

6 Seasonal Dynamics of Lipids in Freshwater Benthic Invertebrates

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6.1. Introduction

Although there is a wealth of information on lipids in marine organisms, especially zooplankton (Kattner and Hagen, 1995; Tande and Henderson, 1988; Clarke et al., 1987; Lee, 1975; Lee and Hirota, 1973), relatively little information is available on freshwater benthic organisms. The benthos of large temperate lakes often experience a seasonal variation in food supply that is similar to the high to midlatitudes of the ocean (Lee, 1975). For instance, in temperate large lakes the diatom bloom that eventually settles to the profundal zone of the lake may be the main source of high-quality food for the benthos during the year (Fitzgerald and Gardner, 1993; Johnson and Wiederholm, 1992; Gardner et al., 1990; Fahnenstiel and Scavia, 1987).

The seasonal variation in lipid content of benthic organisms can provide clues to the ecology of the organisms. The high energy content of lipids ($39.35 \text{ J} \cdot \text{mg}^{-1}$) over proteins ($23.63 \text{ J} \cdot \text{mg}^{-1}$) and carbohydrates ($17.18 \text{ J} \cdot \text{mg}^{-1}$) make it the most efficient energy-storing compound for most freshwater benthic organisms. To survive periods when high-quality food is not reaching the benthic community, cold stenothermic benthic invertebrates often store energy as lipids (i.e., triacylglycerols [TAG]) when food is abundant (Johnson and Wiederholm, 1992; Gardner et al., 1990; Gauvin et al., 1989; Gardner et al., 1985a). The seasonal lipid dynamics of an organism may also depend on their feeding strategy. For example, some benthic animals feed at the sediment surface whereas others feed below the surface. Consequently, animals may feed on particles at various phases of decomposition and nutritional quality depending on their feeding mode. In addition, the trophic state of the water body that the benthic invertebrates inhabit may affect their lipid dynamics. Besides availability of food resources, morphology, life history, habitat, and the reproductive state of a benthic animal may contribute to its seasonal lipid profile.

In this chapter, we explore the seasonal changes of lipids in different benthic invertebrates with emphasis on large temperate lakes. Seasonal lipid dynamics in benthos from lotic environments is limited, so only minimal comparative information is provided on stream invertebrates. Because the location of benthic inverte-

brates in the lake is in part responsible for their seasonal lipid content, this chapter is organized according to habitats. Furthermore, research gaps in lipid dynamics of freshwater benthic invertebrates are explored.

6.2. Results and Discussion

6.2.1. Slope and Profundal Zones

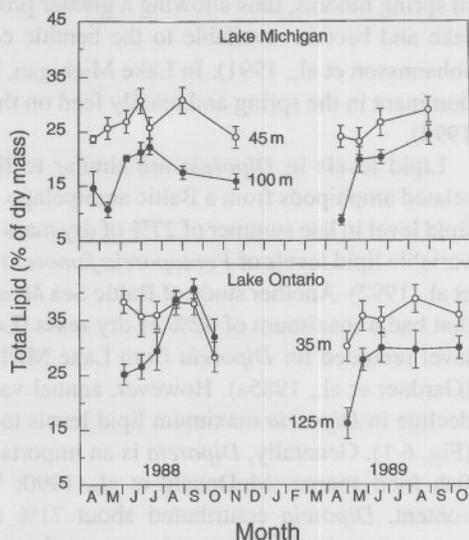
6.2.1.1. Crustacea: Amphipoda

The benthic amphipods *Diporeia* spp. are the most abundant benthic invertebrates in the slope and profundal regions of the upper Laurentian Great Lakes (Nalepa, 1987); they also live in many other glacial lakes from temperate to subarctic zones (Moore, 1979; Dadswell, 1974). In North America, *Diporeia* spp. were formerly known as one species, *Pontoporeia hoyi*; however, recent changes in the taxonomy of these amphipods have identified at least two and perhaps as many as eight species (Bousfield, 1989). Until the taxonomy of these benthic amphipods is resolved, we will refer to the species formerly known as *Pontoporeia hoyi* as *Diporeia*.

Diporeia inhabits the upper 2 cm of sediment and thoroughly mix this upper sediment layer during burrowing and feeding (Robbins et al., 1979). In addition, *Diporeia* prefers feeding in fine silty sediments over coarse ones (Mozley and Howmiller, 1977). The slope region (30–90 m) of the Great Lakes, with its cold temperatures (4–8°C) and an adequate food supply, supports the highest *Diporeia* densities throughout the year (Evans et al., 1990; Nalepa, 1987; Johannsson et al., 1985; Winnell and White, 1984). *Diporeia* is by far the most dominant organism in profundal zones (>90 m); however, overall densities are lower than those found in the slope region, likely because of diminished food supplies (Nalepa, 1991; Evans et al., 1990).

Diporeia lipid levels vary seasonally, mainly because of changes in TAG, the lipid reserve (Cavaletto et al., 1996; Gardner et al., 1985b). A seasonal increase in *Diporeia* lipid reserves occurs sometime following a spring bloom of large diatoms that settle to the bottom before the lake stratifies. However, various lag times occur between the diatom bloom event and accumulation of lipid reserves in the animals that appears to depend on the lake and depth (Fig. 6.1). Evidence of this diatom sedimentation has been shown in the slope region of Lake Michigan by examining alkane composition and biogenic silica fluxes in material collected in a sediment trap located just below the thermocline at a 45-m-deep site in Lake Michigan (Gardner et al., 1989). The ratio of aquatic plankton markers (short alkane length; C₁₇) to terrestrial markers (long alkane length; C₂₉) indicated a large input of plankton/autochthonous material in the spring (late April–May), whereas the ratio during other times of the year indicated a terrestrial/allochthonous input. In addition, high biogenic silica flux in early spring also supported the occurrence of this event (Johengen et al., 1994; Gardner et al.,

FIGURE 6.1. Seasonal variation of total lipid levels in *Diporeia* spp. from 45-m and 100-m sites in Lake Michigan and 35-m and 125-m sites in Lake Ontario. Bars represent standard errors. (Data from Cavaletto et al., 1996.)



1989). It appears that *Diporeia* depends on diatom sedimentation for a high-quality food source. *Diporeia* from the slope has a higher incident of full guts in the spring, when diatom sedimentation to the benthos occurs, than it does during other times of the year (Quigley, 1988).

In the profundal zone of the lake, the percentage of *Diporeia* with full guts is more constant through the seasons, possibly indicating that food resources are relatively consistent throughout the year (Evans et al., 1990). Likely, the relatively long time required for diatoms to settle to the deeper profundal zone results in more decomposition and zooplankton grazing of the diatoms than occurs in the shallower slope region. Thus, the quality of food sources reaching the benthic community may be inversely related to depth. These food differences are evidenced by lower *Diporeia* lipid levels in individuals from the profundal zone compared with those from the slope region (Fig. 6.1) (Cavaletto et al., 1996). However, lipid levels in *Diporeia* are not always lower in the profundal region, and this difference can vary by season. For instance, in Lake Ontario during 1988, *Diporeia* lipid levels were higher in the slope region in the spring, but there was no difference in lipid levels in the slope and profundal regions in late summer (Fig. 6.1) (Cavaletto et al., 1996).

Diporeia from Lake Ontario accumulated lipid levels up to 12% higher than *Diporeia* from Lake Michigan (Cavaletto et al., 1996). This result reflects ecological differences in the two lakes or possibly genetic differences between the two *Diporeia* populations (Bousfield, 1989). One ecological difference between the lakes is that Lake Ontario is more productive than Lake Michigan. This may result in more algal and detrital material provided to the benthos in Lake Ontario (Johengen et al., 1994). In addition, Lake Ontario is dominated by small zooplankton that may not be able to consume large diatoms that are usually dominant

in spring blooms, thus allowing a greater proportion to settle to the bottom of the lake and become available to the benthic community (Mazumder et al., 1992; Johannsson et al., 1991). In Lake Michigan, hypolimnetic calanoid copepods are dominant in the spring and readily feed on the diatom bloom (Vanderploeg et al., 1992).

Lipid levels in *Diporeia* are similar to lipid levels found in two species of related amphipods from a Baltic archipelago. *Monoporeia affinis* had a maximum lipid level in late summer of 27% of dry mass as compared with the less seasonally variable lipid levels of *Pontoporeia femorata* that were 20–23% of dry mass (Hill et al., 1992). Another study of Baltic Sea *M. affinis* revealed higher seasonal lipids that had a maximum of 42% of dry mass (Lehtonen, 1996). The maximum lipid level recorded for *Diporeia* from Lake Michigan was 46% of dry mass in 1984 (Gardner et al., 1985a). However, annual variation occurs as demonstrated by a decline in *Diporeia* maximum lipid levels to 31% of dry mass in 1988 and 1989 (Fig. 6.1). Generally, *Diporeia* is an important pelagic benthic coupling link and fish food source (McDonald et al., 1990; Wells, 1980). Due to its high lipid content, *Diporeia* contributed about 71% of the mean energy content of all macroinvertebrates averaged over southern Lake Michigan as compared with 66% of the biomass (Gardner et al., 1985a).

In addition to providing metabolic fuel when food is scarce, TAGs are important to the reproductive process of *Diporeia*. Adult female *Diporeia* have the highest TAG levels, males have low levels of TAG, and juvenile TAG levels are intermediate (Fig. 6.2) (Quigley et al., 1989). Males are highly active and swim above the sediment surface in search of mates. This high level of activity in males probably rapidly depletes lipid reserves that were accumulated in the juvenile stage. The final molt of the adult male may also be demanding energetically (Hill, 1992). By contrast, the high lipid levels of the females are likely conserved and

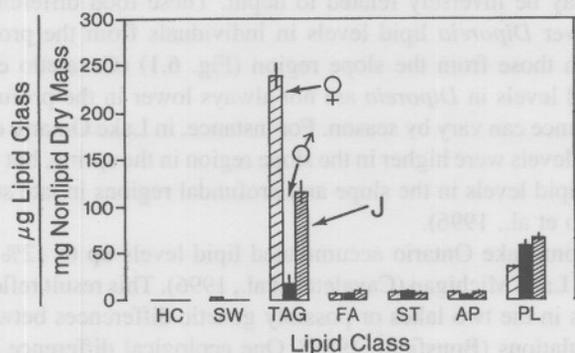


FIGURE 6.2. Mean micrograms (\pm SE) of lipid class per milligram nonlipid dry mass among female, male, and juvenile *Diporeia*. HC, hydrocarbon; SW, sterol ester/wax ester; TAG, triacylglycerol; FA, free fatty acid; ST, sterol; AP, acetone mobile polar lipid; PL, phospholipid. (From Quigley et al., 1989.)

then transferred to their brooded eggs or young to provide them with energy during their first few days of life. In addition, females with high lipid reserves may be able to produce larger broods (Cavaletto et al., 1996).

Lipid levels may also be important to the duration of the life cycle in *Diporeia*. The length of the *Diporeia* life cycle increases with increasing depth. For example, in Lake Michigan, *Diporeia* has a 1-year life cycle in the shelf region (10–20 m), in the slope (30–90 m) it has a 2-year life cycle, and in the profundal zone (>90 m) the life cycle is 2.5–3 years (Winnell and White, 1984). Food availability and increased temperatures during the summer in the shelf region are probably responsible for these varying life cycles; however, a certain lipid level may need to be achieved before completion of the life cycle can occur in the different regions (Hill et al., 1992; Quigley et al., 1989).

6.2.1.2. Mysidacea

Mysis relicta, commonly known as the opossum shrimp, usually inhabit deep, cold, glacial lakes, although they can adapt to a wide range of environmental conditions including temperatures up to 21°C, low oxygen, and eutrophication (Beeton and Gannon, 1991). *Mysis* usually inhabit depths >30 m, but in the Great Lakes they may also be found in shallow regions when the lake is isothermal or during upwelling events (Mozley and Howmiller, 1977). *Mysis* are considered to be epibenthic because they spend the day in the sediments and migrate up into the water column at night (Beeton, 1960). However, in deep regions of a lake (100 m) mysids can occur 7 m above the sediments during the day (Beeton, 1960). *Mysis* are omnivorous, feeding on detrital particles in sediments, algae, zooplankton, and small *Diporeia* (Parker, 1980; Bowers and Grossnickle, 1978; Lasenby and Langford, 1972). *Mysis* can take 1–4 years to reach sexual maturity, depending on food availability (Adare and Lasenby, 1994; Morgan, 1980; Lasenby and Langford, 1972) and temperature (Berrill and Lasenby, 1983). After a female *Mysis* deposits her eggs in the marsupium and breeds with a male, she continues to grow as the embryos and larvae develop. Following release of the young, the female will usually die; however, in some instances *Mysis* have been documented to produce a second brood (Morgan and Beeton, 1978).

Mysis from four Canadian lakes accumulated lipids as they matured. Life cycle length depended on growth rate along with lipid accumulation rate and it varied in the *Mysis* populations from the different lakes. For example, in the first 6 months of life, *Mysis* with a 2-year life cycle grew at a rate of 1.0 mm · month⁻¹ and accumulated 43.5 µg of lipid, whereas *Mysis* with a 1-year life cycle grew 1.8 mm · month⁻¹ and accumulated 125 µg of lipid (Adare and Lasenby, 1994). On maturity, *Mysis* attained their peak lipid levels in summer (Fig. 6.3). Maximum mysid lipid levels ranged from 30 to 40% of dry mass in Canadian temperate lakes (Adare and Lasenby, 1994). These levels are comparable with lipid levels of 33% of dry mass for Lake Michigan *Mysis* (Fig. 6.4) (Gardner et al., 1985a). TAG is the most abundant lipid class (75.6% of total lipid) in *Mysis* from Lake Michigan during late spring (Table 6.1).

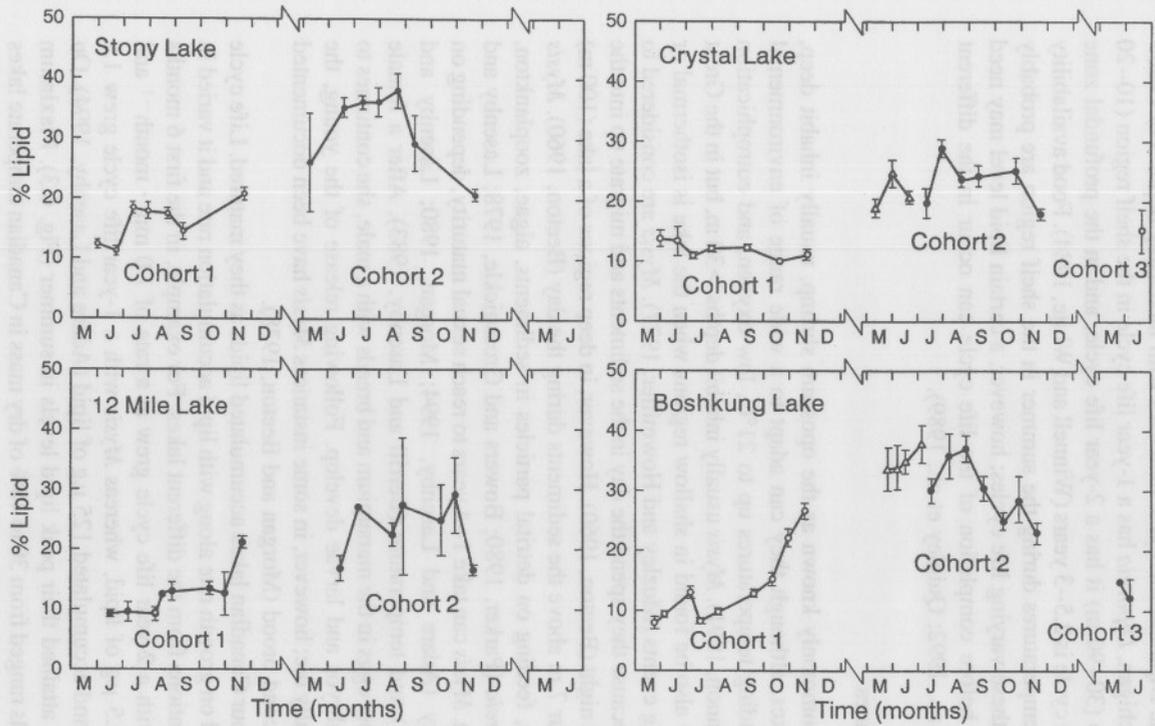


FIGURE 6.3. Seasonal changes in the percentage lipid (of dry mass) of juvenile (open circles), immature (open triangles), and mature (solid circles) mysids from May to November 1990 in the four study lakes. Stony and Crystal lakes are mesotrophic, and 12 Mile and Boshkung lakes are oligotrophic. Mysid cohorts are presented separately for ease of illustration. The time for *Mysis* to reach maturity is 1 year in Stony and 12 Mile lakes and 2 years in Crystal and Boshkung lakes. Bars represent standard errors. (From Adare and Lasenby, 1994.)

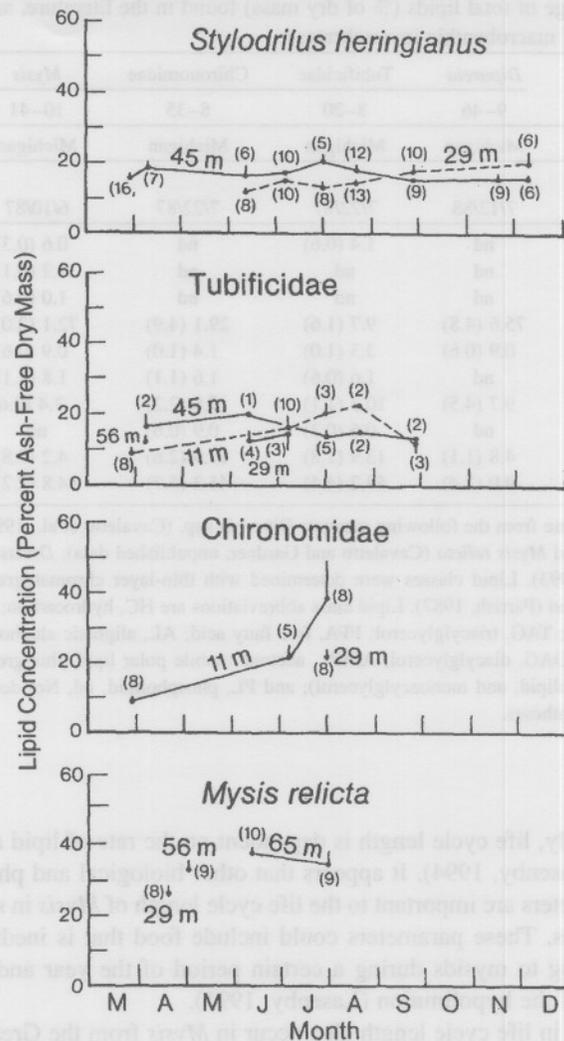


FIGURE 6.4. Total lipid content, expressed as a percentage of ash-free dry mass (ash-free dry mass is approximately 90% of dry mass for oligochaetes and chironomids, and 85% of dry mass for *Mysis relicta*; Johnson and Brinkhurst, 1971) in major species of Lake Michigan macroinvertebrates sampled in southeastern Lake Michigan in 1984. Bars represent standard errors. Numbers in parentheses represent the number of replicate animals analyzed. (From Gardner et al., 1985a.)

The life cycle of mysids in the Canadian lakes study was 1 or 2 years in oligotrophic and mesotrophic lakes, suggesting that lipid accumulation rate was independent of lake trophic status (Fig. 6.3) (Adare and Lasenby, 1994). However, this situation seems unusual because in other *Mysis* studies, life cycle length is considered to be inversely related to lake trophic state (Morgan, 1980), and

TABLE 6.1. Range of total lipids (% of dry mass) found in the literature, and the lipid class profiles of macrobenthic invertebrates.^a

	<i>Diporeia</i>	Tubificidae	Chironomidae	<i>Mysis</i>	<i>Dreissena</i>
Total lipid range	9–46	8–20	8–35	10–41	6–18
Lake	Michigan	Michigan	Michigan	Michigan	St. Clair
Collection date for lipid classes	7/12/88	7/22/87	7/22/87	6/10/87	7/24/90
HC	nd	1.4 (0.6)	nd	0.6 (0.3)	nd
SE	nd	nd	nd	1.2 (0.1)	nd
ME	nd	nd	nd	1.0 (0.6)	2.4 (0.8)
TAG	75.6 (4.8)	9.7 (1.6)	29.1 (4.9)	72.1 (2.0)	17.2 (4.7)
FFA	0.9 (0.6)	3.3 (1.0)	1.4 (1.0)	0.9 (0.6)	3.0 (1.9)
AL	nd	1.6 (0.6)	1.6 (1.1)	1.8 (1.1)	nd
ST	9.7 (4.5)	10.3 (1.1)	7.8 (2.2)	3.4 (0.6)	8.2 (1.8)
DG	nd	0.6 (0.3)	0.9 (0.6)	nd	nd
AMPL	4.8 (1.1)	13.9 (1.8)	17.9 (2.6)	4.2 (0.8)	6.3 (1.2)
PL	9.0 (2.4)	59.2 (4.4)	41.3 (5.7)	14.8 (2.2)	62.9 (6.8)

^aLipid class data are from the following sources; *Diporeia* spp. (Cavaletto et al., 1996); Tubificidae, Chironomidae, and *Mysis relicta* (Cavaletto and Gardner, unpublished data); *Dreissena polymorpha* (Nalepa et al., 1993). Lipid classes were determined with thin-layer chromatography with flame ionization detection (Parrish, 1987). Lipid class abbreviations are HC, hydrocarbon; SE, sterol ester; ME, methyl ester; TAG, triacylglycerol; FFA, free fatty acid; AL, aliphatic alcohol; ST, sterol (alicyclic alcohol); DAG, diacylglycerol; AMPL, acetone mobile polar lipid (this group may include chlorophyll, glycolipid, and monoacylglycerol); and PL, phospholipid. nd, Not detected. Standard errors are in parentheses.

correspondingly, life cycle length is dependent on the rate of lipid accumulation (Adare and Lasenby, 1994). It appears that other biological and physical water-quality parameters are important to the life cycle length of *Mysis* in some of these Canadian lakes. These parameters could include food that is inedible or nutritionally lacking to mysids during a certain period of the year and the average temperature of the hypolimnion (Lasenby, 1991).

Differences in life cycle length also occur in *Mysis* from the Great Lakes. For example, *Mysis* from Lake Michigan reach maturity 8 months faster than *Mysis* from Lake Ontario because the growth rate of *Mysis* from Lake Ontario declines during the winter months, whereas the growth rate of *Mysis* from Lake Michigan remains the same all year long (Johannsson et al., 1994). Furthermore, *Mysis* from Lake Michigan used 11–31% less calories to reach maturity than *Mysis* from Lake Ontario. This result differs from data in a study that compared *Mysis* from an Arctic and a temperate lake. Although the *Mysis* from the Arctic lake had a 2-year life cycle and the *Mysis* from the temperate lake had a 1-year life cycle, the calories used to reach maturity were the same for both populations (Lasenby and Langford, 1972). The lipid level/caloric utilization and life cycle length differences in *Mysis* must be adaptations to differences in food webs between lakes or perhaps a limitation of essential substances in the diet at certain times of the year.

6.2.2. Shelf and Nearshore Zones

6.2.2.1. Crustacea: Amphipoda

Unlike *Diporeia*, the majority of freshwater amphipods inhabit nearshore areas of lakes, ponds, and streams, and they usually live in and around vegetation from the surface to 1 m deep (Pennak, 1978). Seasonal variation in lipid content was determined in two common species of amphipods, *Hyalella azteca* and *Gammarus lacustris*, in conjunction with a contaminant study (Arts et al., 1995). Amphipods were analyzed from three Canadian prairie lakes that are in the vicinity of agricultural herbicide applications.

In *H. azteca*, lipid levels ranged from 2.5 to 16.3% of dry mass and varied seasonally in two of three lakes. In both of these lakes, lipid levels were highest in spring and declined through the summer, with lipid levels increasing again in autumn in *H. azteca* from one of the lakes. In addition, females usually had higher lipid levels than males in spring and early summer during reproduction (Arts et al., 1995). Similarly, total lipid levels in *H. azteca* from a Michigan pond were 17.4% \pm 3.7 (SE) of dry mass in autumn (Cavaletto and Gardner, unpublished data). In *G. lacustris*, lipid levels ranged from 2.4 to 15.7% of dry mass. Like *H. azteca*, lipid levels in *G. lacustris* were highest, especially in females, during the reproductive period in spring and early summer (Arts et al., 1995). TAG was the most abundant lipid class in both *H. azteca* and *G. lacustris*, ranging from 22.6 to 67.3% of total lipid. In addition, the contaminant studied (i.e., triallate) was positively correlated with TAG in both amphipods (Arts et al., 1995).

6.2.2.2. Annelida: Oligochaeta

Oligochaete worms are the most abundant benthic macroinvertebrates in many shallow bays, harbors, and river mouths, and they occur from nearshore areas to the profundal zone (Schloesser et al., 1995; Brinkhurst, 1970, 1967). Many species of oligochaetes are used as water-quality indicators. For example, high densities of *Tubifex tubifex* or *Limnodrilus hoffmeisteri* are usually found in polluted environments. The presence of *Stylodrilus heringianus* is an indication of oligotrophic conditions, and they are more commonly found in the profundal zone of lakes (Nalepa, 1991; Mozley and Howmiller, 1977). Benthic oligochaetes usually feed with their anterior ends 4–6 cm below the sediment–water interface and defecate at the sediment surface (Appleby and Brinkhurst, 1970). Oligochaetes are continuous feeders and derive nutrition from the detritus and bacteria present in the sediment (Wavre and Brinkhurst, 1971; Brinkhurst and Chua, 1969). Lipids have been studied in oligochaetes from the family Tubificidae and *S. heringianus* (Lumbriculidae) (Gardner et al., 1985a). These oligochaetes had no apparent seasonal lipid pattern; however, total lipids varied between 8–20% of dry mass (Fig. 6.4).

Phospholipids (PL) are the most abundant lipid class in tubificids. Oligochaetes have large surface areas of unprotected epidermis (no carapace or cuticle) that require a high portion of structural membrane PL. Sterol (ST; most commonly

cholesterol) is also an important membrane component, and it is fairly abundant in the worms. Combined PL and ST represent 70% of tubificid total lipid (Table 6.1). The acetone mobile polar lipids (AMPL) are polar lipid compounds that are mobile in 100% acetone; this lipid group includes chlorophyll. AMPL may represent a portion of the worm's gut contents. Lipid reserves (TAG) are not a large component of tubificid lipids (Table 6.1). It is possible that because oligochaetes feed below the sediment surface, they have a more constant but probably a low-quality food resource (i.e., detritus and bacteria) compared with organisms that feed closer to the sediment surface. This relatively constant food supply may allow oligochaetes to maintain its growth, respiration, and reproduction with only a minimum of lipid reserves (Gardner et al., 1985a).

6.2.2.3. Insecta

The aquatic midge larvae, members of the family Chironomidae, are ubiquitous in lentic and lotic environments. They are most common in shallow (<8 m) environments where food is relatively abundant. Chironomid larvae feed on surficial sediment, and many species build feeding tubes where they draw in food particles by self-produced currents. Chironomids are selective feeders, and it has been demonstrated that food items in their gut are at a higher concentration than food items in the surrounding sediments (Johnson et al., 1989). Although they feed on detrital particles and bacteria, algae (especially diatoms) can be an important part of their diet (Pinder, 1992; Johnson et al., 1989). In fact, chironomid larvae that were fed detrital particles alone did not survive or grow as well as larvae that were fed both detritus and diatoms (Pinder, 1992). Chironomids inhabiting the near-shore areas of Lake Michigan likely rely on diatoms as an essential part of their diet. Following the spring diatom bloom, chironomid larvae from Lake Michigan show an increase in total lipid levels by midsummer (Fig. 6.4). Storage lipids (TAG) occur at intermediate levels in chironomids as compared with other Great Lakes benthic invertebrates (Table 6.1). These quantities of lipid classes are comparable with levels found in chironomids from a Scottish river where TAG was 54% and PL was 31% of total lipids (Bell et al., 1994).

Chironomids are holometabolous insects, and their metamorphosis from larvae to adult is a high energy activity. A study of biochemical components (protein, carbohydrates, and lipids) of chironomid larvae revealed that the instar prior to prepupal reorganization had a more rapid increase in carbohydrates and lipids than the earlier instars. When prepupal tissue organization did begin, carbohydrates and lipids were the components that were used most rapidly (Beattie, 1978).

Accumulation of lipid reserves was also necessary for proper metamorphosis and reproduction to occur in the caddis fly *Clisornia magnifica*. Caddis fly larvae that were fed a high-quality diet (high carbohydrate) accumulated more lipid, spent less time in the larval form, took longer to pupate, and lived longer as adults than individuals on a low-quality diet (Cargill et al., 1985). Like the chironomid larvae, the majority (i.e., 80%) of lipid reserves that accumulated in the caddis fly larvae occurred during the last instar.

Another similar situation occurs in the aquatic soldier fly larvae, *Hedriodiscus truquii*, which was studied for ecological energetics modeling in thermal springs (Stockner, 1971). The algivorous larvae pass through four instars from egg to adult. Total lipid levels of *H. truquii* may double or quadruple from the second to fourth instar (pupae) and finally reach a maximum lipid level of approximately 20% of dry mass (Stockner, 1971). Energy expenditure during metamorphosis is revealed in the adult's lower lipid levels of 11–12% of dry mass. In addition, the short-lived adults (i.e., a few days) probably do not feed, therefore relying on the lipid acquired as larvae to complete their reproductive cycle.

Mayfly nymphs, members of the order Ephemeroptera, live in diverse habitats from fast-running streams to slow-moving rivers and lakes. Most mayflies are herbivores and detritivores, but a few may be true carnivores (Edmunds, 1978). In addition, they are very sensitive to poor water-quality conditions. Thus, many species were eliminated from their natural habitats due to cultural eutrophication.

Lipid content has been analyzed for studies of mayfly toxicokinetics (Landrum and Poore, 1988) and biochemical composition (Meyer, 1990). Lipid content of the mayfly nymphs varies seasonally. The stream mayfly *Epeorus sylvicola* had its highest values in lipid level, dry mass, and body length in June, just prior to mature nymph emergence to the subimago or preadult stage. The maximum mean lipid level was 12% of dry mass, and the range throughout the year for *E. sylvicola* was from 2 to 20% of dry mass (Meyer, 1990). *Hexagenia limbata*, a burrowing mayfly nymph, had a similar lipid range from 2.4 to 17.7% of dry mass. Like *E. sylvicola*, the mean maximum lipid level in *H. limbata* occurred in June (Landrum and Poore, 1988). In several species of mayflies from a Scottish stream, TAG was determined to be the most abundant lipid class (i.e., 50–60% of total lipid), whereas PL ranked second (i.e., 30% of total lipid) during August (Bell et al., 1994).

Sexual differences in lipid level were found in large nymphs of *E. sylvicola*. Male lipid levels were approximately 15% of dry mass, whereas female lipid levels were approximately 10% of dry mass in individuals >15 mg dry mass (Meyer, 1990). The lower lipid level in females may be due to production of eggs when stored lipid is used for the synthesis of yolk proteins (Meyer, 1990). In compliance with this, protein levels were higher in the >15-mg dry mass female than in male nymphs of the same size.

6.2.2.4. Mollusca: Bivalvia

The mollusk *Diplodon patagonicus* lives in Lake Nahuel Huapi located in the Patagonian Andes Mountains. Total lipid levels varied seasonally in *D. patagonicus*. Lipid values of 4.1% of dry mass (percentage dry mass was converted from wet mass data by assuming that dry mass is 15% of wet mass) occurred in winter, whereas lipid values of 9.7% of dry mass occurred in the spring (Pollero et al., 1981). This lipid increase was likely due to an increase in *D. patagonicus* feeding in the spring but not on a diatom bloom. The spring-melt runoff is low in nutrients in Lake Nahuel Huapi and does not promote a spring diatom bloom. In addition, the lack of seasonal variation in *D. patagonicus* fatty acid (FA) composi-

tion indicated no occurrence of a seasonal algal event. However, FA analysis did reveal an unsaturated FA ratio typical of terrestrial plants. Therefore, it appears that land-based detrital material is an important component of the diet of *D. patagonicus* (Pollero and Brenner, 1981; Pollero et al., 1981b). In addition, reproduction appeared to influence lipid composition of a related species, *Diplodon delodontus* (Pollero et al., 1983). For example, TAG levels of *D. delodontus* increased in both sexes prior to gametogenesis, although TAG levels were higher in females than in males. Furthermore, specific unsaturated FAs also increased with the maturing of the oocytes. Like other benthic invertebrates, lipid production in the spring is important for *Diplodon* spp. to successfully reproduce.

Zebra mussels (*Dreissena polymorpha*) invaded the lakes and rivers of central Europe at the beginning of the past century. In the late 1980s, *Dreissena* invaded the Great Lakes ecosystem (Hebert et al., 1989) and continue to spread into water bodies across the south and to the west in North America. *Dreissena* are nuisance organisms due to their mode of attachment and rapid colonization of hard surfaces. We are only beginning to understand the cascading effects that result from the invasion of this exotic species. For example, dreissenids alter native ecosystems due to their tremendous ability to filter phytoplankton from the water (Fanslow et al., 1995) and shift the main use of primary production from the pelagic zone to the benthos (Lowe and Pillsbury, 1995). Many studies have been done to try to better understand and possibly help control the spread of *Dreissena* (Nalepa and Fahnenstiel, 1995; Nalepa and Schloesser, 1993).

Dreissena are short lived for mollusks (3–4 years), but they still produce many offspring. Unlike most freshwater bivalves that have a parasitic larval stage, *Dreissena* has a free-swimming veliger larva like marine bivalves (Sprung, 1989). *Dreissena* mature rather fast and begin to produce gametes when they are approximately 8 mm in length; they may increase the number of gametes produced as they grow (Sprung, 1991).

Biochemical composition of *Dreissena* soft tissues has been examined in several studies in relation to growth, reproduction, and starvation under natural and experimental conditions (Sprung, 1995; Nalepa et al., 1993; Sprung and Borchherding, 1991; Walz, 1979). *Dreissena* are unusual bivalves whose major energy reserve appears to be lipid rather than glycogen (Sprung, 1995; Sprung and Borchherding, 1991). Lipid content of *Dreissena* varies seasonally (Fig. 6.5). *Dreissena* total lipid was usually highest in the spring and declined throughout the summer and fall, although this may vary with food availability (Sprung, 1995; Nalepa et al., 1993). Lipid is concentrated in the digestive gland of *Dreissena*, and on proper conditions for reproduction (i.e., mainly a temperature of 12°C or greater), some lipid is transferred from the digestive gland to the gonad (Sprung, 1995). Like most freshwater organisms, *Dreissena* storage lipid is TAG. Their TAG concentration peaks in the spring and then declines throughout the remaining seasons (Fig. 6.6) (Nalepa et al., 1993). Structural membrane component lipid (i.e., PL) remains relatively stable from spring until fall and is most often the main lipid class in zebra mussels (Fig. 6.6; Table 6.1).

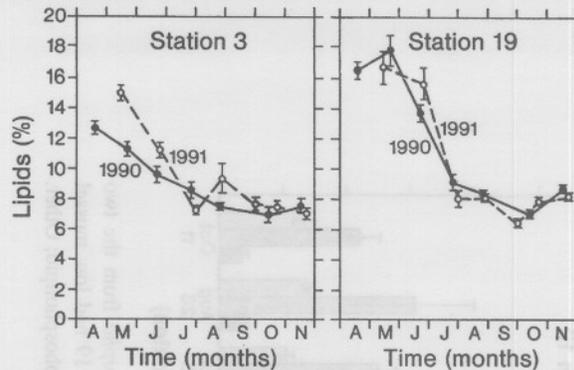


FIGURE 6.5. Mean (\pm SE) lipid content (percentage of dry mass) of *Dreissena polymorpha* from the two sampling sites in southern Lake St. Clair on sampling dates in 1990 and 1991. Station 3 had high mussel densities, and station 19 had low mussel densities. (From Nalepa et al., 1993.)

The seasonal increase in *Dreissena* TAG levels appears to be related to food availability and reproductive state (Garton and Haag, 1993; Walz, 1979). In Lake St. Clair, part of the connecting waterway between Lakes Huron and Erie, *Dreissena*'s lipid composition was studied at two sites (stations 3 and 19) with different zebra mussel densities. At both sites, lipid levels peaked in April or May and then declined. However, spring maximum total lipid and TAG levels were highest at station 19 (Figs. 6.5 and 6.6) (Nalepa et al., 1993). This observation seems to provide some evidence that lipid levels in *Dreissena* are related to food supply because spring chlorophyll concentration was higher at station 19 (i.e., $5.1 \mu\text{g} \cdot \text{L}^{-1}$) than at station 3 (i.e., $2.1 \mu\text{g} \cdot \text{L}^{-1}$). However, other factors are probably involved. For instance, *Dreissena* densities were higher at station 3 than at station 19, and this could limit the food per mussel at station 3. In addition, the water temperature increased earlier in the spring at station 3 than at station 19, a factor that would increase mussel respiration and possibly induce reproduction sooner at station 3 than at station 19. All these factors exerted stress on the *Dreissena* population at station 3 that may have resulted in lower maximum lipid levels.

Another indicator of *Dreissena* condition is the comparison of respiration with ammonium excretion rates or O/N ratio (Quigley et al., 1993). Although the usual biochemical composition of an organism must be considered, some generalizations can be made regarding O/N ratios in starving animals. O/N ratios of ≥ 60 may indicate relatively high use of lipids, a ratio between 50–60 may indicate equal use of lipid and protein, ratios < 50 and > 16 may indicate increasingly more catabolism of protein over lipid, whereas low O/N ratios between 3–16 indicate use of protein (Mayzaud and Conover, 1988). Seasonal O/N ratios of Lake St. Clair *Dreissena* revealed a ratio of 48 in April, signifying relatively equal use of

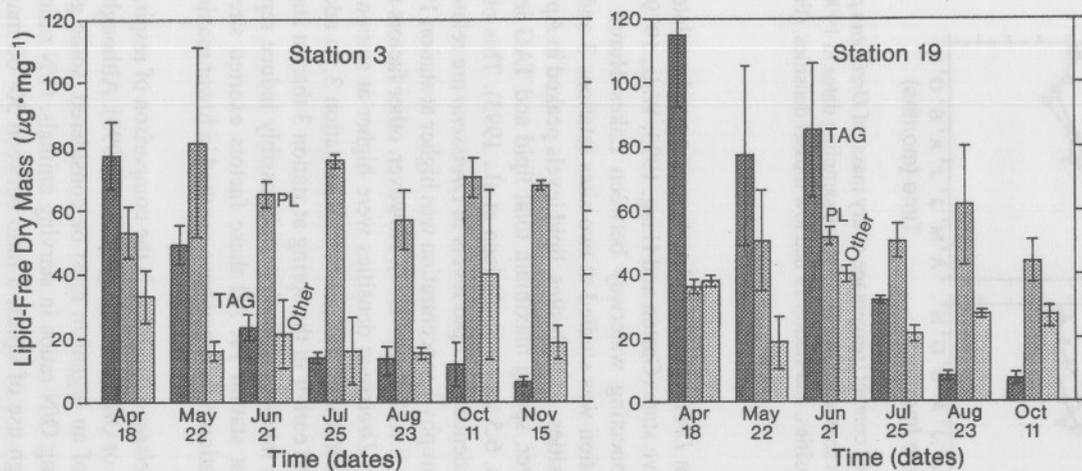


FIGURE 6.6. Seasonal variation (mean \pm SE) in major lipid classes in *Dreissena polymorpha* from the two sampling sites in Lake St. Clair in 1990. Station 3 had high mussel densities, and station 19 had low mussel densities. Values are given as μg lipid \cdot mg lipid-free dry mass $^{-1}$. TAG, triacylglycerol; PL, phospholipid; Other, acetone mobile polar lipid, free fatty acid, sterol. (From Nalepa et al., 1993.)

lipids and protein. An O/N ratio of 50 is considered the lower limit for physiological health in the blue mussel, *Mytilus edulis* (Bayne et al., 1985). In August, *Dreissena* had an O/N ratio of 16 that signified high use of protein, probably from the catabolism of soft body tissues because *Dreissena* mass and lipid declined from April to August (Nalepa et al., 1993). However, a low ratio could also signify the use of a high-protein food source. During the fall months, the zebra mussel's O/N ratio increased to 30, but this number is still below the physiologically healthy ratio (Quigley et al., 1993). Thus, despite *Dreissena*'s rapid increase in densities since their successful invasion of North America, they may not be in a healthy state in all locales, likely due to food limitation during certain times of the year.

6.3. Research Needs

FA characterization in marine organisms has enhanced our understanding of food web dynamics in many marine ecosystems, but this approach has not been used as extensively in freshwater environments. FA biomarkers could likely, in freshwater ecosystems, trace food web dynamics as has been done for marine ecosystems (Kattner et al., 1996; St. John and Lund, 1996; Kattner and Hagen, 1995; Parrish et al., 1995; Kattner, 1989; Napolitano and Ackman, 1989). For example, in Jeddore Harbour, Nova Scotia, the appearance of odd-chain FAs in smelt were eventually traced to *Pontoporeia femorata* (a marine relative of *Diporeia* spp.). *Pontoporeia femorata* was a significant part of the smelt diet in the spring when actively reproductive males swam in the water column (Paradis and Ackman, 1976). The odd-chain FAs may have originated from microbes or allochthonous sources in the harbor (Paradis and Ackman, 1977).

FA characterization of freshwater organisms is very limited, especially for benthic invertebrates. However, some FA analysis has been done for *Diplodon* spp. (Pollero et al., 1983, 1981; Pollero and Brenner, 1981), aquatic insects (Bell et al., 1994; Hanson et al., 1985, 1983; Lee et al., 1975), and nectobenthic amphipods from Lake Baikal (Dembitsky et al., 1994; Morris, 1984). In the Great Lakes, identification of FA biomarkers in *Diporeia* or oligochaetes could possibly be used to trace seasonal changes in their diet, and these biomarkers might eventually be traced to their consumers such as mysids and fish.

Several FAs are essential to organisms at various trophic levels. Invertebrates and fish must obtain essential FAs from their diet for proper development and reproduction. Some FAs are important precursors to hormones. For example, the FA compositions of river invertebrates that are the natural food to salmon were examined and compared with the FA composition of commercial diets fed to farmed salmon (Bell et al., 1994). Although essential FAs were present in the commercial diet, important FA ratios were not optimal for salmon undergoing smoltification. A diet with FA ratios closer to that found in the salmon's natural diet of freshwater invertebrates prevented certain pathologies from developing in the fish.

More extensive FA analysis on benthic macroinvertebrates is necessary to develop a complete understanding of seasonal lipid and food web dynamics in freshwater environments and how FAs may alter development and reproduction. As in the case of *Mysis*, it is unclear whether their maturation time is more dependent on food quantity or quality. An examination of FA profiles of mysids and their potential food items in lakes with different mysid maturation times could be beneficial in understanding why life cycle length varies in *Mysis*. For example, improved growth of juvenile scallops was correlated to the occurrence of the essential FA 22:6 ω 3 in their diet, rather than merely a diet abundant in lipids (Parrish et al. 1995). This essential FA is common to the Cryptophyceae. Seasonal changes in algal composition and the essential FAs that they may provide could contribute to the maturation time of *Mysis* either by direct consumption or indirectly through zooplankton prey.

Long-term monitoring of total lipid content in certain benthic invertebrates could provide additional insight into ecosystem changes. *Diporeia* and other amphipods may be ideal organisms for this approach. In Lake Michigan, seasonal lipid content of *Diporeia* has been analyzed over several years at the same site. In 1984, the yearly mean lipid levels in *Diporeia* were $33.7\% \pm 3.3$ (SE) of dry mass, in 1988 the levels declined to $28.2\% \pm 1.0$ (SE) of dry mass, and in 1989 levels were $25.7\% \pm 1.2$ (SE) of dry mass (Cavaletto et al., 1996; Gardner et al., 1985a). Maximum lipid levels in *Diporeia* reached 46% of dry mass in 1984, and in 1988 maximum levels were only 30% of dry mass. The decline in total lipid could reveal an increase in *Diporeia* population size causing intraspecific competition for food or reflect a decline in the food supply to the benthos. *Diporeia* densities at this site have remained relatively stable through the 1980s (T. Nalepa, personal communication), indicating that food availability to *Diporeia* may have changed from the mid- to late 1980s. However, additional data are necessary to reveal true trends in the lipid levels of *Diporeia*.

Lipid research on freshwater benthic macroinvertebrates has been focused primarily on organisms from temperate to Arctic regions. Little or no information is available for benthic invertebrates in subtropical and tropical lakes. Following results from tropical zooplankton (Lee and Hirota, 1973), lipid energy reserves may not be as important to subtropical/tropical as for temperate and Arctic benthic organisms because the former may have a more continuous food supply. However, it is possible that lipid variation may still occur for reasons other than climatic temperature variation (e.g., high- and low-precipitation periods). It would be interesting to document and compare lipid dynamics in invertebrates from temperate/Arctic regions to those from subtropical/tropical regions. In addition, FA profiles may be interesting to compare in benthic organisms from these two contrasting environments. For instance, to improve membrane fluidity, the degree of unsaturation of membrane FAs appears to be inversely related to temperature (Sargent, 1976). For this reason, FA unsaturation may be less in membrane lipids of benthic species from subtropical/tropical than in those from temperate/Arctic

environments

6.4. Conclusions

The benthic or epibenthic macroinvertebrate species that thrive in cold environments (e.g., slope and profundal zones in the Great Lakes) tend to have higher maximum lipid levels than the benthic invertebrate species that reside in habitats with seasonal changes in water temperatures (e.g., shelf and nearshore zones of lakes) (Fig. 6.7). The high lipid levels may not be from living in cold temperatures per se but from the seasonal variability in food inputs that usually occur in constantly cold environments. For example, *Diporeia* and *Mysis relicta* had the highest maximum lipid levels (>40% of dry mass) of the benthic invertebrates described, and they both reach their highest densities at >30 m or below the thermocline. Food quantity and quality vary seasonally in large temperate lakes, and these seasonal differences are amplified in the hypolimnion. Accumulating lipid reserves is a way for *Diporeia* and *Mysis* to store energy for a period when food is not available and also to support reproduction. Because both *Diporeia* and *Mysis* brood their eggs for many months and release live young, they may have higher reproductive success by transferring more lipid to their young. In addition, both *Diporeia* and *Mysis* have the ability to vary their life cycle length; this appears to be an adaptation to living where food is variable.

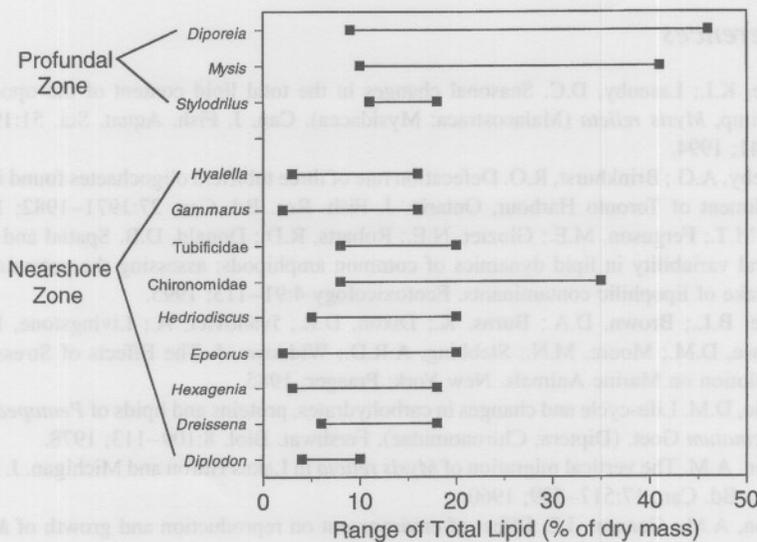


FIGURE 6.7. Summary of freshwater macroinvertebrates ranges of total lipid (% of dry mass). The macroinvertebrates are from the profundal zone (i.e., below the thermocline of deep lakes) and nearshore zones that include the shelf of large lakes and the littoral zone of lakes, ponds, rivers, and streams.

Benthic or epibenthic macroinvertebrate species that generally reside in near-shore zones do not usually accumulate as much reserve lipid or have as great of variation in lipid levels as the macrobenthic invertebrate species that reside in the profundal zone (Fig. 6.7). Usually, nearshore areas are more productive and may provide a more constant food supply to the benthic community. In addition, a reduction in metabolic rate during the "cold" season may conserve energy during this time of the year. Lipid levels often do increase seasonally but do not normally reach the maximum lipid levels found in *Diporeia* and *Mysis* (Fig. 6.7). The increase in lipid levels in chironomids and zebra mussels appears to be related to spring phytoplankton input, and the lipids are then allocated for reproduction. Lipid levels also increased in the amphipods *Hyaella azteca* and *Gammarus lacustris* and in aquatic insect larvae prior to reproduction. The Tubificidae and *Stylodrilus heringianus* differ due to their lack of seasonal variation in lipid reserves. The oligochaete mode of feeding apparently provides them with a relatively constant supply of subsurface bacteria and detritus throughout the year in either nearshore or profundal zones.

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