Chapter 11
Lipids in Marine Copepods: Latitudinal Characteristics and Perspective to Global Warming

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11.1   Introduction

Marine zooplankton represent a very diverse group in the world's oceans, with numerous taxa of high abundance and biomass. Many of these zooplankton species, especially the dominating copepods, are able to accumulate large reserves of energy-rich lipids, exhibiting some of the highest lipid levels in organisms on earth. Their unusual way to store these lipids, namely as wax esters, is another particularity of many zooplankton species. It is generally accepted that wax esters serve as long-term metabolic reserves, whereas triacylglycerols are utilized for short-term demands, although the physiological advantage of wax esters as long-term deposits over triacylglycerols is still unclear. The geographical distribution of wax esters in marine zooplankton was first studied in detail by Lee and co-authors in the 1970s (Lee et al. 1971; Lee and Hirota 1973). They showed that especially herbivorous calanoid copepods from habitats with a marked seasonality intensely synthesize wax esters, which in many herbivorous species consist, to a large degree, of specific long-chain monounsaturated fatty acids (MUFA) and alcohols (reviewed by Sargent and Henderson 1986; Dalsgaard et al. 2003; Lee et al. 2006).

In the transfer of energy through the food web, zooplankton species, especially copepods, play an important role as converters of usually rather lipid-poor phytoplankton (10–20% of dry mass DM) to lipid-rich herbivorous species (>50% DM). Copepods develop from eggs via six nauplii stages (NI-NVI) and five copepodite stages to adult males or females (CI-CVI). Although the earlier developmental stages invest energy into somatic growth, the older copepodids (CIV-CVI) exhibit a massive lipid build-up. This lipid accumulation is usually accomplished via wax ester biosynthesis, at least in most of the larger calanoid species.

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These enormous amounts of lipids fuel major pathways of marine food webs, at the same time essential fatty acids are transferred from primary producers via zooplankton to higher trophic levels.

Fatty acids of dietary origin can be incorporated unchanged into copepod lipids. These so-called fatty acid trophic markers (FATM; Dalsgaard et al. 2003) are useful in the elucidation of dietary relationships. However, differentiation is only possible between larger groups of phytoplankton, e.g., diatoms or dinoflagellates, but not at the species level. Typical fatty acids of diatoms are 16:1n-7 and 20:5n-3 (e.g., Ackman et al. 1968; Kattner et al. 1983). Flagellates and also the haptophyte *Phaeocystis* spp. contain large amounts of 18:4n-3 and 22:6n-3 fatty acids (Harrington et al. 1970; Sargent et al. 1985). The 16:1n-7 and 18:4n-3 fatty acids are mainly incorporated into storage lipids and indicate dietary preferences and thus feeding behavior of the copepods (Graeve et al. 1994a; Dalsgaard et al. 2003). The essential fatty acids, 20:5n-3 (eicosapentaenoic acid, EPA) and 22:6n-3 (docosahexaenoic acid, DHA), are major components of membranes and are also necessary as precursors to bioactive compounds, e.g., eicosanoids. It is still under debate whether copepods are able to produce polyunsaturated fatty acids by de novo synthesis or by chain elongation and desaturation of dietary fatty acids. The ability for these biosynthetic steps seems to exist in copepods, but the de novo biosynthesis route appears not to be utilized due to sufficient amounts of polyunsaturated fatty acids in the diet.

Zooplankton species have developed specific adaptations to cope with the different oceanic regimes that exist between the tropics and higher latitudes. In the tropics, the high continuous turnover of carbon at high temperatures and thus high metabolic rates but generally low primary productivity results in usually lipid-poor zooplankton living in the epipelagic waters (Lee and Hirota 1973). In contrast, polar ocean zooplankton, mainly calanoid copepods and krill, seasonally accumulate enormous lipid deposits, which signifies a major specialization in polar bio-production (Kattner and Hagen 1995). The very effective lipid storage via wax esters is primarily related to a herbivorous life strategy and is not an adaptation to high latitude environments per se. Seasonality in food supply is an important factor determining the life-history traits of these copepods. In temperate and high latitudes, coastal, and in upwelling regions, where pulsed phytoplankton production (blooms) is most common, typical wax-ester storing copepods of the genus *Calanus* and *Calanoides* prevail and play a key role in the short and efficient energy flux to higher trophic levels associated with a high productivity (Hagen and Auel 2001; Lee et al. 2006).

Lipids may also play an important role in buoyancy regulation because of its lower density than seawater. The motionless over-wintering of copepods in diapause at depth may be regulated by lipids (Visser and Jónasdóttir 1999), although small changes in the proportion of lipid classes may have a strong impact on buoyancy (Campbell and Dower 2003).

The large (2–10 mm), lipid-rich *Calanus* species have been studied in great detail, but few lipid studies exist on smaller-sized copepods. Lipid class and fatty acid compositions have been determined for small (ca. 1 mm) calanoid species from Kongsfjorden, Svalbard (Lischka and Hagen 2007), the northern Norwegian Balsfjorden (Norrbin et al. 1990), as well as from temperate regions (Kattner et al. 1981; Peters et al. 2006).

Even less is known about the so-called micro-copepods (<1 mm), the cyclopoids *Oithona* and *Oncaea* (Kattner et al. 2003; Lischka and Hagen 2005).

This review will focus on copepods from the Atlantic Ocean ranging from the tropics to the polar regions. Our knowledge of zooplankton lipids is clearly dominated by species from high latitudes, since lipid accumulation and storage is most pronounced in these extreme environments. The latitudinal comparison will give a general field-oriented overview about the significance and characteristics of copepod lipids in different climatic zones. The discussion about lipid transfer within the food web and some ideas concerning the potential impact of global warming on zooplankton complete this review.

## 11.2 Lipid Patterns of Copepods from Different Latitudinal Regions

Copepod lipids of the world's ocean exhibit various special characteristics. In spite of substantial diversity, there are clear trends in distributional patterns of lipid composition, which are highlighted for the various biomes along a latitudinal gradient.

11.2.1 *High-Latitude Copepods*

Polar ocean ecosystems are typically characterized by a strong seasonality in light regime and ice cover. Light as a limiting factor allows primary production only during the short summer season, when the pack-ice recedes, and intense phytoplankton blooms develop at the marginal ice zones (Sakshaug 1997; Falk-Petersen et al. 2000; Smetacek and Nicol 2005). Although polar oceans have a rather low overall annual primary production of <20 g C m^{-2} year^{-1}, these blooms nourish food webs containing lipid-rich species from zooplankton to fish, seals, and whales. Typically, polar oceans are known for their short food chains from diatoms via zooplankton to higher trophic levels. The short pulses of intense primary production are sufficient to convert algae biomass into enormous amounts of lipids (50–65% of dry mass) by herbivorous copepods (Fig. 11.1). Lipids represent the most efficient energy stores, because they contain about double the calorific density of proteins or carbohydrates, thus providing a compact source of energy-rich food for higher trophic level organisms.

11.2.1.1 Herbivorous Copepods

The life cycle of the herbivorous Arctic copepods is characterized by massive lipid accumulation during the productive season, followed by a descent of older developmental stages to deeper waters, where they survive the food-limited winter period in diapause and reascend in spring (Smith and Schnack-Schiel 1990; Conover and Huntley 1991; Hirche 1996). In the Arctic, the large calanoid copepod *Calanus*
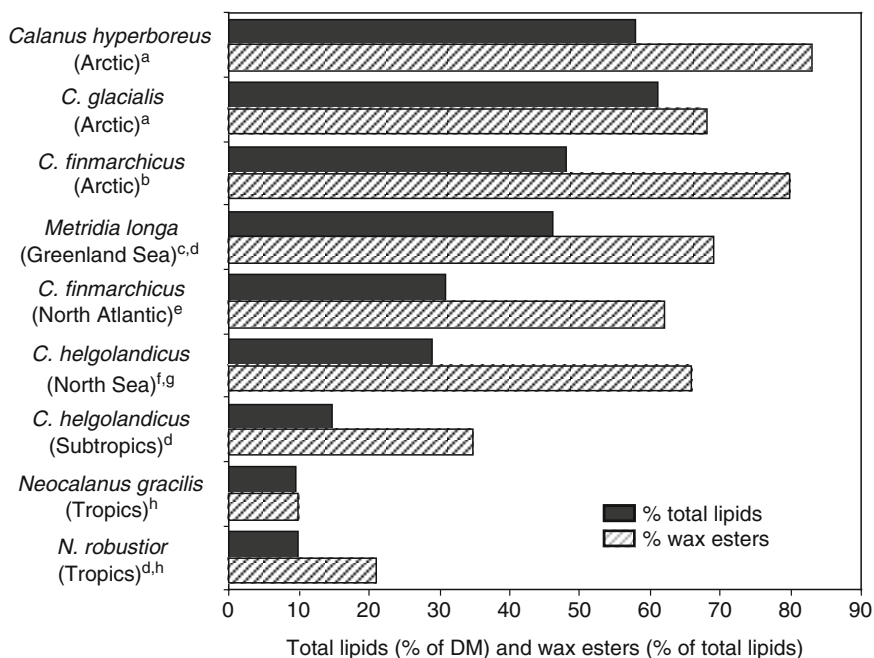
Fig. 11.1 General trends of total lipid content (% of dry mass) and wax esters (% of total lipids) of large copepod species (CV to females) from the Arctic to the tropics. Data compiled from [a]Lee et al. (2006), [b]Hagen (unpublished data), [c]Lee (1975), [d]Lee et al. (1971), [e]Jónasdóttir (1999), [f]Gatten et al. (1979), [g]Kattner and Krause (1989), [h]Kattner (unpublished data)

hyperboreus is a dominant zooplankton species, which represents a prime example of pronounced ontogenetic and seasonal lipid accumulation (Lee 1974; Kattner et al. 1989; Scott et al. 2002). The other herbivorous Arctic species, *C. glacialis*, also accumulates large amounts of lipids. The boreal North Atlantic species, *C. finmarchicus*, which is transported far to the north by Atlantic currents, occurs also in the pack-ice regions of the Greenland Sea (Hirche 1989), and it is present as an expatriate even in the central Arctic Ocean (Mumm 1993). Lipid storage in *C. finmarchicus* is only slightly less pronounced than in the more polar congeners (Fig. 11.1).

These northern *Calanus* species exhibit quite different degrees of independence from primary production to start reproduction. In contrast to *C. glacialis* and *C. finmarchicus*, *C. hyperboreus* relies on its lipids to fuel maturation and egg production independent of the phytoplankton bloom (Conover and Sifferd 1993). The calanoid *C. hyperboreus* reproduces in winter and early spring before the onset of the spring phytoplankton bloom and utilizes lipids accumulated during the previous spring/summer feeding period. Lipid levels of *C. hyperboreus* may decrease from 50 to 15% during reproduction (Hagen unpublished data). In contrast, species such as *C. finmarchicus* usually rely on phytoplankton for successful reproduction (Lee et al. 2006 and references therein), although early in the season initial reproductive processes may also be possible prior to the phytoplankton bloom (Richardson et al. 1999; Mayor et al. 2006).

Total lipids of the calanoid copepods are composed of up to 90% wax esters, which have a very high energy content (Fig. 11.1) (reviewed by Kattner and Hagen 1995; Lee et al. 2006) and consist mainly of long-chain MUFA and fatty alcohols (20:1n-9, 22:1n-11), as well as of fatty acids of dietary origin (Tables 11.1 and 11.2). Up to 50% of the wax esters, biosynthesized de novo by *C. hyperboreus*, may exhibit chain lengths from 40 to 44 carbon atoms, which derive from the combination of 20:1 and 22:1 fatty acid or alcohol units (Kattner and Graeve 1991). C. hyperboreus wax esters reach a higher calorific content when compared with the depot lipids of the other dominant herbivorous species, *C. glacialis* and *C. finmarchicus* from the Arctic and *Calanoides acutus* from the Antarctic (Albers et al. 1996), which have wax esters with shorter chain lengths (34–42 carbon atoms) (Kattner and Graeve 1991). These long-chain monounsaturated fatty acids and alcohols are not present in phytoplankton. They are synthesized de novo only by these herbivorous copepods, which, therefore, exhibit a very characteristic lipid signature (Tables 11.1 and 11.2).

11.2.1.2   Omnivorous and Carnivorous Copepods

Comparable to the herbivorous *Calanus* species, two other highly abundant omnivorous copepod species, *Metridia longa* from the Arctic and *M. gerlachei* from the Antarctic, store lipids mainly as wax esters. However, instead of long-chain monounsaturated fatty acids and alcohols, their major wax ester alcohols are dominated by 14:0 and 16:0 (Table 11.2). This deviation from the typical pattern of herbivorous calanoids probably reflects the more opportunistic feeding behavior and deviating over-wintering strategy (with year-round activity instead of diapause) (Hopkins et al. 1984; Båmstedt and Tande 1988). *M. longa* specimens may reach high lipid and wax ester levels, although not as high as the *Calanus* and *Calanoides* species (Lee 1975; Falk-Petersen et al. 1987; Albers et al. 1996). Fatty acid and alcohol composition are similar to other omnivorous and carnivorous species dominated by shorter-chain fatty acids and alcohols with 14–18 carbon atoms, but usually low percentages of long-chain wax ester moieties (Table 11.1). However, the lipid compositions of *M. longa* are quite variable, and specimens collected during summer contained substantial amounts of, probably dietary, monounsaturated alcohols with 20 and 22 carbon atoms (Table 11.2; Albers et al. 1996). *M. gerlachei* does not strongly rely on internal energy reserves, and the females accumulate only moderate lipid and wax ester levels with maximum lipid values later in the season (Graeve et al. 1994b; Schnack-Schiel and Hagen 1995).

The carnivorous species *Paraeuchaeta antarctica* accumulates large amounts of wax esters, almost exclusively composed of 14:0 and 16:0 alcohol moieties. Another characteristic often found in carnivorous species is the high proportion of the 18:1n-9 fatty acids, which can account for >50% of total fatty acids (Lee et al. 1974; Hagen et al. 1995).

Although wax ester storage is characteristic of most of the copepod species from higher latitudes, there are some exceptions, where triacylglycerols are the principal storage lipid. Copepod species such as *Calanus propinquus*, *C. simillimus*, and

Table 11.1 Large Atlantic copepod species from high to low latitudes. Compositions of major fatty acids and alcohols (mass% of total fatty acids or alcohols) of total lipids

	Calanus hyperboreus[a]	Calanus glacialis[a]	Calanoides acutus[b]	Calanus finmarchicus[a]	Metridia longa[c]	Calanus finmarchicus[d]	Calanus helgolandicus[e]	Neocalanus gracilis[c]	Neocalanus robustior[c]
Location	Arctic	Arctic	Antarctic	Arctic	Arctic	N. Atlantic	North Sea	Tropics	Tropics
Fatty acids									
14:0	3.7	9.8	3.6	16.9	4.1	8.2	11.1	3.3	4.0
16:0	4.3	6.9	3.2	12.7	6.8	15.5	12.5	20.1	22.8
16:1n-7	10.6	25.2	8.5	6.2	29.5	2.7	5.4	2.3	3.1
18:0	0.4	0.4	–	1.5	0.1	1.6	1.5	5.0	6.0
18:1n-9	3.2	3.7	5.0	5.3	29.3	4.6	4.9	7.7	7.9
18:1n-7	0.9	1.0	1.0	0.4	1.1	1.4	–	2.0	1.6
18:2n-6	1.7	0.9	1.7	1.8	2.0	4.3	1.0	1.7	2.5
18:3n-3	0.7	0.5	0.8	1.1	0.5	5.2	2.0	0.5	0.9
18:4n-3	10.3	3.2	9.1	9.5	1.6	12.8	3.4	1.1	1.4
20:1n-9	19.8	12.3	17.9	7.7	3.3	4.1	4.1	1.5	2.0
20:1n-7	1.9	1.0	0.9	1.0	–	–	–	0.5	0.3
20:5n-3	14.1	16.0	20.1	13.2	9.8	14.9	17.4	9.1	9.9
22:1n-11	15.0	7.1	9.1	8.0	1.4	5.0	7.7	6.9	4.6
22:1n-9	3.5	1.1	4.0	0.3	0.1	0.5	–	3.2	2.0
22:5n-3	1.0	0.6	1.4	0.3	–	0.4	–	2.1	1.7
22:6n-3	7.8	5.2	10.1	11.6	8.8	10.7	18.2	20.1	17.6
Alcohols									
14:0	2.8	3.2	7.5	1.7	54.2	2.0	2.5	n.d.	n.d.
16:0	6.1	11.2	8.4	9.6	20.6	16.7	17.0	n.d.	n.d.
16:1n-7	3.6	7.1	4.3	3.2	6.6	1.9	1.4	n.d.	n.d.
18:1n-9	0.4	–	1.6	1.7	–	3.0	1.7	n.d.	n.d.
18:1n-7	0.5	2.1	–	2.6	–	–	1.7	n.d.	n.d.
20:1n-9	32.6	43.4	49.5	36.6	10.6	30.9	27.1	n.d.	n.d.
22:1n-11	55.0	30.4	28.7	44.6	8.0	38.1	46.6	n.d.	n.d.

*n.d.* not determined; – not present or below 0.05%

Compiled from [a]Dalsgaard et al. (2003), [b]Hagen et al. (1993), [c]Kattner et al. (unpublished data), [d]Kattner (1989), [e]Kattner and Krause (1989)

Table 11.2 Fatty acid and alcohol compositions of wax esters and phospholipids, respectively, of Arctic copepod species (data from Albers et al. 1996)

	Wax esters				Phospholipids			
	Calanus hyperboreus	*Calanus glacialis*	*Calanus finmarchicus*	*Metridia longa*	*Calanus hyperboreus*	*Calanus glacialis*	*Calanus finmarchicus*	*Metridia longa*
Fatty acids								
14:0	6.4	13.1	26.3	0.7	4.0	5.2	3.3	2.3
16:0	5.8	6.1	9.8	1.5	25.5	25.8	25.8	20.7
16:1n-7	11.7	32.9	6.7	21.4	2.5	4.6	1.1	1.9
18:0	0.6	–	0.9	0.7	2.3	2.3	3.6	2.6
18:1n-9	5.8	5.5	5.3	30.3	5.1	6.4	2.5	5.3
18:1n-7	1.6	1.1	0.3	1.1	1.4	3.7	1.0	2.2
18:2n-6	3.6	1.0	1.2	2.5	1.8	2.0	1.5	1.4
18:3n-3	1.6	0.3	1.5	0.5	0.5	0.2	0.6	0.2
18:4n-3	6.2	0.5	13.7	1.4	0.8	–	2.5	0.3
20:1n-9	19.0	23.0	7.8	19.5	0.6	0.9	0.2	1.5
20:1n-7	1.5	1.0	0.9	–	–	–	–	–
20:5n-3	7.0	2.7	11.4	7.1	18.6	16.5	19.2	15.9
22:1n-11	17.3	8.3	7.0	9.4	1.2	–	0.2	–
22:1n-9	3.2	2.0	0.2	–	–	–	–	–
22:5n-3	0.5	–	0.2	–	–	–	0.2	–
22:6n-3	2.4	0.8	2.2	0.5	33.8	30.5	37.4	43.9
Alcohols								
14:0	4.4	2.1	3.9	46.1	–	–	–	–
16:0	11.2	9.3	14.6	17.7	–	–	–	–
16:1n-7	1.6	5.3	3.4	0.9	–	–	–	–
20:1n-9	27.8	58.4	39.3	15.5	–	–	–	–
22:1n-11	55.0	25.0	38.8	19.8	–	–	–	–

Euchirella rostromagna store large amounts of triacylglycerols (Hagen et al. 1993, 1995; Kattner et al. 1994; Ward et al. 1996). The primarily herbivorous Antarctic copepod, *C. propinquus*, exclusively stores triacylglycerols, which seems to be related to a more opportunistic feeding behavior and active overwintering without diapause (Hopkins and Torres 1989; Schnack-Schiel and Hagen 1995). This species has, however, developed a very effective fatty acid biosynthesis, which at least partially compensates for the lack of wax esters. This is achieved by producing long-chain MUFA comparable to wax ester-storing copepods, made even more effective by elongating the 20:1n-9 fatty acid to 22:1n-9 (Hagen et al. 1993). Usually, this 22:1 fatty acid isomer is either absent or only found in very small amounts in marine zooplankton organisms. The addition of two carbon atoms results in a higher calorific content and allows for more efficient lipid utilization, since every fatty acid has to be activated by one ATP for catabolism (β-oxidation), independent of its chain length.

Few lipid analyses exist of small and micro-copepods (Fig. 11.2, Table 11.3). Only lipids of the abundant Arctic cyclopoids *Oithona similis* and *Oncaea borealis* have been studied in detail (Kattner et al. 2003; Lischka and Hagen 2007). The latter species appears to be a genuine cold-water species and is suggested to be the only true Arctic *Oncaea* species (Sewell 1947; Richter 1994; Auel and Hagen 2002), while in the Antarctic, *Oithona similis, Oncaea curvata*, and *O. antarctica* dominate the copepod assemblages (Schnack et al. 1985; Hopkins and Torres 1989; Metz 1995).
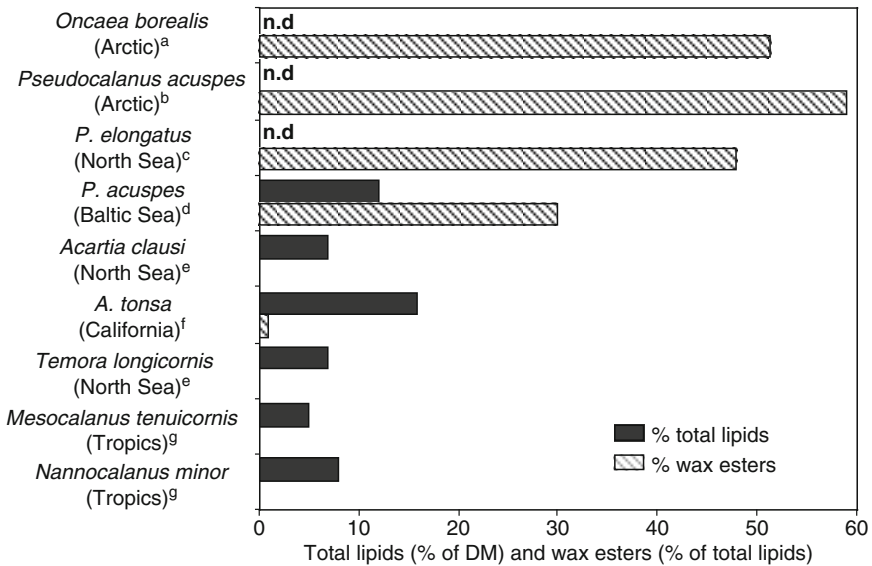
Fig. 11.2 General trends of total lipid content (% of dry mass) and wax esters (% of total lipid) of small copepod species (CV to females) from the Arctic to the tropics; no bar means no wax esters; *n.d.* not determined. Data compiled from [a]Kattner et al. (2003), [b]Norrbin et al. (1990), [c]Kattner and Krause (1989), [d]Peters et al. (2006), [e]Laakmann (2004), [f]Lee and Hirota (1973), [g]Kattner (unpublished data)

Table 11.3 Small Atlantic copepod species from high to low latitudes. Compositions of major fatty acids and alcohols (mass% of total fatty acids or alcohols) of total lipids

	Oncaea borealis[a]	Oithona similis[b]	Pseudocalanus minutus[b]	Pseudocalanus acuspes[c]	Acartia clausi[d]	Temora longicornis[d]	Mesocalanus tenuicornis[e]	Nannocalanus minor[e]
Location	Arctic	Arctic	Arctic	Baltic Sea	North Sea	North Sea	Tropics	Tropics
Fatty acids								
14:0	3.9	4.0	1.8	1.0	2.2	2.5	2.5	2.3
16:0	13.4	20.6	11.9	15.0	14.7	15.5	17.1	17.6
16:1n-7	5.0	8.1	14.4	2.4	1.5	3.3	1.3	1.3
18:0	3.0	5.4	0.7	2.5	4.7	3.1	8.5	8.5
18:1n-9	27.9	21.2	26.2	18.9	5.0	3.1	5.0	4.6
18:1n-7	3.4	2.9	2.6	2.0	1.4	2.9	1.2	1.2
18:2n-6	2.0	2.7	0.2	5.6	0.9	0.8	2.0	1.8
18:3n-3	0.8	–	–	3.3	1.1	0.9	0.5	0.4
18:4n-3	2.6	–	–	3.6	4.0	4.1	0.8	0.6
20:1n-9	10.0	–	–	–	0.9	1.2	0.4	0.4
20:1n-7	0.4	–	–	–	0.8	0.7	–	–
20:5n-3	13.9	16.7	24.1	15.2	17.9	22.4	11.8	12.1
22:1n-11	6.7	–	–	–	0.5	0.6	–	0.2
22:1n-9	1.7	–	–	–	0.5	0.8	–	0.1
22:5n-3	1.4	–	–	–	0.6	0.6	1.0	0.9
22:6n-3	13.3	16.9	12.4	22.0	38.4	30.9	37.7	39.3
Alcohols								
14:0	23.3	22.3	50.0	26.7	–	–	–	–
16:0	46.2	40.0	47.7	62.7	–	–	–	–
16:1n-7	0.9	–	–	–	–	–	–	–
18:0	–	8.2	0.4	5.1	–	–	–	–
18:1n-9	–	–	–	5.2	–	–	–	–
20:1n-9	15.7	25.8	–	0.5	–	–	–	–
22:1n-11	14.1	–	–	–	–	–	–	–

Compiled from [a]Kattner et al. (2003), [b]Lischka and Hagen (2007), [c]Peters et al. (2006), [d]Laakmann (2004), [e]Kattner et al. (unpublished data)

In addition, the lipid class and fatty acid compositions of *Pseudocalanus acuspes* and *Acartia longiremis* have been studied in Balsfjorden, northern Norway (Norrbin et al. 1990), and the seasonal lipid dynamics of *Pseudocalanus minutus* in the Arctic Kongsfjorden, Svalbard (Lischka and Hagen 2007).

The accumulation of considerable wax ester deposits (in % total lipids) in these smaller copepods (Fig. 11.2) is comparable to that of the larger polar species. Small copepods may use their lipid reserves during periods of food shortage in winter and for somatic growth, whereas reproductive processes are usually fuelled by the spring phytoplankton bloom, although in *Oithona similis* overwintering and gonad maturation seems to rely on internal lipid reserves (Lischka and Hagen 2007). Their lipids are not composed of long-chain fatty acids and alcohols typical of the larger species. The wax ester moieties are usually dominated by the shorter-chain alcohols 14:0 and 16:0, which is also indicative of opportunistic feeding (Table 11.3) (Graeve et al. 1994b). High percentages of the 18:1n-9 fatty acid during all seasons (Table 11.3) also point to a generally non-selective diet (Dalsgaard et al. 2003; Kattner et al. 2003; Lischka and Hagen 2007). This suggests that the small copepods are generally opportunistic feeders, as proposed by Paffenhöfer (1993), although their life cycles are related to the pronounced seasonality of food availability in polar regions (Metz 1995). It should be noted that higher proportions of long-chain monounsaturated fatty acids/alcohols in some species probably also reflect carnivory on other zooplankton organisms, including early stages of calanoid copepods.

11.2.2 Mid-Latitude Copepods

From polar to temperate regions, there is a gradual transition in the lipid characteristics among copepod species, which inhabit both areas (Fig. 11.1). This holds true for several smaller species as well as for *Calanus finmarchicus*, a species, in which these differences also depend on water mass distribution (Heath et al. 2004). In temperate regions, phytoplankton production is not as limited as in the Arctic due to the less seasonal light regime, which, together with the elevated temperatures, supports life-cycle strategies of herbivorous copepods characterized by shorter generation times. Primary production cycles in the temperate North Atlantic, for example, are governed mostly by nutrient supply and classically exhibit a spring bloom dominated by diatoms. Thereafter, a phytoplankton community exists at lower levels throughout the summer and in autumn a second smaller bloom may occur due to vertical mixing of the nutrient-depleted surface waters with nutrient-rich deeper waters.

11.2.2.1 Large Copepods

Similar to the Arctic Ocean, phytoplankton blooms are utilized by the larger copepods from temperate regions, such as *Calanus finmarchicus*, *C. helgolandicus*, *C. pacificus*, and *Neocalanus* spp., to accumulate lipids, although total lipid levels

are lower than in the polar species (Fig. 11.1). These boreal copepods also exhibit a life cycle with seasonal vertical migration, diapause, and deposition of mainly wax esters in an oil sac. Although not quite reaching the levels of polar species, wax ester values of temperate copepods are also high (mean of 65% of total lipids). During their ontogenetic development from copepodite stage CI to adult stage (*C. finmarchicus* s.l.), wax ester levels increased from a minimum of 20 to 87% of total lipids (Kattner and Krause 1987). Off California, CIII to adult specimens of *C. pacificus* showed wax ester accumulation from 1 to 50%, whereas younger stages had no wax esters (Lee et al. 1972). The later copepodite stages of *C. helgolandicus* may range seasonally between 23 and 90% wax esters of total lipids with means ranging from ~66% (Kattner and Krause 1989) to 80% (Gatten et al. 1979). Wax esters of these temperate species, although more variable, closely resemble those of polar copepods with high percentages of long-chain monounsaturated fatty acids and alcohols (Table 11.1). Since dietary fatty acids change seasonally with the availability of phytoplankton species, the fatty acid and alcohol patterns seem to be more dependent on phytoplankton peak events than on temperature regimes and latitude.

Comparing specimens of *C. finmarchicus* from high latitude and temperate regions, Kattner (1989) found that *C. finmarchicus* from temperate seas exhibited a significantly smaller size and dry mass. Specimens from warmer regions are often smaller and have more generation cycles than their congeners in cold regions (Mauchline 1998). In addition, the percentage of long-chain monounsaturated alcohols was lower in temperate specimens (Table 11.1). The de novo synthesis of these energy-rich lipids seems to be less pronounced in the temperate species, probably due to a more reliable year-round food availability. The portion of wax esters synthesized also tended to be slightly smaller than in the Arctic congeners (Fig. 11.1).

When compared with the North Atlantic, production cycles are different in the subarctic Pacific, and phytoplankton blooms do not develop in spring and autumn. Micrograzers, e.g., heterotrophic microflagellates and ciliates, seem to control the developing algal biomass, whereas the assumed top-down control by "major grazers," the dominant copepods of the genus *Neocalanus*, *Eucalanus*, and *Metridia*, could not be verified due to insufficient grazing rates (Miller 1993).

Copepods of the genus *Neocalanus* exhibit an interesting life-cycle strategy: they go into diapause in summer/fall and produce lipid-rich eggs fuelled by internal energy reserves, which are spawned at depth during winter. There is another interesting but not yet understood difference between the Atlantic/Arctic *Calanus* species and the Pacific calanoid copepods *Neocalanus cristatus* and *N. flemingeri*, which synthesize mainly 20:1n-11 wax ester moieties (Saito and Kotani 2000) rather than 20:1n-9.

The Pacific copepod *Metridia okhotensis* stores wax esters comparable in amount and composition with its Atlantic counterpart *M. longa*. Other Pacific copepod species, e.g., *Eucalanus bungi* and *Euchirella* spp., store primarily triacylglycerols (Lee et al. 1971; Saito and Kotani 2000), as do the high-latitude species *Calanus propinquus*, *C. simillimus*, and *Euchirella rostromagna* (Hagen et al. 1993, 1995; Ward et al. 1996).

11.2.2.2 Small Copepods

The herbivorous Atlantic copepod *Pseudocalanus elongatus* occupies an intermediate position between the large herbivorous northern and the small omnivorous copepods of the temperate regions. The lipid composition of *P. elongatus* is similar to the Arctic and northern North Atlantic species due to its wax ester storage (~50% of total lipids; Fig. 11.2). These wax esters are also primarily composed of the short-chain alcohol moieties 14:0 and 16:0 (Table 11.3) (Fraser et al. 1989; Kattner and Krause 1989). During a seasonal study in the Baltic Sea, Peters et al. (2006) found similar results for *P. acuspes* with wax ester levels between 17 and 44% and triacylglycerol levels between 15 and 35% of total lipids. Fatty alcohols were also clearly dominated by 14:0 and 16:0 and fatty acids by 18:1n-9. The feeding behavior for *P. acuspes* is suggested to be opportunistic, and important food items are ciliates and cyanobacteria, in addition to diatoms and flagellates. In contrast to the primarily herbivorous *Calanus* species, the smaller calanoid species of the genus *Acartia (longiremis, tonsa), Temora (longicornis)*, and *Centropages (typicus)* favor life strategies which include opportunistic feeding behavior, high metabolic rates, a limited lipid accumulation and in some cases (e.g., *Acartia*) resting eggs as survival mechanisms (e.g., Peters et al. 2007). Therefore, reproductive effort is directly dependent on food availability and is not buffered by lipid reserves. The lipid compositions of these species are usually characterized by high phospholipid and low neutral lipid levels (little triacylglycerols, no wax esters; Fig. 11.2). Accordingly, fatty alcohols are missing and principal fatty acids include 20:5n-3, 22:6n-3, and 16:0 typical of biomembranes (Table 11.3). Very little is known about the fatty acid composition of the neutral lipid fraction due to the minute amounts available. Few fatty acid compositions have been determined of separate lipid classes of small species: *Temora longicornis* from the North Sea (Fraser et al. 1989), *P. acuspes*, *T. longicornis*, and *A. longiremis* from the Baltic Sea (Peters et al. 2006, 2007). Dietary fatty acids such as 16:1n-7 and 18:4n-3 are found to be quite abundant in the neutral lipid fraction. We assume that the lipid biochemistry of these smaller copepods is less important for survival and reproduction and is less dependent on bloom events when compared with the large *Calanus* species.

11.2.3 Low-Latitude Copepods

In one of the first latitudinal comparisons Lee and co-authors described the minor importance of lipids and wax esters in some copepod species, e.g., *Neocalanus gracilis, N. robustior, Euchaeta marina*, from the upper 250 m of tropical waters. Many species lack wax esters, some have minor to moderate amounts of wax esters (range: trace to 40% of total lipids, median: trace) and most species have moderate amounts of triacylglycerol (range: 3–18.5%, median 6%). In deeper layers (below 500 m), however, lipids and wax esters were increasingly accumulated (wax ester range: 11–72%, median 63%) (Lee and Hirota 1973).

In the oligotrophic, epipelagic tropical oceans lipid deposits are not a key component in the life strategies of copepods (Figs. 11.1 and 11.2) and correspondingly,

the lipid data-base is rather limited. In these latitudes, evolutionary pressure has selected against a sophisticated lipid biochemistry and favored opportunistic feeding. Typical life strategies include continuous feeding and rapid utilization of available food items for growth and reproduction, which results in a high turnover with short generation times.

Our lipid data of typical epipelagic tropical and subtropical copepod species from the East Atlantic with different ecological niches and feeding behavior support the general patterns of low lipid contents and little storage lipids (Figs. 11.1 and 11.2). These species include herbivorous and omnivorous species of the genus *Neocalanus*, *Mesocalanus*, *Nannocalanus*, and *Clausocalanus*, which are all widespread in tropical and subtropical waters and well adapted to oligotrophic conditions (Bradford-Grieve et al. 1999). Their lipids are essentially composed of phospholipids, except for the larger *Neocalanus* species, which have small amounts of wax esters (~10% of total lipids). The lipid compositions are clearly dominated by the fatty acids 16:0, 22:6n-3, and 20:5n-3 typical of membrane phospholipids. Additional fatty acids include 18:0 and 18:1n-9 (Tables 11.1 and 11.3).

Similar results were reported for *Clausocalanus farrani*, *C. furcatus*, and *Ctenocalanus vanus* from the subtropical Gulf of Aqaba (Red Sea), which showed low wax ester levels. Wax ester moieties consisted of shorter-chain alcohols (14:0, 16:0, 18:0), and fatty acid compositions were similar to those described above (Cornils et al. 2007).

11.2.4   Upwelling-System Copepods

The limited lipid accumulation of low-latitude epipelagic copepods is in stark contrast to copepod species living in major coastal upwelling areas, as well as deeper-living species (>500-m depth) found in tropical and subtropical waters (Lee et al. 1971, 2006). The high-productivity regions periodically or seasonally generate strong pulses of primary production, usually diatom blooms, which typically support short food chains with calanoid copepods and clupeiform fishes (e.g., anchovies, sardines) as major components. This periodicity is comparable to the seasonal food supply at temperate and high latitudes and thus creates a similar strategy of lipid accumulation. The same might be true for deeper-living species outside of the upwelling zones, which feed infrequently during occasionally occurring sedimentation events, but generally experience low prey densities.

Major coastal upwelling regions include the California and Humboldt Current systems in the East Pacific, the Canary and Benguela Current systems in the East Atlantic and the monsoon-driven Somali Current system in the Indian Ocean. These areas are dominated by calanoid copepods, e.g., *Calanus marshallae*, *C. pacificus*, *C. chilensis*, and *Calanoides carinatus* (Mauchline 1998; Petersen 1998; Lee et al. 2006). The latter species, the herbivorous *C. carinatus*, is a key component of the Atlantic and Indian Ocean upwelling systems including the Benguela region, where it exhibits typical life-history traits of *Calanus* and *Calanoides* species from high latitudes. Major features include intense feeding on phytoplankton in productive

surface waters, use of surplus energy for rapid biosynthesis of wax esters with long-chain monounsaturated fatty acids and alcohols and accumulation of these lipid deposits in oil sacs, as well as vertical migration to deeper layers >500 m and diapause at depth to survive periods of food paucity (Petersen 1998; Verheye et al. 2005).

11.3   Essential Fatty Acids and Phospholipid Structure

Essential fatty acids, transferred and exchanged within the food web, are crucial components not only in marine life but also for human nutrition (e.g., Arts et al. 2001, and see Chap. 14). The term essential means that animals are unable to synthesize these specific fatty acids, or that these fatty acids are produced in insufficient amounts by animals. There is still an ongoing discussion about the biosynthesis and amount of essential fatty acids produced by zooplankton and animals in general (see Chap. 13) and those from precursor fatty acids ingested with the diet.

In the marine environment, the omega-3 fatty acids, EPA and DHA, are generally thought to be essential fatty acids. Phytoplankton is the primary source of these fatty acids in the oceans. However, phytoplankton groups have clearly different fatty acid compositions. Diatoms, for example, are rich in EPA and dinoflagellates are rich in DHA. Hence, spring blooms will offer high amounts of EPA, whereas later in the year during the summer season with a lower standing stock of phytoplankton, higher proportions of DHA are available for secondary production. To satisfy their physiological demands for essential fatty acids, herbivorous copepods, which play a pivotal role in the initial transfer of essential fatty acids along the food web, need to feed on a variety of phytoplankton species throughout the year.

In copepods, but also in marine animals in general, EPA and DHA represent the dominant fatty acids in phospholipids, which are the principal membrane constituents and thus a major source of essential fatty acids for higher trophic levels. Together with the saturated 16:0 fatty acid, they can comprise up to 80% of total phospholipid fatty acids. Membrane fatty acids reflect structural requirements and vary only somewhat with dietary changes. Copepods have a quite uniform composition of phospholipid fatty acids (Table 11.2, Fig. 11.3), and variations mostly occur within the proportions of the three major fatty acids.

In general, phospholipid molecules are composed of a saturated or monounsaturated fatty acid at the first carbon atom of the glycerol backbone (position *sn-1*) and a polyunsaturated fatty acid at the second carbon atom (position *sn-2*). This asymmetric fatty acid distribution is thought to be of major importance in the functional and structural roles of biomembranes (see Chap. 10). In many copepod species, there is, however, a surplus of polyunsaturated fatty acids in the phospholipids, which means that a polyunsaturated fatty acid is also located in *sn-1* position. The major phospholipid class in *Calanus hyperboreus* and *C. finmarchicus* is phosphatidylcholine (PC) followed by phosphatidylethanolamine (PE). The fatty acid composition differs in that PC is composed of equal amounts of EPA and DHA (both ~35%), whereas in PE half of the fatty acids are composed of DHA with smaller contributions of EPA
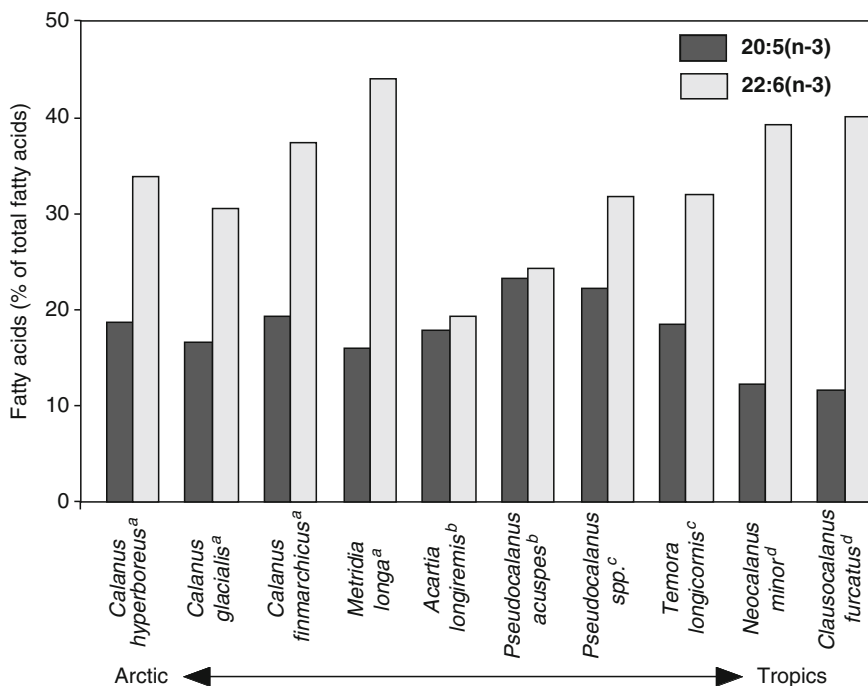
Fig. 11.3 Distribution of the polyunsaturated fatty acids 20:5n-3 and 22:6n-3 in phospholipids of copepods from high to low latitudes. Data compiled from [a]Albers et al. (1996), [b]Norrbin et al. (1990), [c]Fraser et al. (1989), [d]Kattner data of total lipids, mainly composed of phospholipids (unpublished)

(~10%; Table 11.4). Thus, the distribution of fatty acids in PE follows the general pattern of phospholipids, however, with mainly DHA in the *sn-2* position. In PC, a high proportion of EPA is also located in *sn-1* position (Fig. 11.4). Little is known about the advantages and reasons for this remarkable phospholipid pattern. The ratio of PE to PC reflects compensatory mechanisms that allow maintenance of physical–chemical membrane properties with changing temperatures (Shinitzky 1984).

Increasing amounts of polyunsaturated fatty acids in phospholipids are reported to be important in regulating membrane fluidity at cold temperatures (e.g., Farkas 1979; Hall et al. 2002). This regulatory mechanism is still under discussion, and it should be taken into account that the phase transition temperature of highly unsaturated phospholipids is not markedly lower than that of phospholipids composed of fatty acids with fewer double bonds (reviewed by Stillwell and Wassall 2003). The high proportions of EPA and DHA in tropical zooplankton phospholipids (Fig. 11.3) further challenge the reasoning with regard to membrane fluidity. There are still many open functional questions, which need to be studied in the context of biomembrane structure and function.

In addition, the dominant polar euphausiids accumulate PC simultaneously with increasing lipid levels (Hagen et al. 1996). Most of these phospholipids were found

Table 11.4 Fatty acid composition of phosphatidylcholine (PC) and phosphatidylethanolamine (PE) of *Calanus hyperboreus* and *C. finmarchicus* (Kattner and Farkas, unpublished data)

Phospholipid	*Calanus hyperboreus*		*Calanus finmarchicus*	
	PC	PE	PC	PE
Fatty acids				
14:0	3.6	1.1	2.7	0.6
16:0	12.4	23.2	10.8	24.7
16:1n-7	3.6	0.6	0.7	0.2
18:0	0.5	0.8	0.8	2.4
18:1n-9	2.5	2.7	1.5	0.4
18:1n-7	0.5	0.7	1.7	0.7
18:2n-6	1.0	0.3	1.1	0.1
18:3n-3	0.8	0.4	1.1	0.3
18:4n-3	2.4	0.8	3.0	0.6
20:4n-6	0.7	–	1.4	0.2
20:5n-3	36.5	12.1	35.3	8.0
22:5n-3	0.4	0.2	0.6	0.6
22:6n-3	32.6	54.7	37.6	57.3
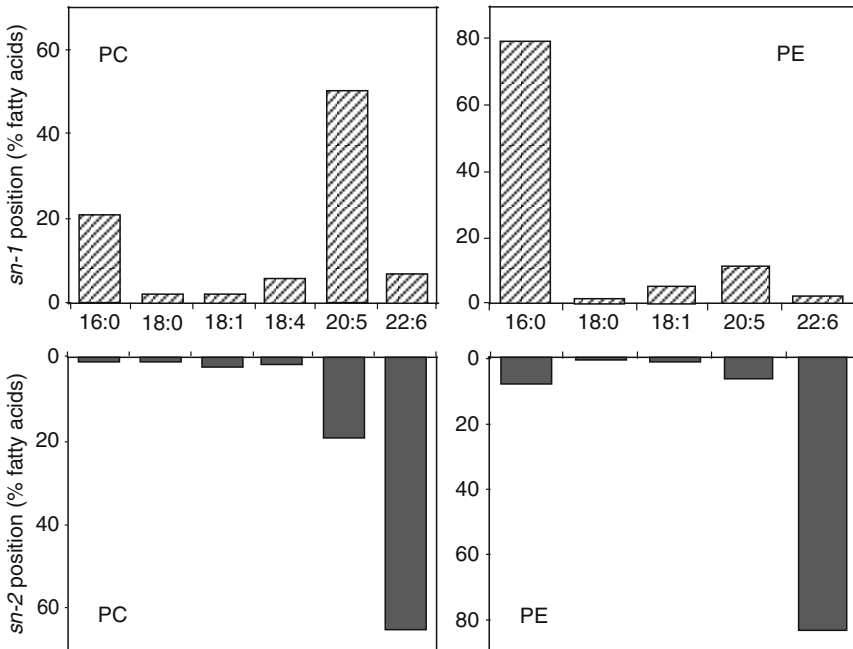
Fig. 11.4 Position-specific distribution of fatty acids of phosphatidylcholine (PC) and phosphatidylethanolamine (PE) of *Calanus finmarchicus*. The fatty acid distribution of *C. hyperboreus* phospholipids is similar (Kattner and Farkas, unpublished data)

in the free form in tissue surrounding the hepatopancreas, i.e., not incorporated into membranes (Stübing 2004). These lipids are an additional source of essential fatty acids because their high percentages of EPA and DHA are comparable to those of membrane lipids (Hagen et al. 2001).

The neutral lipids, wax esters and triacylglycerols, contain clearly lower percentages of EPA and DHA. EPA is usually more abundant, but comprises mostly <10%, whereas DHA occurs in even lower percentages (Table 11.2; Albers et al. 1996; Scott et al. 2002). Owing to the huge amounts of wax esters in high-latitude copepods, neutral lipids do improve the overall food quality (total essential fatty acid content) of copepods for higher trophic level organisms.

11.4 Impact of Global Warming on Lipid Dynamics

Polar oceans are characterized by an enormous lipid accumulation in major components of the pelagic food web with an intensive and fine-tuned energy transfer from copepods via fish to seabirds and marine mammals. This lipid-based energy flux in high-latitude ecosystems may be easily disturbed, since Polar Regions are especially sensitive to global changes (Flato et al. 2000). Recent investigations and modeling have shown that the Arctic ice cover is already strongly reduced in size and thickness (e.g., Serreze et al. 2007). The Fourth Assessment Report "Climate Change 2007" of the IPCC has unequivocally declared that global warming will likely continue in the near future, unless dramatic political measures are taken.

If we expect a poleward shift of ecosystem boundaries, i.e. tropical species expanding toward temperate regions and temperate species in turn moving to higher latitudes, then the dominance of lipid-rich species at high latitudes will probably decrease. This could have a tremendous impact on the food quantity and energy flux to higher trophic levels in polar oceans. In contrast, food quality will probably be less affected concerning essential fatty acids, since temperate and tropical species are also rich in these components. In the north, there might be competition between the three dominant *Calanus* species, as *C. finmarchicus* will probably shift toward the Arctic Ocean shelf areas competing with *C. hyperboreus* and *C. glacialis* during spring phytoplankton blooms (Gradinger 1995), which might then be more comparable to blooms in temperate regions. In some Arctic regions, these spring blooms might become less pronounced, since nutrient concentrations are currently low in Siberian shelf waters, and the nutrient input from the large Russian rivers is relatively small (Dittmar and Kattner 2003). However, the discharge of nutrients might also change due to melting of the huge permafrost areas (Wu et al. 2005). If nutrient supply by riverine discharge increases, phytoplankton blooms associated with river plumes may become more important in the Arctic Ocean than marginal ice zone blooms, and the whole ecosystem will change to a more temperate system. These shelf blooms may increasingly replace marginal ice zone blooms and, consequently, ice algae production will decline, a resource crucial to many herbivorous copepods.

The reduction in ice cover will have a general effect on the food supply of dominant zooplankton species in polar regions. At the underside of the ice, epontic phytoplankton communities adapted to very low light intensities grow early in the season, and various animals feed on these algae such as Antarctic krill and Arctic amphipods. Some zooplankton species, e.g., *Calanus glacialis* and *Pseudocalanus* spp., are known to migrate into the ice for feeding (Runge et al. 1991).

The light regime will still be a limiting factor at high latitudes, but an earlier break-up and later freezing or even disappearance of the sea-ice may prolong the productive season. It has been postulated that herbivorous copepods are affected primarily by changes in phytoplankton species composition and abundance, not so much by temperature shifts per se (Hirche 1987; Richardson and Schoeman 2004). These changes may have a strong impact on the timing of bloom events, which are again intertwined with the reproduction cycles of, for example, the *Calanus* species in the Arctic, which may no longer match with primary production cycles (Hansen et al. 2003). These modifications may in turn favor smaller and more flexible zooplankton taxa known from temperate waters such as copepods of the genus *Metridia*, *Temora*, and *Acartia*. It is difficult to predict the influence on the overall lipid flux within the food web, because this is dependent on the abundance of these species. Such a change in zooplankton species composition will obviously change the energetic value of the lipids because of the reduction of species with large amounts of lipids rich in long-chain wax ester moieties. The occurrence of essential fatty acids, such as EPA and DHA, is probably less impacted by global changes, since they are structural components of all marine bio-membranes, largely independent of latitudinal distribution. The amount of these essential lipids, however, is again dependent on zooplankton biomass, but the balance of food quality and food quantity is difficult to predict.

If global warming leads to the disappearance of key biomass species especially adapted to polar ice-covered regions, thus diminishing the present lipid-based energy flux (Falk-Petersen et al. 2007), this may induce a regime shift from a higher to lower-level energy system with cascading effects up the food web that will eventually threaten the entire intricately balanced system, in which lipids play a central role. Hence, biodiversity and energy flux of polar systems could be severely influenced by these changes.

The impact of global warming on the Southern Ocean ecosystem will be quite different, because the system is less pulsed when compared with the Arctic Ocean, due to differences in the light regime, iron-limitation of phytoplankton growth, and a more pronounced seasonal sea-ice cover, which is reduced to ~20% during summer. In contrast to the Arctic, the Southern Ocean is a krill-dominated region, and the life strategies of this key group are intensely linked to the seasonality of the ice regime. Hundred million tons of krill biomass strongly rely on the seasonal development of ice algae and exhibit a pronounced seasonal lipid accumulation, mainly triacylglycerols, and PUFA-rich phospholipids (Hagen et al. 2001). In the past, colder winters have been associated with stronger year classes of krill in the following year, indicating that the survival of the Antarctic krill, *Euphausia superba*, is strongly dependent on ice cover, which allows successful over-wintering of the

larvae (Loeb et al. 1997; Siegel 2005). In contrast, warmer winters in the Antarctic with a less pronounced ice coverage are advantageous for salp stocks (*Salpa thompsoni*), which extend their distribution centers southward under favorable conditions. Of course, such a regime shift from lipid-rich krill to low-calorie gelatinous salps will lead to severe perturbations at higher trophic levels and a dramatic change in food availability for e.g., seals, whales, penguins, and other seabirds. The effects of such changes can already be observed today (Atkinson et al. 2004).

11.5   Conclusions and Perspectives

Lipids in marine organisms are highly diverse and complex and exhibit various special characteristics. Typical marine lipids include wax esters as energy depots, long-chain polyunsaturated omega-3 fatty acids synthesized by phytoplankton as well as long-chain monounsaturated fatty acids and alcohols synthesized by calanoid copepods. Even if we restrict our view to lipids in copepods, the numerous life cycle strategies of copepods make it difficult to establish general features. It is clear that high-latitude copepods are much more lipid-dependent than tropical species. However, copepods in upwelling regions and deeper-living species also accumulate huge amounts of lipids for survival. It is now generally accepted that the seasonality or periodicity in food supply is the driving force for the evolution of specific life-cycle strategies in these cold-water systems, including lipid accumulation and wax ester storage. The more pronounced the seasonality the higher the amounts of lipids produced and accumulated. Lipid levels of zooplankton in polar regions can comprise more than half of the total carbon, whereas zooplankton in warm epipelagic waters of the tropics store almost no lipids.

In spite of many detailed lipid studies of various zooplankton species, there are still important discoveries to be made. Examples are the finding that the important 20:1n-9 component in North Atlantic *Calanus* species is substituted by 20:1n-11 in North Pacific *Neocalanus* species (Saito and Kotani 2000). Reasons for this difference are unknown. Another example is the predominance of the 18:1n-9 and 18:1n-7 alcohols in the wax esters of the Antarctic *Thysanoessa macrura* (Kattner et al. 1996). These alcohols are usually only minor lipid components in zooplankton species. The lipid class compositions can also be very unusual: for instance, the pteropod *Clione limacina* produces significant amounts of diacylglycerol ethers in combination with odd-chain fatty acids (Kattner et al. 1998). These unusual biosynthetic pathways are still unexplained.

We suppose that many of the deeper-living zooplankton species have also developed special lipid adaptations, which still need to be elucidated. The lipid compositions of frequently occurring copepods, especially of small species, have not yet been determined, although we suspect that such species will probably exhibit a "normal" lipid composition. A large gap exists concerning the early developmental stages. Almost no lipid data are available for most of the nauplii and early copepodids, which all are, of course, difficult to collect in sufficient numbers and to differentiate into

their respective stages. Data sets on the seasonality of lipid levels and composition need to be improved. Experimental studies following lipid assimilation via labeled diets (Graeve et al. 2005) will considerably improve our knowledge on pathways of lipid biosynthesis and the incorporation of essential fatty acids. We know that lipids undergo various changes during development and are influenced by environmental conditions, but the results are still fragmentary and sometimes contradictory. Lipid research is also needed on biosynthetic pathways, metabolism, and membrane structure and functioning.

The lipid data base for prognostic modeling is thus still insufficient, which makes it difficult or even impossible to make sound predictions. However, all these data are important to predict changes in zooplankton distribution and migration to higher-latitude regions, which become more favorable to temperate species due to future changes in climate. Because zooplankton, especially herbivorous copepods, represent the crucial link between primary producers and consumers at higher trophic levels, changes in species distribution and biochemical (lipid) composition of copepods will have a decisive effect on future life in the oceans.

Many questions have been summarized during a recent workshop on lipids in marine zooplankton (Kattner et al. 2007). A close cooperation between biologists, chemists, physicists, and modelers is necessary to improve and complete our knowledge on lipids and zooplankton in general. Interdisciplinary research including life cycles, migration, biochemical compositions, ecophysiological experiments, and climate scenarios should be better coordinated for optimal utilization of the available expertise.

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