the rods in increasingly polar solvent systems (Parrish 1986, 1987). Between solvent developments, rods were scanned with an Iatroscan Mark IV connected to a Hewlett-Packard 3392A integrator. A mixed lipid standard was used for TLC-FID calibration and quantification. It included one compound from each of the following lipid classes: hydrocarbon, sterol ester, triacylglycerol, free fatty acid, alcohol (aliphatic), sterol (alicyclic alcohol), and phospholipid.

Statistical analyses—Linear regression analysis was used to investigate how lipid content varied with the size (dry mass or length) of the amphipods and to predict lipid content for a given size of animal. Analysis of covariance (ANCOVA) was used to compare the mean lipid content of groups of animals, by adjusting for differences in size, according to Sokal and Rohlf (1981). These ANCOVAs required that there was a significant linear relationship between lipid content and size and that the regression coefficients of the groups were not significantly different. Values for lipid mass were log(x + 1)-transformed when variances were not homogeneous between groups.

Results

Seasonal changes in lipid levels—Lipid levels in 1-yr-old *M. affinis* (the generation born in 1988) were ~17% of the dry mass in winter, dropped to a low of 13% in March, rose to a maximum of 27% in late summer, then declined during autumn (Fig. 1A). Lipid levels in 1-yr-old *P. femorata* were initially higher and remained more constant throughout the year (Fig. 1B). Lipids accounted for 20–23% of the dry mass, except in May, when the mean value was 16%. The young of the year (the generation born in spring 1989) had lower lipid levels than the 1-yr olds. In August, September, and October mean lipid levels were 19, 11, and 15% in juvenile *M. affinis* and 12, 15, and 16% in juvenile *P. femorata*.

The 1-yr olds started to mature in July, and the gonads became visible through the dorsal cuticle. By October, when males of both species had started developing long antennae and the females had bright orange ovaries, the mean lipid level of male *P. femorata* was low (13%) compared to that of females (19%) (Fig. 1B). The maturing adults sampled in October 1988 had higher mean lipid levels than in 1989 (*M. affinis* 23%, *P. femorata* 22%, Fig. 1). The 1988 animals were a mixture of maturing males and females. They were also considerably larger than those from 1989 and may have been older than 2 yr (mean dry mass was 5.3 mg in *M. affinis* and 7.8 mg in *P. femorata*, compared to about 3 mg for 1-yr olds of both species in October 1989).

Lipid content in relation to size—The individual dry mass of 1-yr-old amphipods increased from ~1 mg in December 1988 to ~3 mg in October 1989. Some of the seasonal variation in lipid levels may have

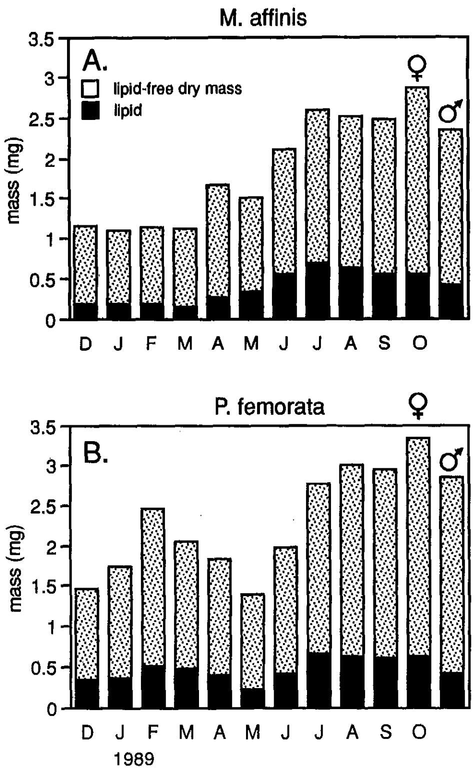

Fig. 2. Mean dry mass (whole bars) and lipid content (black) of the 1-yr-old cohort of *Monoporeia affinis* and *Pontoporeia femorata.*

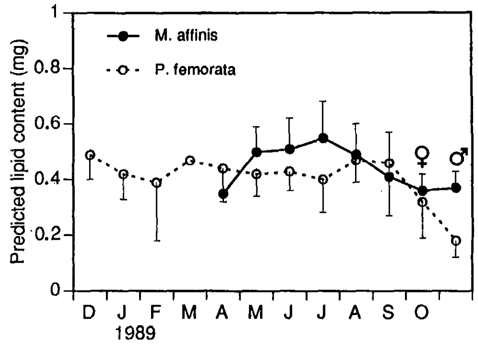

Fig. 3. Prediction of lipid content of a "standard-sized" amphipod weighing 2.0 mg, based on significant linear regressions between lipid content and dry mass. Bars show standard errors of the predicted values. The March value for *Pontoporeia femorata* is the measured mean lipid content (mean dry mass was 2.05 mg), as the regression was not significant. The September value for *P. femorata* is from the amphipods that were shipped live to the U.S.

been due to differences in size, both between months and within the samples from each month. In both species the mean lipid content generally increased during the year, but also varied with the mean size in different months (Fig. 2). The relationship between lipid content (mg) and dry mass (mg) was examined by linear regression analysis.

The lipid content of 1-yr olds of each species increased significantly with dry mass in all months except March 1989 ($P < 0.05$). The lipid content of juveniles sampled in September and October 1989 increased significantly with dry mass ($P < 0.01$), except for *M. affinis* from October ($P > 0.05$). These trends indicate that adults and juveniles gained lipids as they grew. The formulas from the significant regression lines were used to predict values for the lipid content of a standard-sized (2.0 mg), 1-yr-old animal in each month (Fig. 3). Predictions were not made for *M. affinis* from December to February because none weighed as much as 2.0 mg. The pattern of seasonal variation is similar to that shown by the lipid percentages: the lipid content of *M. affinis* increased throughout spring to a maximum in July, then declined gradually. The lipid content of *P. femorata* remained steady during the year, then dropped in October.

In October 1989, the predicted lipid content of male *P. femorata* was only about half that of the females (Fig. 3). Males of both species were at the penultimate stage of maturity, in which the second antennae were shorter than the body (Segerstråle 1950). The mean lipid content in males and females of each species was compared with an ANCOVA that adjusted for differences in lipid-free dry mass (Fig. 4). Lipid content did not differ significantly between the sexes in *M. affinis* (df = 19, $F = 1.02$, $P > 0.05$).

In *P. femorata,* the maturing animals included two exceptionally large animals (one male and one female with a lipid-free dry mass of 5 mg) that may have been 2-yr olds (Fig. 5A). There was no significant difference in lipid content between the sexes (df = 17, $F = 2.92$, $P > 0.05$). When the two largest animals were excluded (Fig. 5B), the lipid content of females was significantly higher than that of males (df = 15, $F = 28.85$, $P < 0.001$). In the latter test, the variances for lipid-free dry mass were still heterogeneous after log-transformation

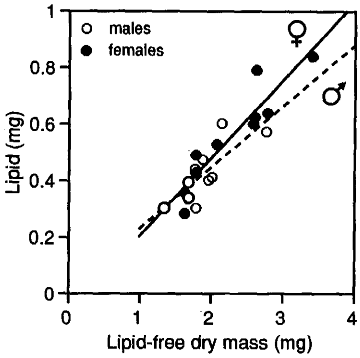

Fig. 4. Relationship between total lipid content and lipid-free dry mass in maturing male and female *Monoporeia affinis* in October 1989. ANCOVA based on significant linear regressions showed no significant difference in lipid content between the sexes.

(Cochran's *C*-test, $P = 0.03$). The results suggest that 1-yr-old male *P. femorata* depleted lipids in connection with sexual maturation.

Lipid composition—The five major classes of lipids were: triacylglycerols, phospholipids (structural lipids), acetone-mobile polar lipids (pigments and other polar lipid compounds), sterols, and free fatty acids. On average, triacylglycerol and phospholipid together accounted for 89–95% of the lipids, and none of the three other lipid classes constituted >4.5%.

In 1989, the spring bloom was early; it was dominated by the diatom *Skeletonema costatum* and began to decline in mid-March, after which the ciliate *Mesodinium rubrum* became abundant (U. Larsson et al. unpubl.).

In March, phospholipid was the main lipid class in *M. affinis* (49% of total lipid on average), and the percentage of triacylglycerol was smaller (40%). In June, after the spring bloom, the mean triacylglycerol content was more than four times higher than in March (Fig. 6), and this component had become the main lipid (76%). In September, the percentage of triacylglycerol was still high (77% of lipid mass).

Triacylglycerol was always the main lipid class in *P. femorata*. This component increased steadily in importance from March to June to September (59, 66, and 72% on average of lipid mass). The mean triacylglycerol content doubled between March and June (Fig. 6). However, the March animals were small ($n = 11$, mean dry mass was 1.5 mg) and their mean lipid content was low (0.2 mg, 11% of the dry mass) compared

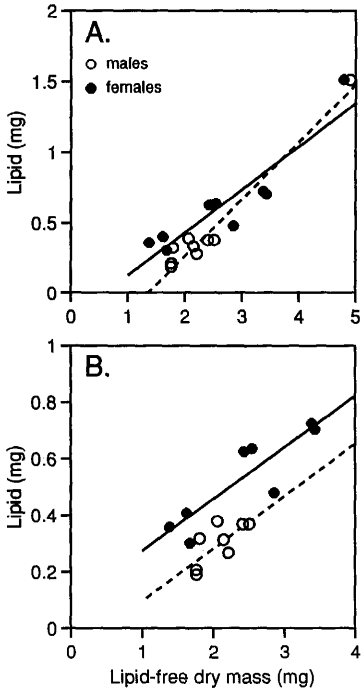

Fig. 5. Relationship between total lipid content and lipid-free dry mass in maturing male and female *Pontoporeia femorata* in October 1989. A—All animals; B—without the two largest animals. ANCOVA based on significant linear regressions in panel B showed lipid content was significantly higher in females.

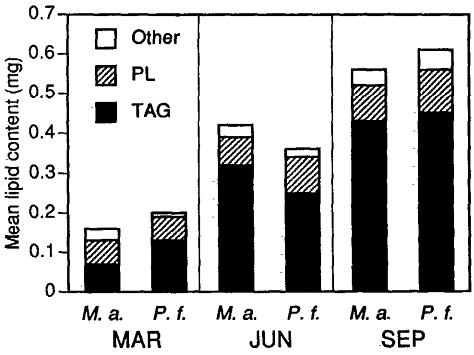

Fig. 6. Mean lipid content and lipid composition of *Monoporeia affinis* (*M.a.*) and *Pontoporeia femorata* (*P.f.*) before (March) and after the spring phytoplankton bloom (June and September) in 1989. Main lipid classes were triacylglycerol (TAG) and phospholipid (PL). Other lipid classes were acetone-mobile polar lipids, sterols, and free fatty acids.

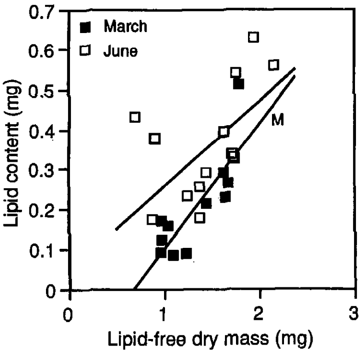

Fig. 7. Relationship between total lipid content and lipid-free dry mass in *Pontoporeia femorata* before (March) and after the spring bloom (June) in 1989. ANCOVA based on significant linear regressions showed lipid content was significantly higher in June.

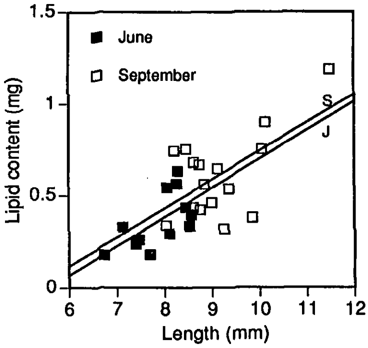

Fig. 8. Relationship between total lipid content and length in *Pontoporeia femorata* in June and September, after the spring bloom in 1989. ANCOVA based on significant linear regressions showed no significant difference in lipid content between these months.

with the *P. femorata* dried earlier in March for determining seasonal changes in lipid levels ($n = 10$, mean dry mass was 2.1 mg, mean lipid content was 0.5 mg, 23% of the dry mass). Therefore, the size of the amphipods was taken into account to compare lipid composition between months.

The amphipods were largest in September, as shown by one-way ANOVA followed by a posteriori analyses with Tukey's test. In *M. affinis,* dry mass increased each month (df = 39, $F = 65.93$, $P < 0.001$), and in *P. femorata,* dry mass was greater in September than in March and June (df = 38, $F = 20.71$, $P < 0.001$). The length of both species was greater in September than in the two earlier months (*M. affinis,* df = 39, $F = 13.55$, $P < 0.001$; *P. femorata,* df = 38, $F = 9.62$, $P < 0.001$).

The lipid content increased significantly with dry mass in both species in all months (linear regression analyses, $P < 0.05$), that is, the amphipods accumulated lipids as they grew larger. Two measures of size, lipid-free dry mass and length, were used to investigate changes in lipid content in relation to the spring bloom.

In *M. affinis,* the amount of total lipid was not significantly related to lipid-free dry mass or length ($P > 0.05$). The lipid content differed significantly among months (one-way ANOVA, df = 39, $F = 25.34$, $P < 0.001$) and was lower in March than in both June and September (a posteriori Tukey test). Thus, lipids were accumulated after the spring bloom and maintained at a high level until September. The triacylglycerol and phospholipid contents increased significantly with lipid-free dry mass in September only ($P < 0.01$ and $P < 0.05$) and were not significantly related to length ($P > 0.05$). The triacylglycerol content was significantly greater in June than in March (two-sided t-tests, df = 22, $t = -5.77$, $P < 0.001$). There was no difference in the phospholipid content between these 2 months (df = 22, $t = -0.36$, $P > 0.05$). Thus, the increase in total lipid after the spring bloom was probably due to storage of triacylglycerol.

In *P. femorata,* lipid content increased significantly with lipid-free dry mass in March ($P < 0.01$) and June ($P < 0.05$) and with length in June and September ($P < 0.05$). The mean lipid content in March and June was compared with an ANCOVA that adjusted for differences in lipid-free dry mass (Fig. 7). Lipid content was significantly higher in June than in March (df = 22, $F = 7.26$, $P < 0.05$). When lipid content was adjusted for differences in length (Fig. 8), there was no significant difference in lipid content between June and September (ANCOVA, df = 27, $F = 0.64$, $P > 0.05$). These two analyses indicate that *P. femorata,* like *M. affinis,* accumulated lipids during and immediately after the spring bloom and maintained them at a high level until September.

The amount of triacylglycerol in *P. femorata* increased significantly with lipid-free

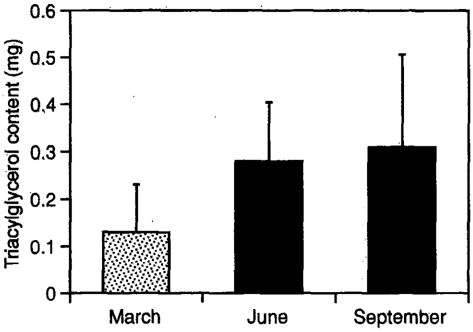

Fig. 9. Predicted values (±SE) for the triacylglycerol content of *Pontoporeia femorata* in June and September, after the spring bloom in 1989. The predicted values are based on significant linear regressions of triacylglycerol mass on length and are for amphipods 8.08 mm long, the mean length in March. Also shown is the measured mean triacylglycerol content (±SD) in March, before the spring bloom.

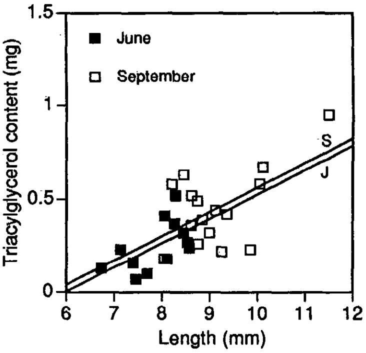

Fig. 10. Relationship between triacylglycerol content and length in *Pontoporeia femorata* in June and September, after the spring bloom in 1989. ANCOVA based on significant regressions showed no significant difference in the mass of triacylglycerol between these months.

dry mass in March only ($P < 0.01$) and with length in June and September ($P < 0.05$). The two significant regressions based on length were used to predict the triacylglycerol content of amphipods of 8.08 mm (the mean length in March). The predicted values for triacylglycerol content in June and September—after the spring bloom—were twice as high as the mean value observed in March (Fig. 9). When the triacylglycerol content was adjusted for differences in length (Fig. 10), there was no significant difference between June and September (ANCOVA, df = 27, $F = 0.43$, $P > 0.05$). These analyses indicate that triacylglycerol was accumulated after the spring bloom and maintained at a high level until September. The phospholipid content was not significantly related to lipid-free dry mass or length in any month ($P > 0.05$). There was a significant difference in the phospholipid content among months (one-way ANOVA, df = 38, $F = 5.42$, $P < 0.01$) and it was higher in September than in March (a posteriori Tukey test). Thus, storage of triacylglycerol after the spring bloom was the main reason for the increase in total lipid between March and June, but phospholipid also accumulated during the entire 6 months.

Discussion

Lipid content increased with dry mass in *M. affinis* and *P. femorata,* which indicates that the animals gained lipids during growth. Juveniles had lower lipid levels than adults, as in the closely related freshwater species *D. hoyi* (Quigley et al. 1989), the Antarctic amphipod *Paramoera walkeri* (Rakusa-Suszczewski and Dominas 1974), and the mysid-like amphipod *Macrohectopus branicki* from Lake Baikal (Morris 1984). The Baltic species are thus similar to *D. hoyi,* which accumulates lipids progressively, in particular triacylglycerol, throughout its lifetime (Quigley et al. 1989).

Studies of lipid dynamics in amphipods must take account of the size, sex, and reproductive status of the animals (Clarke et al. 1985) because these factors, as well as physiological condition, affect the lipid content and composition of marine benthic invertebrates (Clarke 1983). Some of the seasonal variation in the lipid content of *M. affinis* and *P. femorata* was due to differences in the size of the amphipods. Lipid-free dry mass and length are not ideal measures of the somatic growth of the animals. For instance, the cuticle may constitute a large proportion of the dry mass, and this proportion may vary with amphipod size and the molt cycle. Estimates of length depend on the degree to which an amphipod's body is bent, even when the body outline is traced with a digitizer. It may therefore be more useful to relate the lipid content to a measure such as ash-free dry mass.

In *D. hoyi,* growth rate and lipid content were high in spring due to an increase in the quality of the food supply during the diatom bloom (Gardner et al. 1985*b*, 1989). In other benthic amphipods, lipid levels rose when the amount or quality of food resources increased in summer (Percy 1979; Nair and Anger 1980). In contrast, in habitats where food was always available, amphipods did not accumulate large lipid reserves (Napolitano and Ackman 1989) or showed little variation in lipid levels during the year (Moore 1976).

In *M. affinis* and *P. femorata* from our study, lipid levels were not as high as those of *D. hoyi* from Lake Michigan, where the mean value was 30–40% of dry mass (Gardner et al. 1985*b*; Gauvin et al. 1989), but they are high compared with those of other amphipods (table 10 of Clarke et al. 1985). Both *M. affinis* and *P. femorata* stored additional lipid (more than that accumulated due to growth) in the form of triacylglycerol between March and May. Such storage suggests that they assimilated food resources from diatoms that settled on the sediment surface during the spring bloom. *M. affinis* and *P. femorata* absorbed ~40% of the carbon from surficial sediment in spring, but fed less on surficial sediment collected in autumn (Lopez and Elmgren 1989). In our study, *M. affinis* assimilated the food resources more rapidly in spring, as there was a change in the dominant lipid class from phospholipid in March to triacylglycerol in June and September. In contrast, the lipids of *P. femorata* had a constantly high proportion of triacylglycerol.

The Baltic amphipods may use stored lipids as reserves when food is scarce or of poor quality. In *M. affinis*, the growth of adults increases immediately after the spring bloom, but then declines or ceases (Cederwall 1977; Sarvala 1986; Uitto and Sarvala 1991). The lipid reserves of *M. affinis* were low in the first few months of 1989, before the spring bloom (Fig. 1).

Lipids are probably also used by *M. affinis* and *P. femorata* for development of the gonads and by females for the production of eggs and young. In females of two iteroparous gammarids, lipids accumulated and the percentage of triacylglycerol increased as the ovary matured (Clarke et al. 1985); in an Arctic amphipod, the lipid levels of brooding females were higher than in the rest of the population (Percy 1979). The increase in phospholipid between March and September in *P. femorata* may be connected with sexual maturity because female amphipods accumulate structural lipids when their eggs develop (Clarke et al. 1985).

Lipids were probably depleted by the metabolic costs associated with the metamorphosis of maturing males of *P. femorata*. In October 1989, the mean lipid level of such males was only 13% of the dry mass, which is similar to that of sexually mature males of *P. femorata* caught off the coast of Nova Scotia (Paradis and Ackman 1976). In *D. hoyi*, lipid levels of males were lower than those of females in December when the males matured, stopped feeding, and became pelagic (Quigley et al. 1989). Males of the intertidal amphipod *Echinogammarus marinus* depleted their lipid reserves when carrying the females in amplexus (Clarke et al. 1985). Males and females of *M. affinis* did not differ significantly in lipid content in October 1989, perhaps because this species matured later in the year than *P. femorata*.

The differences between the seasonal patterns of lipid storage in the two Baltic species can be related to differences in their feeding rates and activity levels. Both species are equally effective at absorbing particulate organic carbon from surface layers of spring sediment, but *M. affinis* has a faster feeding rate (Lopez and Elmgren 1989). The higher total food intake would enable *M. affinis* to accumulate greater amounts of lipid, in the form of triacylglycerol, after the spring bloom.

Monoporeia affinis has higher metabolic costs because it is more active and expends more energy on respiration (Cederwall 1979). The energy reserves would therefore be depleted more quickly during periods when food is scarce. The mean lipid levels of this species were only ~15% of the dry mass in winter and early spring. Lipids may also be depleted when the animals swim at night. A large proportion of the animals in field populations swim from July onward (Donner et al. 1987).

Although *P. femorata* has a lower feeding rate, it accumulated lipids after the spring bloom. It is the least active of the two species and can regulate its oxygen consumption (Cederwall 1979). Lower metabolic costs would enable it to maintain constantly large reserves of lipid, in the form of triacylglycerol, during most of the year. *P. femorata* may also feed during autumn and winter or utilize another food source in the sediment, since a growth period can occur in late autumn (Uitto and Sarvala 1991).

As *M. affinis* and *P. femorata* breed only once in their lifetime, it is important for them to acquire energy resources for the production of gonads and young. However, in the Baltic Sea, populations of these amphipods seldom complete the life cycle in a single year and must overwinter one or more times. The length of the life cycle is inversely related to the growth rate in *M. affinis* (Segerstråle 1950). Leonardsson et al. (1988) suggested that the growth rate of individual *M. affinis* determined when a size threshold for reproduction was reached. It is also possible that individual amphipods need a certain level of energy reserves, in the form of lipids, before reproduction can take place in autumn. In July, when the gonads started developing, mean lipid levels in *M. affinis* and *P. femorata* were 27 and 23% of the dry mass. Mean lipid levels of gravid females were 23% in *D. hoyi* (Quigley et al. 1989). If food resources are not plentiful enough to enable the amphipods to grow to a size where they can store lipid to a level of ~20% of their dry mass, they may have to postpone reproduction until the following year.

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