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REVIEW

Lipid storage in marine zooplankton

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ABSTRACT: Zooplankton storage lipids play an important role during reproduction, food scarcity, ontogeny and diapause, as shown by studies in various oceanic regions. While triacylglycerols, the primary storage lipid of terrestrial animals, are found in almost all zooplankton species, wax esters are the dominant storage lipid in many deep-living and polar zooplankton taxa. Phospholipids and diacylglycerol ethers are the unique storage lipids used by polar euphausiids and pteropods, respectively. In zooplankton with large stores of wax esters, triacylglycerols are more rapidly turned over and used for short-term energy needs, while wax esters serve as long-term energy deposits. Zooplankton groups found in polar, westerlies, upwelling and coastal biomes are characterized by accumulation of large lipid stores. In contrast, zooplankton from the trades/tropical biomes is mainly composed of omnivorous species with only small lipid reserves. Diapausing copepods, which enter deep water after feeding on phytoplankton during spring/summer blooms or at the end of upwelling periods, are characterized by large oil sacs filled with wax esters. The thermal expansion and compressibility of wax esters may allow diapausing copepods and other deep-water zooplankton to be neutrally buoyant in cold deep waters, and they can thus avoid spending energy to remain at these depths. Lipid droplets are often noted in zooplankton ovaries, and a portion of these droplets can be transferred to developing oocytes. In addition to lipid droplets, zooplankton eggs have yolks with lipovitellin, a lipoprotein with approximately equal amounts of protein and lipid. The lipovitellin lipid is predominantly phosphatidylcholine, so during reproduction females must convert a portion of their storage lipid into this phospholipid. Developing embryos use their lipovitellin and lipid droplets for energy and materials until feeding begins. The various functions storage lipids serve during the different life history stages of zooplankton are very complex and still not fully understood and hence offer a multitude of fascinating research perspectives.

KEY WORDS: Zooplankton · Lipids · Wax esters · Triacylglycerols · Diapause · Reproduction · Ontogeny · Biomes

INTRODUCTION

This review will concentrate on the accumulation and utilization of storage lipids by zooplankton from different ocean biomes. Storage lipids provide energy for reproduction, periods of low food supply, obtaining food, escaping predation and for vertical migration. The high-energy content of lipids (ca. 39 kJ g^{-1}) offers an advantage over proteins and carbohydrates (both ca. 17 to 18 kJ g^{-1}). We will discuss various types of storage lipids in different tissues, including dietary markers, and techniques used for lipid quantification. Lipids are also important components of membranes (phospholipids, cholesterol), as hormones regulating various processes (ecdysone), as antioxidants (tocopherol, pigments) and for buoyancy (neutral lipids).

One of the earliest mentions in the scientific literature of zooplankton lipid accumulation is a description by Claus (1863) of the fat sac and fat droplets in the copepod *Calanus* sp. collected from the island of Helgoland, Germany. Seventy years later Marshall et al. (1934) described the buildup of lipids in *C. finmarchicus* copepodite stage 5 and adults associated with a spring phytoplankton bloom off the coast of Scotland.

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Lovern (1935) reported high amounts of lipid and long-chain alcohols in *C. finmarchicus* from the North Sea, which suggested the presence of wax esters. In the 1950s and 60s there were several papers showing the accumulation of lipids by zooplankton, but these papers reported only total lipid and not the type of lipid present. Nakai (1955) and Blumer & Mullin (1964) noted that lipid accounted for more than 50% of the dry mass (%DM) of *C. finmarchicus* from the Gulf of Maine and *C. cristatus* from the North Pacific. Petipa (1964a) showed that the oil sac volume in *C. helgolandicus* in the Black Sea changed during diurnal migrations, while Ikeda (1974) described oil sacs with different shapes and sizes in copepods from various ocean biomes. Littlepage (1964) found lipid accumulation in the Antarctic euphausiid *Euphausia crystallorophias* in summer followed by utilization during the long dark Antarctic winter. Lee et al. (1970) reported that *C. helgolandicus* (= *C. pacificus*) from the California coast had high lipid contents, primarily wax esters contained within a prominent oil sac. Thus, there was good evidence by the 1970s that copepods, as well as other zooplankton groups, were able to accumulate large amounts of storage lipid.

A major part of this review will summarize the extensive studies over the past 3 decades showing the important role played by storage lipids in the life history of many zooplankton species, especially those from high latitudes. It is advantageous, particularly in herbivorous zooplankton from these oceanic areas, to accumulate large lipid stores during the relatively short phytoplankton blooms. The lipid stores can be utilized during the long winter, and for many species the storage lipid provides both energy and materials for reproduction before the onset of the spring phytoplankton bloom. Longhurst (1998) divided the ocean into 4 major biomes, referred to as polar, westerlies, trades/tropical and coastal biomes. Herbivorous copepods from polar and westerlies biomes go through a fall and winter diapause at great depths and use accumulated lipid stores, largely wax esters, for energy and reproductive needs. Because of their thermal expansion and compressibility properties, wax esters have an advantage for zooplankton in cold deep water (Yayanos et al. 1978, Køgeler 1987, Visser & Jónasdóttir 1999). Owing to these properties, zooplankton with large stores of wax esters become neutrally buoyant in cold deep water, so energy is not required to maintain them at these depths. In upwelling coastal biomes herbivorous copepods diapause at depths during non-upwelling periods. Until upwelling returns these diapausing copepods utilize wax ester stores. Instead of lipid accumulation in the late stages, some copepod species form diapause eggs during low food periods (Marcus 1996 and references therein). In contrast to species from high latitudes or upwelling areas, zooplankton from tropical biomes generally do not accumulate large lipid stores; however, lipid droplets have been noted in gonads of tropical copepods. Gelatinous zooplankton species belonging to the phyla Cnidaria, Ctenophora and Tunicata do not accumulate large lipid stores, and extensive feeding results in rapid growth, but not in lipid accumulation (Madin et al. 1981, Youngbluth et al. 1988, Deibel et al. 1992, Nelson et al. 2000, Ju et al. 2004), although there may be exceptions in polar regions (Falk-Petersen et al. 2002).

While freshwater zooplankton are not covered in this review, there are studies showing the importance of storage lipids, both triacylglycerols and wax esters, for reproduction, growth and survival of zooplankton in freshwater ecosystems (Tessier & Goulden 1982, Boudier & Amblard 1989, Cavaletto et al. 1989, Butler 1994, Brett & Müller-Navarra 1997, Vanderploeg et al. 1998, Ackman 1999, Arts 1999).

TECHNIQUES FOR ANALYZING STORAGE LIPIDS

Chemical analysis

Many analytical methods have been described for the characterization of lipids. Therefore, we only briefly touch this topic in our review. Zooplankton storage lipids are extracted along with other lipids by organic solvents, e.g. methanol and chloroform (more recently the less toxic dichloromethane), mostly based on procedures of Folch et al. (1957) or Bligh & Dyer (1959). After extraction the different lipid classes can be separated by silicic acid thin-layer chromatography and quantified by thin-layer chromatography-densitometry methods (Armenta 1964, Sargent et al. 1977, Olsen & Henderson 1989). Another approach used to quantify the different types of lipids is the thin-layer chromatography/flame-ionization detection (TLC-FID) method (Ackman 1981, Parrish & Ackman 1983, 1985, Fraser et al. 1985, Volkman et al. 1986, Parrish 1987, 1999, Bergen et al. 2000, Hagen 2000). In this method lipid extracts are applied to quartz rods coated with a thin layer of silica, and the passage of solvent mixtures separates different lipid classes, which are quantified with a flame ionization detector. Separation by silicic acid column chromatography with gravimetrical quantification and confirmation of lipid classes by nuclear magnetic resonance (NMR spectroscopy) is used by Saito & Kotani (2000). Separation and quantification of lipids has also been carried out by high performance liquid chromatography (HPLC) combined with evaporative light-scattering detection (Christie 1997, Nordbäck & Lundberg 1999). A spectrofluorometric method has been developed, which allows quantitation of

neutral and polar lipids after water extraction of tissues (Hentschel 1998, Alonzo & Mayzaud 1999).

Collection of lipid classes from silicic acid columns or silicic acid thin-layer plates can be followed by analysis of constituent fatty acids and fatty alcohols. The derivatives of fatty acids and fatty alcohols can be analyzed by gas-liquid chromatography using capillary columns and flame ionization detection. Kattner & Fricke (1986) developed a procedure in which fatty acid methyl esters and free alcohols are simultaneously analyzed. A suite of authentic standard fatty acids and alcohols are used to help in the identification of the individual fatty acids and alcohols. Gas-liquid chromatography-mass spectrometry (GC-MS) allows structural confirmation of fatty acids, fatty alcohols, 1-alkylglycerols and double-bond positions (for GC and GC-MS techniques see Lee et al. 1971b, Christie 1982, 1989, Kattner & Fricke 1986, Tande & Henderson 1988, Kattner et al. 1998 as well as many other references on slightly modified methods). Intact wax esters not hydrolyzed to constituent fatty acids and alcohols are applied to gas-liquid chromatography to determine the total chain length and structure of the wax esters (Lee et al. 1971b, 1974, Kattner et al. 1990). For example, major wax esters of the Arctic copepod *Calanus hyperboreus* were 40:2, 42:2 and 44:2, which are composed of 20:1 and 22:1 fatty acids combined with the corresponding alcohols (Graeve & Kattner 1992).

Microscopic analysis

Because many copepods have oil sacs filled with storage lipids, several techniques have been developed to quantify the oil volume under the microscope. Petipa (1964b) determined oil sac volumes and oil mass, assuming lipid density of 0.91 g ml^{-1}, in *Calanus helgolandicus* from the Black Sea. Using this technique she noted large increases in oil sac lipid mass from 0.6 to 45.4 µg, when copepodids developed from stage 2 to 5. Miller et al. (1998) quantified the oil sac volume of *C. finmarchicus* using a video image of live animals and found that storage lipid determined by the TLC-FID method correlated well with oil sac volume. Corkett & McLaren (1969) developed an oil sac index to indicate the amount of assimilable food available to *Pseudocalanus* spp. with a calibration curve based on laboratory studies, where copepods were fed on different food concentrations. As *Pseudocalanus* spp. was fed increasing concentrations of phytoplankton food, there was a corresponding increase in the oil sac index (Corkett & McLaren 1978). Oil sac volumes in *Pseudocalanus* spp. collected in the North Atlantic (Scotian shelf) were related to recent trophic history (Reiss et al. 1999). Paffenhöfer & Harris (1976) noted well-developed oil sacs in copepodids and adults of *Pseudocalanus* spp. at food concentrations of 50, 100 and 200 µg carbon l^{-1}, but no evidence of oil sacs at a food concentration of 25 µg carbon l^{-1}. The seasonal moulting pattern of *C. finmarchicus* has been related to body size and oil sac volume (Arashkevich et al. 2004)

Many zooplankton species fed high food amounts do not develop well-defined oil sacs but rather accumulate oil droplets. Costlow (1982) suggested that the lipid reserves in barnacle nauplii could be estimated from the total volume of the 'oil cells', which were attached to the outer surface of the midgut. Goulden & Hornig (1980) counted the number and size of oil droplets in a freshwater daphnid. Arts & Evans (1991) developed a simple optical-digital method, which was used to follow changes in seasonal patterns of lipid droplets, i.e. triacylglycerols, in the freshwater copepod *Diaptomus sicilis*. Lipid-specific staining in combination with microscopy/photometry has been used to quantify storage lipid in zooplankton larvae derived from benthic adults, such as barnacle nauplii and bivalve veligers (Gallager & Mann 1981, 1986). Some of the stains which can be used for such studies include Oil Red O, Sudan IV, Sudan Black B, Phosphine 3R and Nile Red (Croll 1972a,b, Gallager & Mann 1981, 1986, Carman et al. 1991, Locke & Sprules 1993).

TYPES OF STORAGE LIPIDS

Lipid classes

Four principal types of storage lipid have been found in marine zooplankton: triacylglycerols, wax esters, phospholipids and diacylglycerol ethers (1-alkyldiacyl-*sn*-glycerols) (Fig. 1). Triacylglycerols, composed of a glycerol backbone esterified with 3 fatty acids, are the most common storage lipid in animals. While triacylglycerols are present in almost all zooplankton, wax esters are major storage lipids in high-latitude species. Wax esters consist of simple esters of long-chain primary alcohols and long-chain fatty acids. The nomenclature used here for alcohols and fatty acids gives the carbon length, the number of double bonds and the position of the first double bond in relation to the terminal methyl group.

Phospholipids are a key component of biomembranes. In zooplankton these polar lipids consist of 3 major fatty acids, 22:6 (n-3), 20:5 (n-3) and 16:0, largely independent of dietary changes (Lee et al. 1971b, Falk-Petersen et al. 2000). However, one of the important phospholipids, phosphatidylcholine, also appears to serve as a storage lipid in high-latitude euphausiids, e.g. *Euphausia superba*, *E. crystallorophias* and *Thysanoessa macrura* (Hagen et al. 1996, Mayzaud 1997).

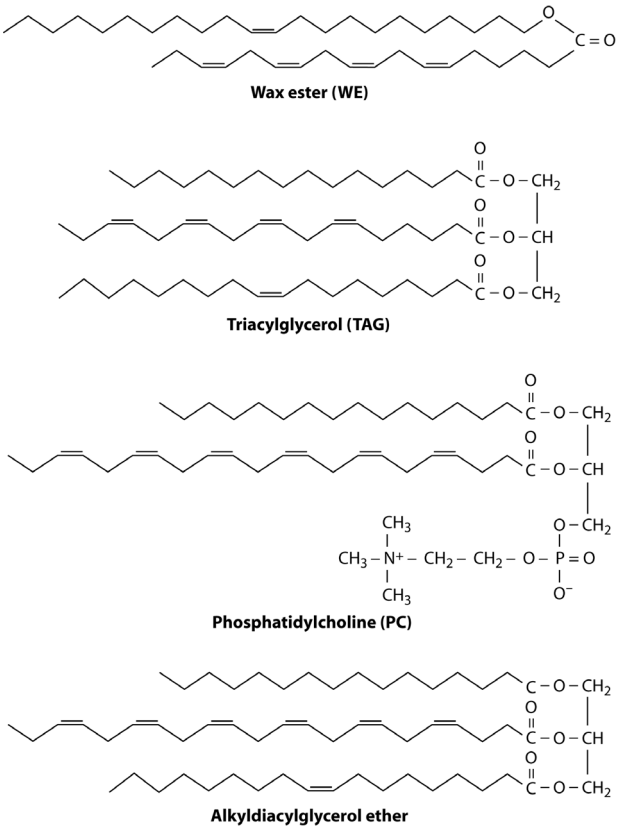

Fig. 1. Chemical structures of different storage lipids in zooplankton. Wax ester (22:1 alcohol; 18:4 fatty acid); triacylglycerol (16:0, 18:4 and 18:1 fatty acids); phosphatidylcholine (16:0 and 22:6 fatty acids); alkyldiacylglycerol ether (16:0 alcohol; 22:6 and 17:1 fatty acids)

Phosphatidylcholine is composed of a glycerol backbone with fatty acids at positions 1 and 2 and cholinephosphate on position 3. It is unusual for this lipid to serve for energy storage. This function is only suggested for phosphatidylcholine, but not for phosphatidylethanolamine, the other important marine zooplankton phospholipid. Membrane phospholipids generally have an asymmetric fatty acid distribution, where there is an unsaturated fatty acid at position 2 and a saturated fatty acid at position 1 (Hadley 1985). This asymmetric fatty acid distribution is thought to be of major importance in the functional and structural roles of membranes. Zooplankton phospholipids differ from this scheme since polyunsaturated fatty acids are in excess of saturates (Albers et al. 1996). Thus, polyunsaturated fatty acids are also in position 1, particularly 20:5(n-3) in phosphatidylcholine (Kattner 1991). Since the principal lipid of crustacean lipovitellin is phosphatidylcholine, we propose a possible transfer of phosphatidylcholine to euphausiid lipovitellin during reproduction.

The 4th type of storage lipid reported in marine zooplankton are diacylglycerol ethers, which have been reported as a major storage lipid in the pteropod genus *Clione* from polar and temperate regions (Lee 1974a, 1975, Phleger et al. 1997, Kattner et al. 1998, Falk-Petersen et al. 2001, Böer et al. 2005). Up to 41% of the lipid of the pteropod *C. limacina* in polar oceans can be diacylglycerol ethers (Kattner et al. 1998). They are characterized by one ether-linked alkyl chain and 2 fatty acid esters at the glycerol backbone. These lipids are not found in the diet of this pteropod and are presumed to be made de novo from the diet, consisting exclusively of the pteropod *Limacina helicina*. The diacylglycerol ethers of *C. limacina* are unique with up to 1/3 of their total fatty acids being odd-chain fatty acids, mainly 17:1(n-8), 15:0 and 17:0. It is not yet clear why pteropods store high amounts of diacylglycerol ethers with odd-chain fatty acids, in addition to the more commonly occurring triacylglycerols.

Dietary fatty acids

There is a large body of literature showing that fatty acid compositional changes can be used to determine the contribution of different microalgae groups in the food of herbivorous zooplankton and how these phytoplankton fatty acid patterns are modified in omnivorous and carnivorous zooplankton species (see the recent review by Dalsgaard et al. 2003). Since our review deals with storage lipids, we have restricted the discussion to fatty acids and fatty alcohols found in triacylglycerols and wax esters and how such compositional lipid data can be related to the diet. Principal fatty acids of triacylglycerols and fatty acids and alcohols of wax esters of selected copepods and euphausiids are presented in Tables 1 & 2.

Generally, phytoplankton fatty acids are incorporated unmodified into zooplankton storage lipids. The 16:1(n-7) and 20:5(n-3) are the principal diatom fatty acids (Kates & Volcani 1966), while 18:4(n-3) and 22:6(n-3) are typical of dinoflagellates (Harrington et al. 1970, Graeve 1993). The presence of 16:1(n-7) and 18:4(n-3) in storage lipids was used by Graeve et al. (1994b) and Scott et al. (1999) to indicate the relative importance of diatoms and dinoflagellates in the zooplankton diet. Other studies supported this observation, finding high concentrations of 16:1(n-7) and 18:4(n-3) in storage lipids of copepods and euphausiids after feeding in phytoplankton blooms, with 16:1 and 18:4 accounting for up to 45 and 23% of the total fatty acids, respectively (Sargent et al. 1985, Kattner & Krause 1987, Kattner 1989, Norrbin et al. 1990, Kattner & Hagen 1998, Miller et al. 1998, Falk-Petersen et al. 2000). The relatively high levels of 16:4(n-1), 18:4(n-3) and phytanic acid in the triacylglycerols of *Euphausia superba* have been used as an indicator of the impor-

Table 1. Major fatty acids of storage lipids including wax ester alcohols in copepods from different biomes (mass% of total fatty acids and alcohols, respectively). *Neocalanus tonsus* (Ohman et al. 1989), *N. plumchrus* (Lee 1974a, Lee & Nevenzel 1979), other data from Albers et al. (1996). TAG = triacylglycerols; WE = wax esters

	Calanoides acutus Antarctic		*Metridia gerlachei* Antarctic		*Euchaeta antarctica* Antarctic		*Neocalanus tonsus* Subantarctic	*Calanus finmarchicus* Arctic		*Metridia longa* Arctic	*Calanus hyperboreus* Arctic		*Neocalanus plumchrus* North Pacific	
	TAG	WE	TAG	WE	TAG	WE	WE	TAG	WE	WE	TAG	WE	TAG	WE
Fatty acids														
14:0	8	4	13	1	13	1	14	12	26	1	7	6	8	11
16:0	9	2	20	4	16	1	11	30	10	2	26	6	18	12
16:1(n-7)	6	8	11	13	12	24	6	4	7	21	6	12	10	8
16:4(n-1)	6	3	2	3	0.2	1	–	–	1	1	–	2	3	5
18:0	1	4	4	0.3	2	0.2	2	6	1	1	12	1	7	0.2
18:1(n-9)	6	4	12	34	19	48	7[a]	10	5	30	18	6	8[a]	3[a]
18:1(n-7)	1	1	6	1	9	–		2	0.3	1	2	2		
18:4(n-3)	9	13	8	9	1	2	1	6	14	1	1	6	3	7
20:1(n-9)	13	24	1	1	9	2	23	–	8	20	1	19	6	14
20:5(n-3)	15	17	9	17	4	8	5	9	11	7	2	7	17	21
22:1(n-11)	5	8	0.1	–	1	0.1	19	2	7	9	–	17		9
22:6(n-3)	9	6	6	8	3	7	2	6	2	1	3	2	2	2
Alcohols														
14:0		11		51		64	1		4	46		4		1
16:0		10		46		27	2		15	18		11		5
16:1(n-7)		2		4		3	0.2		3	1		2		7
20:1(n-9)		56		–		4	57		39	16		28		33
22:1(n-11)		21		–		1	25		39	20		55		44

[a]Sum of 18:1(n-9) and 18:1(n-7)

Table 2. Major fatty acids of storage lipids including wax ester alcohols in euphausiids from different biomes (mass% of total fatty acids and alcohols, respectively). *Thysanoessa inermis* collected during bloom conditions, Balsfjord, Norway (Falk-Petersen et al. 1990), *T. inermis* Kongsfjord, Svalbard (Falk-Petersen et al. 2000), *Euphausia crystallorophias* (Kattner & Hagen 1998), *E. superba* (Hagen et al. 2001), *T. macrura* (Hagen & Kattner 1998), *E. pacifica* (Lee 1974a). TAG = triacylglycerols; WE = wax esters

	Thysanoessa inermis Northern Norway Adults		*Thysanoessa inermis* Svalbard Adults		*Euphausia superba* Antarctic		*Euphausia crystallorophias* Antarctic				*Thysanoessa macrura* Antarctic		*Euphausia pacifica* North Pacific Juveniles
					Furciliae	Females	Furciliae		Adults		Furciliae	Adults	
	TAG	WE	TAG	WE	TAG	TAG	TAG	WE	TAG	WE	WE	WE	TAG
Fatty acids													
14:0	3	1	5	1	7	21	4	2	9	0.4	32	38	9
16:0	29	4	30	3	27	23	10	5	19	1	23	26	18
16:1(n-7)	8	4	30	14	5	9	9	5	15	8	5	6	13
18:0	5	2	2	51	9	2	3	3	2	0.2	2	1	1
18:1(n-9)	10	59	8	14	8	24	13	34	20	65	11	17	12[a]
18:1(n-7)	11	10	13	3	3	6	6	16	7	20	3	5	
18:4(n-3)	10	2	2	0.1	11	4	15	7	7	1	8	–	5
20:1(n-9)	1	2	1	2	3	1	4	–	1	3	6	1	0.2
20:5(n-3)	6	8	3	4	13	1	17	18	9	0.3	6	2	8
22:1(n-11)	1	1	1	1	–	–	0.4	–	0.1	–	–	0.2	–
22:6(n-3)	2	1	0.1	0.1	2	1	6	5	5	0.1	1	0.5	1
Alcohols													
14:0		12		22				74		63	–	–	
16:0		51		58				26		34	–	–	
16:1(n-7)		4		14				–		–	–	–	
18:1(n-9)		–		0.1				–		–	40	40	
18:1(n-7)		–		0.1				–		–	34	41	
20:1(n-9)		–		2				–		2	23	16	
22:1(n-11)		–		2				–		0.2	1	4	
Phytol		23		–				–		–	–	–	

[a]Sum of 18:1(n-9) and 18:1(n-7)

tance of diatoms in the diet of this Antarctic euphausiid (Clarke 1980, 1984, Clarke & Morris 1983) (Table 2).

In zooplankton with large wax ester stores, the fatty acids of triacylglycerol may be more reflective of recent food, whereas wax ester fatty acids and alcohols reflect both dietary influences and de novo synthesis. Triacylglycerols are utilized more rapidly than wax esters, which serve as energy reserves during longer fasting periods. Assimilation of dietary fatty acids and de novo biosynthesis are rapid processes (Graeve et al. 2005). The wax esters of many herbivorous copepods are characterized by considerable amounts of the long-chain monounsaturated fatty acids 20:1(n-9), 20:1(n-11), and 22:1(n-11) (Tables 1 & 2), which are not present in significant amounts in their phytoplankton diet. The 20:1 and 22:1 fatty acids are reduced to the corresponding alcohols, which are the principal alcohols of these zooplankters. Omnivorous and carnivorous zooplankton species are characterized by wax esters with high amounts of the 18:1(n-9) fatty acid (Tables 1 & 2). Carnivorous zooplankton feeding on wax-ester-rich herbivorous copepods have triacylglycerols with high amounts of 20:1(n-9) and 22:1(n-11) fatty acids. These are assumed to be derived from the 20:1 and 22:1 alcohols and fatty acids in their copepod diet (Ackman et al. 1970, Ratnayake & Ackman 1979a,b, Sargent & Falk-Petersen 1981).

Fatty alcohols

Since wax esters are usually absent in marine phytoplankton lipids, wax ester alcohols in herbivorous zooplankton originate either from reduction of phytoplankton fatty acids or from de novo synthesis from phytoplankton protein and carbohydrate. The biosynthesis of fatty alcohols and esterification with a fatty acid to wax esters results in rapid lipid accumulation since there is both de novo synthesis and incorporation of dietary lipids (Sargent et al. 1981, Sargent & Henderson 1986, Graeve et al. 2005).

There are major differences between the principal alcohols of different zooplankton species (Tables 1 & 2). The most important wax ester alcohols are 14:0, 16:0, 18:1(n-9), 18:1(n-7), 20:1(n-9), 20:1(n-11) and 22:1(n-11). The 20:1(n-9) and 22:1(n-11) are the most common alcohols of the wax esters found in herbivorous zooplankton, while omnivorous and carnivorous zooplankton have a predominance of 14:0 and 16:0 alcohols. However, in the Antarctic euphausiid *Euphausia crystallorophias* and the copepod *Rhincalanus gigas*, which are considered to be herbivorous or omnivorous, the 14:0 and 16:0 accounted for 90% of the wax ester alcohols. It appears that the 20:1(n-9) and 22:1(n-11) alcohols only occur in copepods that undergo diapause (Graeve et al. 1994a, Kattner et al. 1994a, Kattner & Hagen 1998). A principal wax ester alcohol of the north Atlantic euphausiids *Thysanoessa raschii* and *T. inermis* at one collection site in northern Norwegian waters was phytol, which was hypothesized to be due to feeding on phytoplankton detritus (Falk-Petersen 1981, Falk-Petersen et al. 1981, 1982, Sargent & Falk-Petersen 1981). However, *T. raschii* and *T. inermis* collected from another fjord did not have phytol in their wax esters (Table 2). In addition, *E. crystallorophias* also contained considerable amounts of phytol at one under-ice location in Antarctica (Falk-Petersen et al. 1999). The fatty alcohol composition of the Antarctic euphausiid *Thysanoessa macrura* is unique because it has both 18:1(n-9) and (n-7) as its principal alcohols (Kattner et al. 1996, Hagen & Kattner 1998).

Kattner & Krause (1989) reported 22:1 alcohol to account for 43 to 72% of the alcohols in *Calanus finmarchicus* from the North Sea, whereas Miller et al. (1998) reported an absence of this alcohol in *C. finmarchicus* from the Gulf of Maine. This is the only report where the 20:1 alcohol in herbivorous copepods was not accompanied by large amounts of the 22:1 alcohol.

LIPID STORAGE IN DIFFERENT TISSUES

Marine zooplankton accumulates storage lipids in oil sacs, oil droplets, hepatopancreas/fat bodies, digestive tracts and gonadal tissues. The location of storage lipids is best observed in photomicrographs of sections from fixed tissues.

Oil sac

Many species of the copepod genera *Calanus*, *Euchaeta*, *Paraeuchaeta*, *Eucalanus*, *Rhincalanus* and *Pseudocalanus* are characterized by large oil sacs that can occupy a large part of the body cavity. Ultrastructure studies have shown oil sacs filled with triacylglycerols or wax esters, to be surrounded by a single layer of epithelial cells (Figs. 2 & 3a) (Lee et al. 1970, Benson et al. 1972, Bauermeister & Sargent 1979, Henderson & Sargent 1980, Blades-Eckelbarger 1991). In *Euchaeta japonica* the alimentary canal, which produces triacylglycerols, lies in close proximity to an oil sac containing only wax esters. Since membrane preparations from oil sacs of this copepod form wax esters from fatty acids, it seems likely that triacylglycerols formed in the alimentary canal are converted to wax esters by oil sac membrane cells (Henderson & Sargent 1980). Similarly, Holtz et al. (1973) found that oil sac membrane cells from *C. pacificus* carried out wax ester synthesis. Sev-

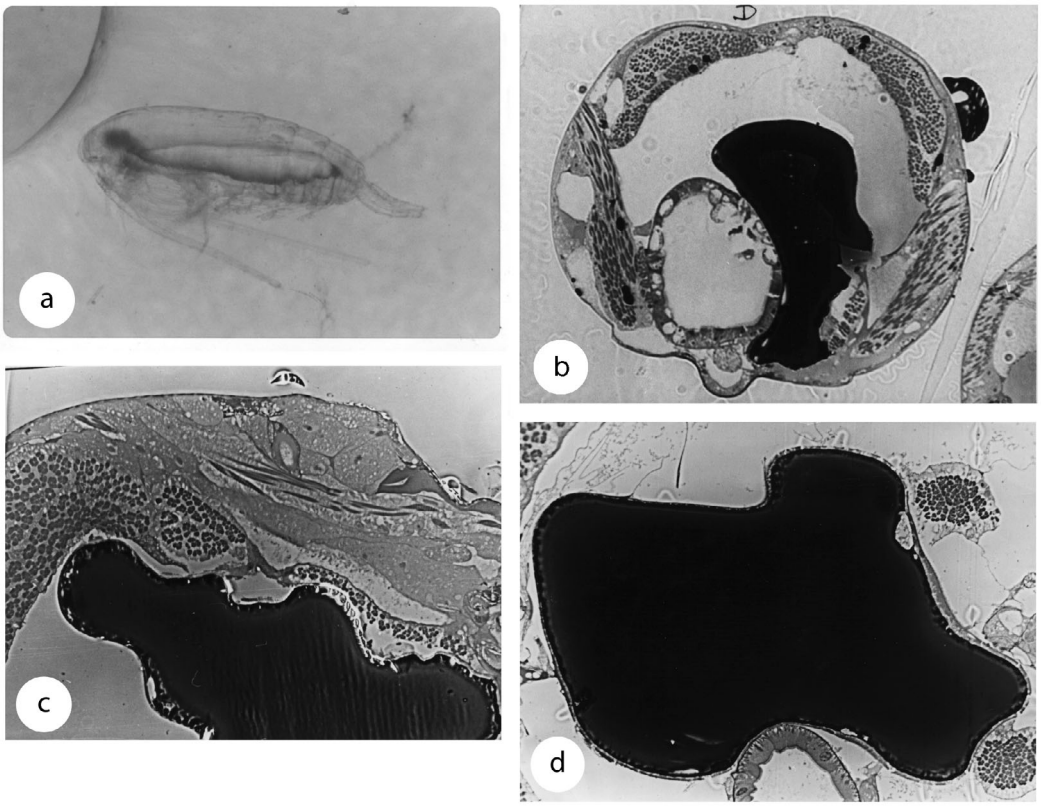

Fig. 2. *Calanus plumchrus*. (a) Photomicrograph of a living specimen with large oil sac; (b) section of fixed tissues from C5 with large dark oil sac adjacent to digestive lumen; (c) section showing large dark oil sac and adjacent muscle tissues; (d) electron micrograph showing membrane surrounding oil sac and section of lumen

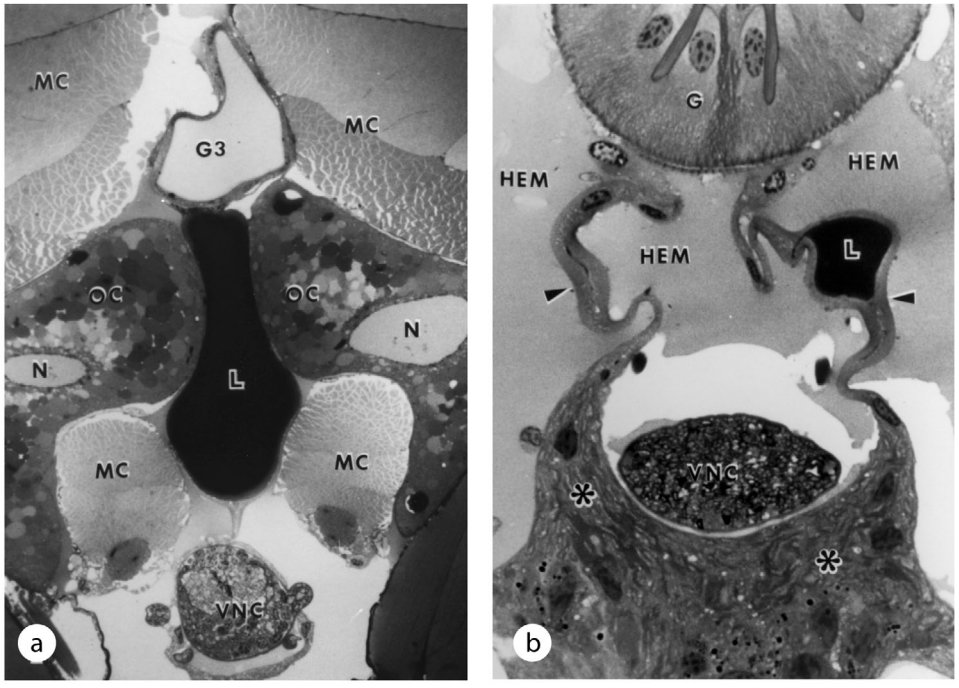

Fig. 3. *Euchaeta marina* from subtropical region of Gulf Stream. Light micrograph section showing (a) lipid sac (L), midgut (G3), musculature (MC), ventral nerve cord (VNC), oocytes (OC) with nucleus (N) (magnification 260×); (b) small lipid inclusion (L), midgut (G), ventral nerve cord (VNC) and hemolymph (HEM). Arrowheads indicate end of lipid sac; branches of the lipid sac extend around VNC and border on an unidentified gland (*). Lipid inclusion is closely connected to midgut and surrounded by hemolymph (magnification 600×). With permission from Blades-Eckelbarger (1991)

eral investigators have commented on the similarity of copepod oil sacs to adipose tissue cells of higher vertebrates. Electron micrographs of oil sacs of *Euchaeta norvegica* and *C. finmarchicus* showed membranous structures within the oil sac. This led Sargent & Henderson (1986) to conclude that copepod oil sacs are similar to higher animal adipose tissues, which are composed of adipocytes or fat cells. Blades-Eckelbarger (1986), based on light microscopy studies, suggested that the cells surrounding the oil sac in *Euchaeta marina* (Fig. 3b) resembled mammalian white adipose tissue cells. These oil sacs also show similarity to the adipocytes of fish tissues (Zhou et al. 1996).

During reproduction or periods of low food, oil sac wax esters or triacylglycerols are used for energy and materials. Blades-Eckelbarger (1991) noted the presence of micropinocytotic activity and invaginations along the membrane surrounding the oil sac, which along with many mitochondria suggested active lipid metabolism at the surface of the lipid in the oil sacs. In vertebrate animals a protein, perilipin, plays an important role in regulating utilization of triacylglycerol oil droplets in the adipocytes (Greenberg et al. 1991), and we suggest a perilipin-like protein may play a role in regulating storage and utilization of the storage lipids found in many zooplankton species.

Oil droplets

In addition to lipids within oil sacs, oil droplets and so-called lipid inclusions have been found distributed throughout the body cavity in zooplankton, particularly in those from higher latitudes and deeper waters (Figs. 3b & 4) (Lee & Hirota 1973, Bauermeister & Sargent 1979, Defaye et al. 1985, Larson & Harbison 1989, Blades-Eckelbarger 1991). Electron micrographs of these lipid droplets show the close proximity of mitochondria, suggesting that lipids within the droplets can be rapidly metabolized (Fig. 4b). In copepods with oil sacs filled with wax esters, the lipid droplets were found to be composed of triacylglycerols (Bauermeister & Sargent 1979). Studies on copepods, where triacylglycerols and wax esters are spatially separated, have shown that triacylglycerols serve as rapidly used energy stores, while wax esters are more slowly used over longer periods (Lee et al. 1971a, Lee & Barnes 1975, Håkanson 1984, Sargent & Henderson 1986).

Hepatopancreas and fat bodies

The different cell types found in crustacean hepatopancreas tubules, including crustacean zooplankton, are E-, F-, R- and B-cells, where the F-, R- and B-cells are derived from embryonic or E-cells. The R-cells are the primary storage cells and can contain large accumulations of lipid droplets and lipoproteins (Arnaud et al. 1978, 1980, Halberg & Hirche 1980, Robinson & Dillaman 1985, Al-Mohanna & Nott 1987, 1989, Sagrista & Durfort 1991, Vogt 1994, Wright & Ahearn 1997). Hepatopancreas or digestive glands of many zooplankton groups, including copepods and euphausiids, are characterized by lipid droplets and high lipid contents (Herring 1973, Raymont et al. 1974, Arnaud et al. 1980, Henderson et al. 1981, Sargent et al. 1981, Saether et al. 1983, Blades-Eckelbarger 1991, Virtue et al. 1993, Pond et al. 1995). The hepatopancreas of the euphausiid *Thysanoessa inermis* had a high wax ester content, possibly associated with lipid droplets (Sargent et al. 1981). For the decapod *Notostomus auriculatus*, 93% of the lipid in the animal's body is associated with the hepatopancreas (Herring 1973). In contrast, in *Euphausia superba*, less than 2% of its lipids are located in this organ (Clarke 1980).

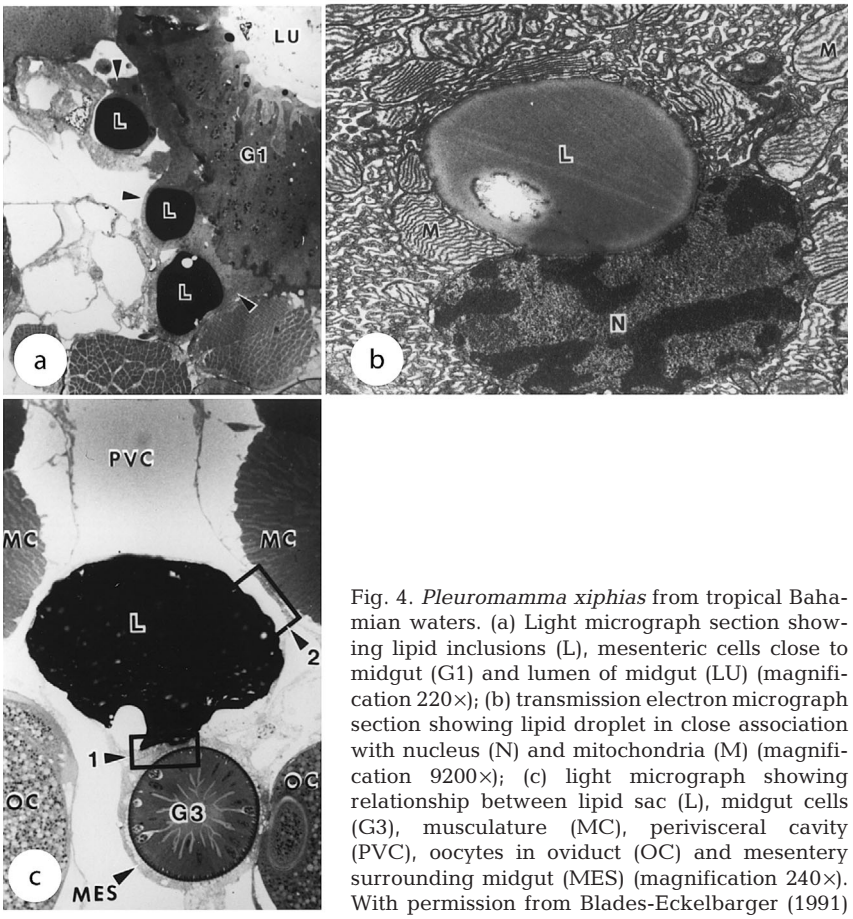

Fig. 4. *Pleuromamma xiphias* from tropical Bahamian waters. (a) Light micrograph section showing lipid inclusions (L), mesenteric cells close to midgut (G1) and lumen of midgut (LU) (magnification 220×); (b) transmission electron micrograph section showing lipid droplet in close association with nucleus (N) and mitochondria (M) (magnification 9200×); (c) light micrograph showing relationship between lipid sac (L), midgut cells (G3), musculature (MC), perivisceral cavity (PVC), oocytes in oviduct (OC) and mesentery surrounding midgut (MES) (magnification 240×). With permission from Blades-Eckelbarger (1991)

Various polar euphausiids appear to utilize phosphatidylcholine as a storage lipid (Hagen 1988, Hagen et al. 1996, Mayzaud 1997). Phosphatidylcholine is the major lipid in high-density lipoproteins found in arthropod hemolymph (Lee & Puppione 1988, Lee 1991, Walker et al. 2003). These lipoproteins play an important role in transporting lipids from different tissues, e.g. hepatopancreas/liver to muscle. Some euphausiids may store phosphatidylcholine in lipoproteins within a storage tissue. In vertebrates, liver parenchymal cells and the Golgi apparatus carry out the synthesis and assembly of plasma lipoproteins (Dolphin 1985, Havel 1987). In decapod crustaceans lipoproteins are assembled in the hepatopancreas (Walker et al. 2003), while in insects and isopods they are assembled in the fat body (Picaud 1980, Kanost et al. 1990).

Since the hepatopancreas of *Euphausia superba* is not an important tissue for lipid storage, other euphausiid tissues have been examined as lipid storage sites. Recently Stübing (2004) found evidence of phosphatidylcholine storage within the cephalothorax of *E. superba*, possibly within tissues similar to the fat bodies of insects and isopods. Phospholipid staining showed a relatively uniform distribution of phosphatidylcholine within the fat body cells. Sucrose gradients of extracts from *E. superba* indicated that much of the phosphatidylcholine was not associated with the membrane fraction but was found in a less dense supernatant fraction. One possibility is that phosphatidylcholine-rich lipoproteins accumulate in the cytosol of the euphausiid storage tissue. Since phosphatidylcholine is the principal lipid component of crustacean lipovitellin, phosphatidylcholine-rich particles in euphausiid storage tissues may be used in the assembly of *E. superba* lipovitellins for developing oocytes.

Ovary

Oil droplets, composed of triacylglycerols or wax esters, have been observed in ovarian sections of euphausiids and copepods (Fig. 5a) (Saether et al. 1983, Blades-Eckelbarger 1991). Oil sacs, when present, are often in close proximity to developing oocytes (Fig. 4c). Lipovitellin, the major constituent of yolks in crustaceans, polychaetes and molluscs, consists of 30 to 50% lipid. Lipovitellins are utilized for energy and materials by the newly hatched larvae. Phosphatidylcholine is generally the major lipid component of lipovitellin with lesser amounts of cholesterol and triacylglycerols (Lee 1991). In *Artemia salina*, and presumably in other crustacean zooplankton, the lipovitellin is associated with egg-yolk granules (deChaffoy & Kondo 1980).

ACCUMULATION AND UTILIZATION OF STORAGE LIPIDS

Reproduction

A great deal of energy and materials are required for reproduction processes. After copepod reproduction is completed the female has a lower lipid content and smaller oil sac than the copepodite stage 5 (Figs. 6 & 7). A feature of reproduction is the accumulation of lipid droplets and yolk lipovitellin in the developing ovary and oocytes (Fig. 5) (Hilton 1931, Ross et al. 1982, Blades-Eckelbarger & Youngbluth 1984, Blades-Eckelbarger 1986, Cuzin-Roudy & Amsler 1991, Ianora & Santella 1991, Laabir et al. 2001). Lipovitellins are associated with yolk spheres or granules within the oocytes. Lipid droplets (wax esters or triacylglycerols) and lipovitellins are utilized by zooplankton embryos for energy, membranes and hormones (Lee & Walker 1995). Females with large stores of wax esters or triacylglycerols convert a portion of these lipids into phospholipids, and these newly formed phospholipids are used to assemble lipovitellin in the developing oocytes. A schematic diagram is presented in Fig. 6 showing a female copepod with a large oil sac produc-

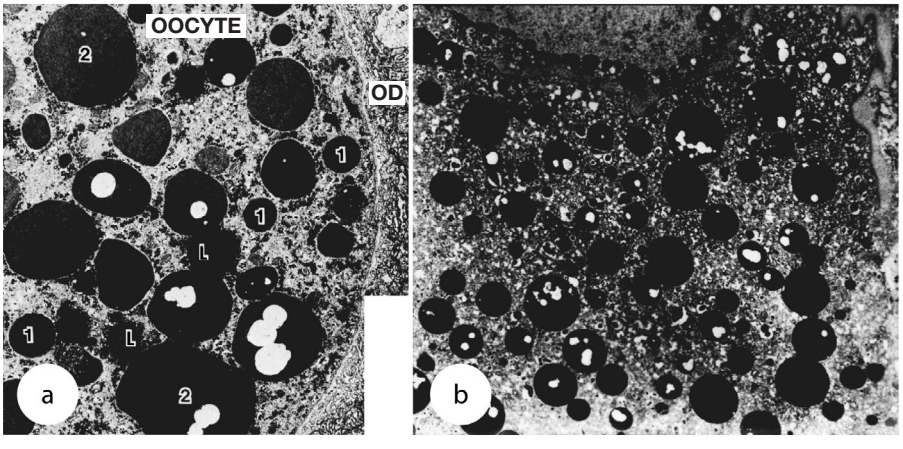

Fig. 5. Transmission electron micrographs. (a) *Labidocera aestiva* from subtropical south Florida waters showing poration of mature oocytes that have passed through the oviduct (OD); lipid droplet (L), type 1 yolk sphere (1) and type 2 bodies (2) (magnification 3200×). With permission from Blades-Eckelbarger & Youngbluth (1984). (b) *Temora stylifera* from Bay of Naples showing large number of yolk spheres filled with lipovitellin (magnification 1800×). With per-mission from Laabir et al. (2001)

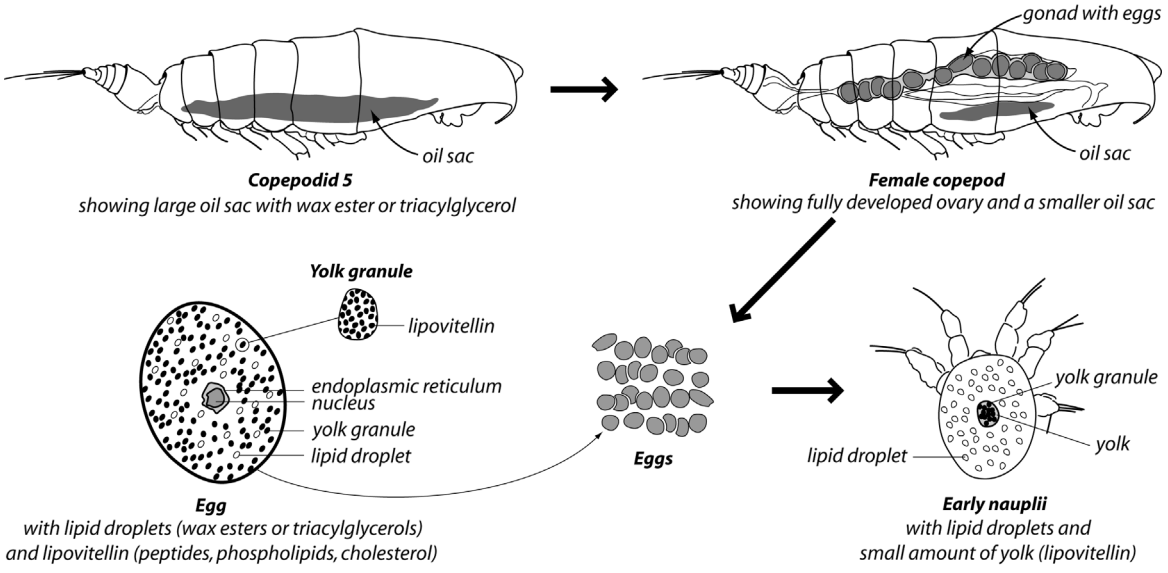

Fig. 6. Formation of eggs in oil sac containing copepod with lipid droplets (wax esters or triacylglycerols) and lipovitellin associated with yolk granules; note reduction of oil sac size from C5 to female as lipid in oil sac is utilized to provide lipid for assembly of lipid droplets and lipovitellin. Early nauplii utilize lipid droplets and lipovitellin for energy and to form membranes and organelles

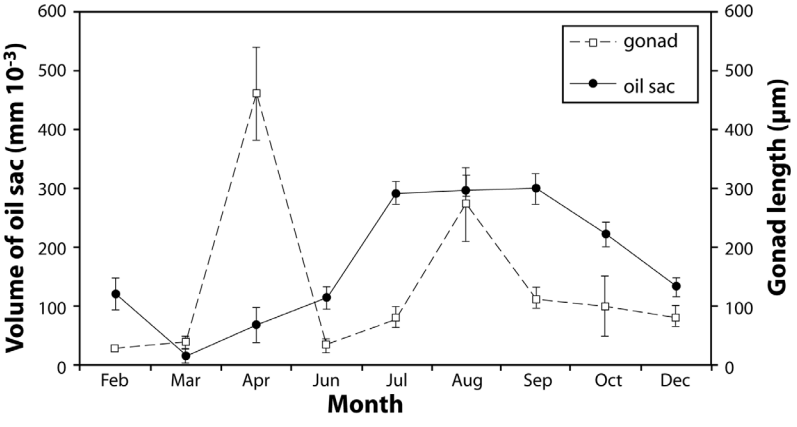

Fig. 7. *Calanus hyperboreus* (C5) off northern Norway. Seasonal changes in oil sac volume and gonad length. Modified from Pasternak et al. (2001)

ing lipid-rich eggs, which hatch into nauplii that have lipid droplets and yolk granules with lipovitellin. Female northern krill *Meganyctiphanes norvegica* undergoing oogensis and vitellogenesis were found to accumulate large amounts of phospholipids synthesized in the digestive gland and fat body (Cuzin-Roudy & Buchholz 1999, Cuzin-Roudy et al. 1999, Albessard et al. 2001). The eggs of this species are rich in phospholipids containing 75% phospholipids and 9% triacylglycerols, and we suggest that the egg phospholipids are associated with egg lipovitellin.

Wax esters in the form of lipid droplets are the major storage lipid of eggs of *Acanthephyra pelagica*, *Calanus hyperboreus*, *Euchaeta japonica*, *E. marina*, *E. media* and *Euphausia crystallorophias*, while triacylglycerols in lipid droplets are the important neutral lipid class of the eggs of *C. helgolandicus*, *C. pacificus* and *Euphausia superba* (Table 3) (Lee et al. 1972, 1974, Lee & Hirota 1973, Herring & Morris 1975, Gatten et al. 1980, Conover 1988, Kattner & Hagen 1998, Hagen & Auel 2001). The importance of egg lipid droplets is likely related to the amount of energy required by the early developmental stages. Eggs of the shrimp species *Penaeus setiferus*, *Crangon crangon* and *C. allemanni* lack or have only trace amounts of storage lipids (Kattner et al. 1994b, Lee & Broudy unpubl. data). Their eggs hatch soon after release, and the naupliar stages immediately start feeding. In contrast, the eggs of the copepods *Euchaeta japonica* and *C. plumchrus* are full of lipid droplets, and feeding does not begin until the late naupliar stages, i.e. after 20 to 30 d (Lee et al. 1974, Saito & Tsuda 2000).

Based on the time of reproduction and the amount of storage lipid accumulated for reproduction, zooplankton can be separated into 3 groups (Fig. 8). Group 1 comprises zooplankton with large lipid stores, which are able to reproduce during a period when food is either not available or at very low concentrations. This group consists of copepods and euphausiids in polar and westerlies biomes including *Calanus hyperboreus*,

Table 3. Total lipids (mass per egg or ind.)and lipid class compositions of eggs and females of copepods, euphausiids, decapods and mysids (n: number of eggs per female)

	Lipid mass (µg)	Lipid (%DM)	WE (%TL)	TAG (%TL)	PL (%TL)	Location	Source
Copepoda							
C. carinatus eggs (n = 1400)	0.6	75	–	–	–	Benguela Current	Borchers & Hutchings (1986)
C. carinatus C5	131	71	–	–	–		Borchers & Hutchings (1986)
C. finmarchicus eggs (n = 600)	0.07	15	17	15	69	Gulf of St. Lawrence	Ohman & Runge (1994)
C. finmarchicus female	105	31	71	2	25		Diel & Tande (1992)
E. japonica eggs (n = 14)	40	64	58	19	21	Strait of Georgia,	Lee et al. (1974)
E. japonica female	600	52	60	17	20	Canada	Lee et al. (1974)
N. tonsus eggs (n = 285)	0.14	66	11	6	66	New Zealand	Ohman et al. (1989)
N. tonsus female	150	30	88	1	9		
P. antarctica eggs (n = 60)	6.2	36	–	–	–	Antarctic	Alonzo et al. (2000a,b)
P. antarctica female	2800	47	94	3	3	Antarctic	Alonzo et al. (2000a,b)
Euphausiacea							
E. crystallorophias eggs (n = 135)	23	51	62	–	–	Weddell Sea	Kattner & Hagen (1998)
E. crystallorophias female	28 000	50	56	6	34		Hagen (1988), Hagen & Auel (2001)
E. superba eggs (n = 14 500)	9.4	35	–	31	29	South Georgia	Clarke & Morris (1983)
E. superba female	98 000	35	1	29	29		Clarke (1980, 1983, 1984)
Decapoda							Clarke (1983)
A. pelagica eggs (n = 132)	390	49	11	47	23	North Sea	Herring (1973), Herring & Morris (1975)
A. pelagica female	115 000	33	7	73	16		Herring (1973), Herring & Morris (1975)
Mysidacea							
Gnathophausia sp. eggs (n = 220)	2700	82	11	71	6	North Pacific	Lee (unpubl. data)
Gnathophausia sp. female	2 200 000	42	12	69	16		Lee et al. (1971a), Lee (unpubl. data)

C. cristatus, *Neocalanus plumchrus*, *Euchaeta japonica*, *E. norvegica* and *Thysanoessa macrura*. These zooplankters reproduce in winter and early spring before phytoplankton has appeared, and they utilize lipid accumulated from the previous spring/summer feeding period (Fig. 9a) (Hagen 1988, Conover & Siferd 1993, Kattner & Hagen 1998, Falk-Petersen et al. 2000, Hagen & Auel 2001, Ringuette et al. 2002). In the Antarctic euphausiid *Thysanoessa macrura*, lipids decreased from 40 to 9 %DM (Sep to Nov) after reproduction was completed. The lipid utilized was not replaced until the phytoplankton bloom later in the year (Hagen et al. 1996, Hagen & Kattner 1998). Similarly, female *C. hyperboreus* had a winter/early spring spawn during which lipids decreased from 50 to 25 %DM (Conover & Corner 1968). The importance of storage lipids for late winter reproduction in *C. hyperboreus* is illustrated in Fig. 7, where there was a decrease in the oil sac volume followed by an increase in gonad size (Pasternak et al. 2001). After reproduction was completed and a summer phytoplankton bloom had begun, the oil sac increased in size.

Eggs of group 1 zooplankton are characterized by large yolks, many lipid droplets, lower density than seawater (except *Euchaeta*) and non-feeding by early larval stages (Nakai 1969, Conover 1988, Hagen & Auel 2001, Auel et al. 2003). Since *Calanus hyperboreus*, *Neocalanus cristatus*, *N. plumchrus* and *N. flemingeri* discharge their eggs in deep waters, the early nauplii may ascend more quickly to surface waters due to the positive buoyancy as a result of many lipid droplets. Both *Euchaeta japonica* and *E. norvegica* have major spawns in winter, when little food is available (Hopkins 1977, Båmstedt 1979, Hopkins et al. 1982). The egg yolk allows development without feeding through all naupliar stages and the first copepodite stage (Fig. 9) (Lee et al. 1974). *E. norvegica* females decreased from 1800 to 600 µg lipid/individual after spawning with each egg sac containing 500 µg lipid, while *E. japonica* females used most of their lipids for reproduction, since an egg sac and a gravid female had 560 and 600 µg lipid, respectively (Table 3) (Båmstedt & Matthews 1975). *C. glacialis* seems to have an intermediate position between groups 1 and 2, since it appears to have enough lipid to carry out

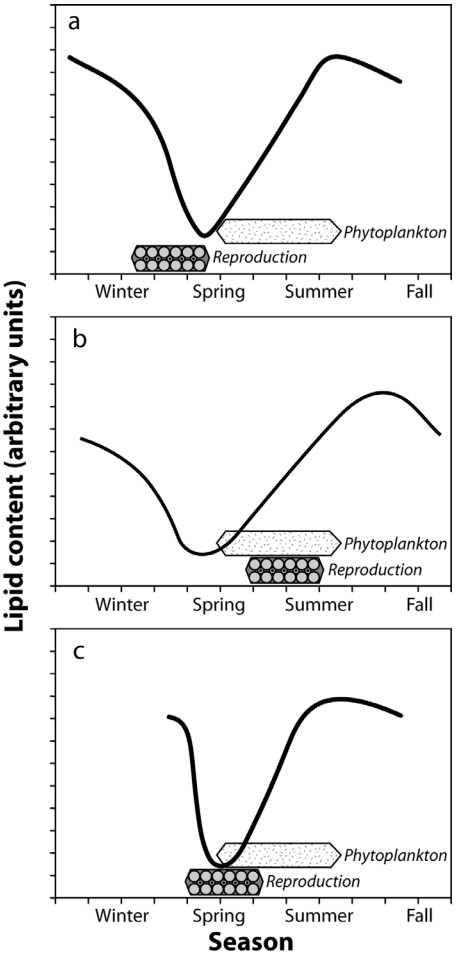

Fig. 8. Changes in lipid content during reproduction of different zooplankton groups. (a) Group 1 zooplankton with reproduction fueled by accumulated lipid; (b) Group 2 zooplankton with reproduction fueled by diet due to insufficient lipid stores; (c) Group 3 zooplankton with reproduction possible before and during phytoplankton bloom. Modified from Falk-Petersen et al. (2000)

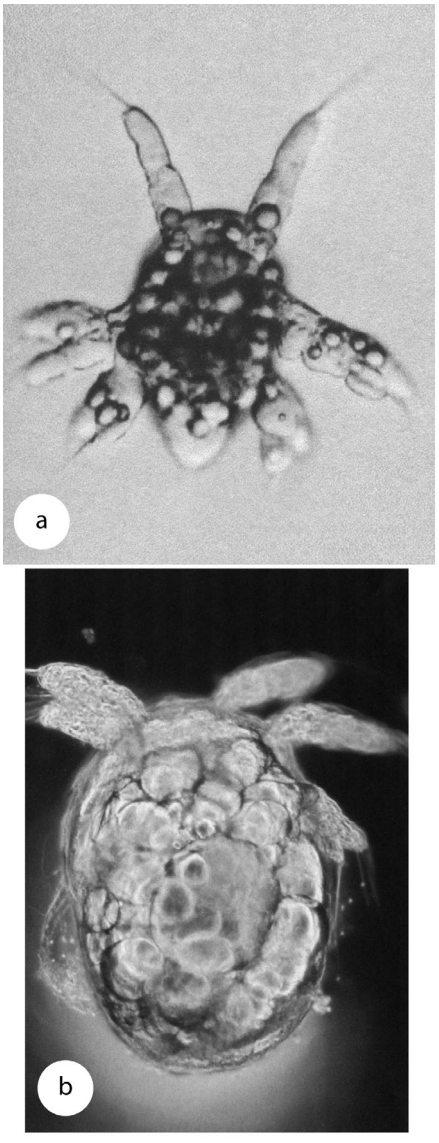

Fig. 9. Light photomicrograph of nauplii. (a) *Neocalanus flemingeri* with large number of lipid droplets (magnification 28×; with permission from Saito & Tsuda 2000); (b) *Euchaeta japonica* with yolk still present in center of nauplius (magnification 70×)

reproduction without additional food, although egg production rates increased up to 6 times when food was offered (Hirche & Kattner 1993).

In contrast, group 2 females need to feed for successful reproduction because they have insufficient amounts of storage lipids. Species including *Calanus australis*, *C. finmarchicus*, *Calanoides carinatus*, and *Euphausia superba* utilize stored lipids during winter but must feed on the spring/summer phytoplankton blooms to produce large amounts of eggs (Fig. 8b) (Hirche & Kattner 1993, Hagen et al. 1996, Falk-Petersen et al. 2000, Hagen & Auel 2001, Quetin & Ross 2001, Niehoff 2004). *C. finmarchicus* egg production has been shown to depend on the concentration of phytoplankton with 600 eggs per female produced under bloom conditions but much lower egg production under low food concentrations (Diel & Tande 1992, Nielsen & Hansen 1995). A female with 105 µg of lipid would need to transfer 42 µg of this lipid into 600 eggs (Table 3). Early in the season a few gravid *C. finmarchicus* females enter surface waters before the phytoplankton bloom, and these early females use lipid stores for egg production (Richardson et al. 1999). However, most females require phytoplankton food for successful reproduction. *E. superba* has 136 and 98 mg lipid in eggs and females, respectively (Table 3). Thus, *E. superba* reproduction takes place during summer,

when phytoplankton concentrations are high enough to provide sufficient energy for successful reproduction.

Group 3 zooplankton (Fig. 8c) are species in which some of the females have sufficient lipid for reproduction while other females require additional food to reproduce successfully. Examples of group 3 include *Euphausia crystallorophias* and *Neocalanus tonsus.* Female *N. tonsus* in deep water in winter (145 µg lipid/female) spawned in the absence of food, but spring females (47 µg lipid/female) in surface waters required food before spawning (Ohman 1987). Based on the amount of lipid per female it was calculated that deep-living females would have a predicted reproductive potential of 285 eggs, as compared to females at the surface in spring with only 4 eggs. In *E. crystallorophias* first spawning takes place before the phytoplankton bloom but the final spawning overlaps with the beginning of the phytoplankton bloom (Kattner & Hagen 1998). *E. crystallorophias* collected before the bloom had 3.1 and 28 mg lipid in eggs and female, respectively, so these females had sufficient lipid stores to supply lipids for the eggs (Table 3).

Most work on the utilization of stored lipids for spawning has been done on zooplankton from polar or westerlies biomes since these animals often build up large lipid stores before reproduction (Båmstedt & Matthews 1975, Herring & Morris 1975, Corkett & McLaren 1978, Båmstedt 1979, Clarke 1980, Gatten al. 1980, Falk-Petersen et al. 1981, 2000, Sargent & Henderson 1986, Hirche 1989, Nicol et al. 1995). Small lipid sacs and lipid droplets in the ovaries during oogenesis have been observed in several tropical and subtropical zooplankters, including *Euchaeta marina*, *Pleuromamma xiphias*, *Anomalocera patersoni* and *Labidocera aestiva* (Figs. 4c & 5a) (Blades-Eckelbarger 1991, Ianora & Santella 1991). Such studies suggest that storage lipids can also play an important role in tropical and subtropical zooplankton reproduction.

Ontogeny

Some zooplankton species produce larvae which must begin feeding soon after hatching (planktotrophic), but others have non-feeding larval stages (lecithotrophic) which rely on yolk lipid stores. In addition, coastal and estuarine benthic invertebrates often produce planktonic larvae which depend on lipid droplets and lipovitellin in their yolks. For example, the non-feeding cyprid larvae of the barnacle *Balanus balanoides* contain numerous large triacylglycerol droplets, which are gradually consumed until the larvae have found a suitable settlement substrate (Holland & Walker 1975, Lucas et al. 1979). Oyster larvae (*Ostrea edulis*) rely on oil droplets, which can have up to 12%DM as triacylglycerols (Holland & Spencer 1973, Holland & Hannant 1974).

Euphausiids have a long and complex larval sequence with 2 naupliar, 1 metanaupliar, 3 calyptopis and 6 furcilia stages before metamorphosis into juveniles. *Euphausia superba* eggs descend to great depth below 1000 m (Marr 1962), and the nauplii and metanauplii must utilize lipids as they migrate to the surface. Krill start feeding with the first calyptopis stage, 20 to 40 d after spawning, so that development from egg to this stage relies on stored lipids. Freshly spawned embryos, gastrulae and limb bud stages of *E. superba* contained 9.4, 7.7 and 5.9 µg of lipid per individual, respectively, showing lipid utilization by the early larval stages of this Antarctic euphausiid (Clarke 1984, Amsler & George 1985). Development of the non-feeding stages from egg to calyptopis, which takes 20 to 40 d in *E. superba*, *E. crystallorophias* and *Thysanoessa longicaudata*, must rely on stored lipids (Fevolden 1980, Clarke & Morris 1983, Hagen 1999). In *E. crystallorophias* the amount of wax esters increases from larvae to adults, as shown in Fig. 10. The role of phosphatidylcholine for energy storage in *E. superba* was discussed above.

Most of the triacylglycerols found in eggs may have been converted from phosphatidylcholine in the storage tissues of the female. The calyptopis and furcilia stages feed in surface waters on the summer phytoplankton bloom, and immature stages, emerging from the furcilia, can accumulate large lipid stores by the end of summer (Kattner & Hagen 1998). However, the furciliae have only a relatively short period in summer to accumulate enough storage lipids if they are to survive as furciliae over winter. The lipids of furcilia III larvae of *E. superba* were 15%DM (early autumn col-

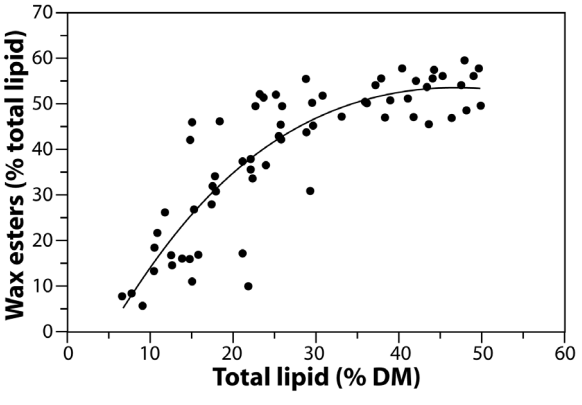

Fig. 10. Antarctic euphausiid *Euphausia crystallorophias*. Increases in wax esters levels (%total lipid) and total lipid (%DM) from larvae to adults. With permission from Kattner & Hagen (1998)

lection) with lipids consisting of 70 and 25% triacylglycerols and phospholipids, respectively (Meyer et al. 2002). Because of their relatively low lipid content, Hagen (1988) calculated that furcilia may last only 9 to 18 d without food. It has been suggested that, because of their relatively low lipid stores and their inability to withstand starvation, overwintering furciliae need to feed on ice algae to survive the winter (Daly 1990, Ross & Quetin 1991, Hagen et al. 1996, 2001, Hagen 1999, Meyer et al. 2002).

Calanoid copepods undergo 12 molts between egg and adult, including 6 naupliar stages (N1 to N6) and, following metamorphosis, 6 copepodite stages, C1 to C5 plus C6, the adult male and female. The first feeding stages for the copepods *Oithona davisae* and *Acartia* spp. are N1 and N2, respectively (Landry 1983, Uchima & Hirano 1986), while N3 is the first feeding stage of *Pseudocalanus* spp., *Calanus hyperboreus*, *C. finmarchicus* and *C. marshallae* (Conover 1967, Marshall & Orr 1972, Corkett & McLaren 1978, Peterson 1986, Williams et al. 1987). In the North Pacific copepod *Euchaeta japonica* and in the Antarctic copepod *E. antarctica*, there are sufficient resources in the egg yolk to allow development through 6 naupliar stages and the 1st copepodite stage before feeding is required (Lee et al. 1974, Yen unpubl. data).

The Arctic copepod *Calanus hyperboreus* reproduces continuously at depth in winter before the spring/summer phytoplankton bloom. The non-feeding stages, N1 & N2, full of lipid droplets (B. Hansen pers. comm.), swim to the surface utilizing their storage lipids. The first feeding stages, N3 to N6, reach the surface with the onset of phytoplankton production (Conover & Huntley 1991, Hirche & Niehoff 1996). It is likely that naupliar and early copepodite stages, which first enter surface waters before phytoplankton is present, will die because they have depleted both lipid droplets and lipovitellin. Similarly, the eggs of the subarctic copepods *Neocalanus cristatus*, *N. plumchrus* and *N. flemingeri* are discharged in deep waters (500 to 2000 m), and the nauplii migrate to the surface (Miller et al. 1984, Miller & Nielsen 1988, Kobari & Ikeda 1999). Photomicrographs of early naupliar stages show that these stages are full of lipid droplets (Fig. 10a), and as result of their lipid stores *N. cristatus* nauplii can develop to C1 without feeding (Saito & Tsuda 2000). In contrast, photomicrographs of early naupliar stages of *Calanus finmarchicus* and *C. pacificus* indicate a relatively small number of lipid droplets, and thus these species must begin feeding by N3 (Hygum et al. 2000a, Lee unpubl. data). Fernandez (1979) found that N3 and N4 of *C. pacificus* could withstand starvation for only 4 to 6 d.

Yolk lipid is utilized while copepods are in their naupliar and early copepodite stages. Lipid does not accumulate during this part of the life history even during extensive feeding. Håkanson (1984) noted that *Calanus pacificus* nauplii did not accumulate storage lipids even in the presence of excess phytoplankton. Similarly, the first 2 copepodite stages did not increase their very low wax ester content when fed higher food concentrations. *Pseudocalanus minutus* early copepodite stages lacked a visible oil sac, while late copepodite stages showed a distinct oil sac (Corkett & McLaren 1969, Klein Breteler & Gonzalez 1988).

High-latitude copepods have low levels of wax esters and triacylglycerols in the first 2 copepodite stages with a gradual increase of these lipids as development proceeds to later copepodite stages (C3 to C5) (Lee et al. 1972, 1974, Håkanson 1984, Kattner & Krause 1987, Hygum et al. 2000b). Fig. 11a shows the accumulation of wax esters in *Calanus finmarchicus* C3 while feeding on a diatom bloom (Hygum et al. 2000c). The study showing increased accumulation of wax esters and triacylglycerols as *C. finmarchicus* developed from C3 to C5 stages was followed by Hygum et al. (2000c) during a spring/summer bloom near Tromsø, northern Norway (Fig. 11b). In mesocosms with different phytoplankton concentrations (100, 200 and 688 µg phytoplankton carbon l^{-1}) there were corresponding increases in *C. finmarchicus* lipids as these copepods developed from C3 to C5 (Fig. 12) (Hygum et al. 2000c, Marker et al. 2003). Phytoplankton concentrations of 100, 300 and 900 µg carbon l^{-1} fed to *C. pacificus* (C4 to C5) corresponded to wax ester contents of 1, 3.2 and 5.5 µg per copepodid, respectively (Fig. 13).

An exception to the gradual accumulation of lipid in later copepodite stages is described for the Antarctic copepod *Paralabidocera antarctica*. It spends much of its life in the sea ice and is an example of copepods with nauplii that accumulate storage lipid. The early naupliar stages of this species enter the sea ice in early autumn, feed on ice algae, build up large stores of triacylglycerols and spend the winter as lipid-rich N4 in the ice (Swadling et al. 2000). In addition, Gannefors et al. (2005) found that the Arctic pteropod *Limacina helicina* overwinters as triacylglycerol-rich veligers.

Coping with food scarcity

The utilization of storage lipids allows zooplankton to survive periods of low food supply. Table 4 gives examples of zooplankton species from 2 groups separated by their differences with respect to lipid accumulation and the ability to withstand starvation. Species of group 1 have little or no storage lipid and can withstand only short periods of starvation, while species of group 2 accumulate large lipid stores to survive long starvation periods.

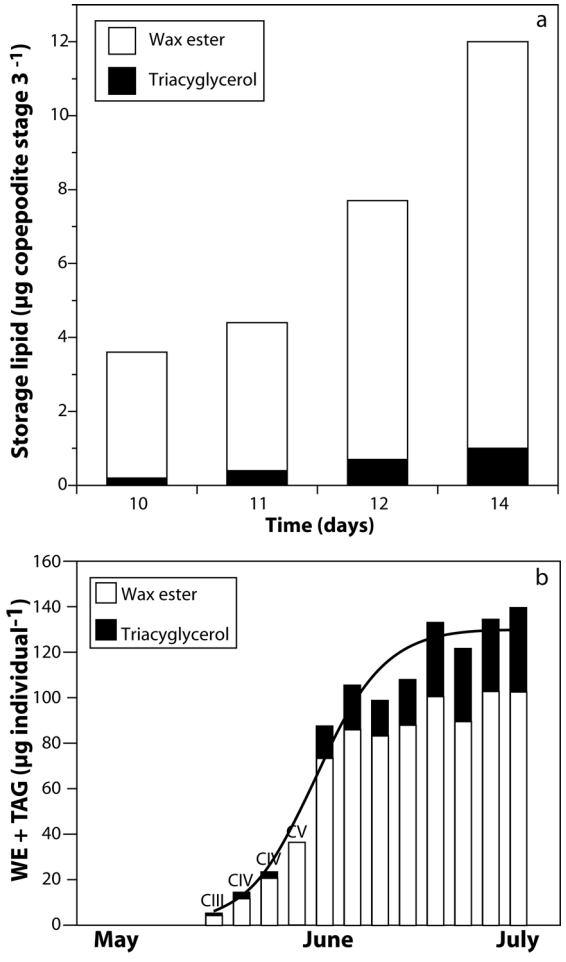

Fig. 11. *Calanus finmarchicus*. (a) Increases in wax ester and triacylglycerol levels of C3 (reared from C1) fed mainly on diatoms in Norwegian fjord mesocosm; modified from Hygum et al. (2000c). (b) Accumulation of wax esters and triacylglycerols (µg/copepodite) by C3–C5 during summer (Tromsø, Norway). Unmarked bars are C5 stages. With permission from Marker et al. (2003)

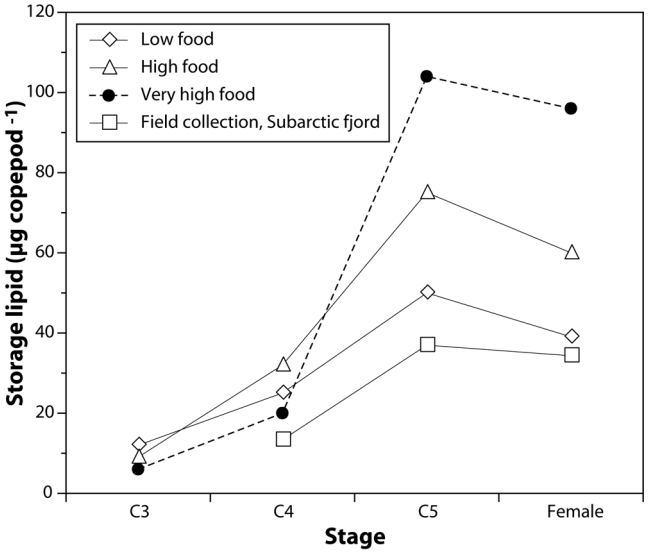

Fig. 12. *Calanus finmarchicus* from field and mesocosms located in Bergen, Norway. Changes in wax ester content from C3 to female. The mesocosms contained different phytoplankton concentrations, primarily diatoms, but dinoflagellates and ciliates were also present. Low, high and very high food concentrations comprised 100, 200 and 688 µg phytoplankton C l^{-1}, respectively (Hygum et al. 2000c, Marker et al. 2003). Field-collected sample came from a subarctic Norwegian fjord (Scott et al. 2000)

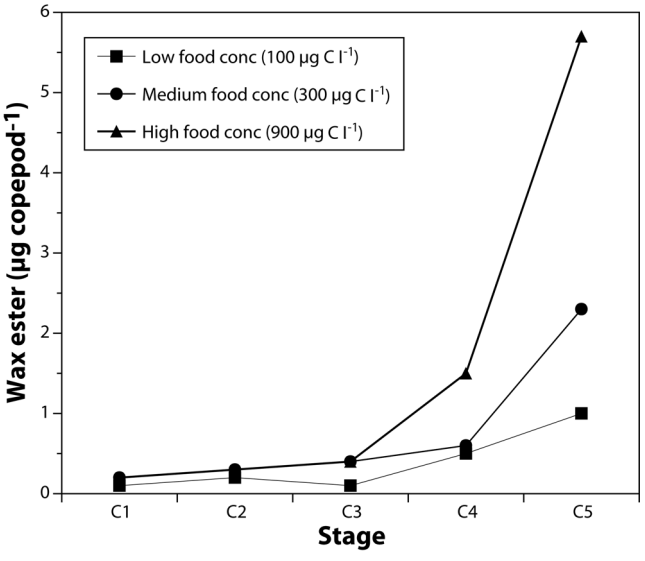

Fig. 13. *Calanus pacificus*. Changes in wax ester levels in C1–C5 fed on different concentrations of diatom *Thalassiosira weissflogii*. With permission from Håkanson (1984)

Lipid-poor species include some inshore and estuarine copepods, epipelagic chaetognaths, cnidarians, ctenophores and tunicates. They grow rapidly during high food periods, but excess food is not converted into large lipid stores. Many of these copepods (*Acartia* spp., *Labidocera acuta*, *L. aestiva*, *Pontella mediterranea*, *Tortanus forcipatus*, *Anomalocera patersoni*) produce resting eggs during low food periods (Fleminger 1957, Zillioux & Gonzalez 1972, Uye et al. 1979, Grice & Marcus 1981, Heinle 1981, Matsuo & Marumo 1982, Miller 1983, Uye 1985, Sullivan & McManus 1986, Marcus 1989, Marcus & Fuller 1989, Lindley 1990, Ianora & Santella 1991). Low food concentrations are generally available year round to zooplankton in tropical or subtropical waters. Zooplankton from these warm-water areas is characterized by low amounts of storage lipids and generally cannot withstand more than a few days of starvation (Reeve et al. 1970, Nival et al. 1974, Cosper & Reeve 1975, Uye 1981, Gardner & Paffenhöfer 1982, Feigenbaum & Maris 1984, Feigenbaum 1991).

Table 4. Total lipid data in relation to starvation tolerance of lipid-poor (group 1) and lipid-rich zooplankton species (group 2)

	Lipid mass (µg ind.$^{-1}$)	Lipid (%DM)	Starvation (d)	Location	Source
Group 1					
Copepoda					
A. clausi	1.4	3	3–6	N Atlantic/N Pacific	Mayzaud (1976), Harris et al. (1977), Kayama & Mankura (1980), Uye (1981)
A. tonsa	2	16–19	6–10	Inshore & estuarine	Lee & Hirota (1973), Dagg (1977), Houde & Roman (1987)
C. typicus	7.8	13	3–6	Mediterranean estuaries	Dagg (1977), Harris et al. (1977), Nival et al. (1990)
E. pileatus	–	–	8	NW Atlantic shelves	Gardner & Paffenhöfer (1982)
L. trispinosa	30	14	2–3	California Current	Lee & Hirota (1973), Lee (unpubl. data)
T. stylifera	–	–	27	Mediterranean Sea	Nival et al. (1990)
Ctenophora					
Mnemiopsis leidyi	–	4	5	Tropical Caribbean Sea	Kremer & Reeve (1989), Lee (unpubl. data)
Pleurobrachia pileus	300	2–9	2–14	N Pacific	Lee (1974a), Hoeger (1983)
Chaetognatha					
Sagitta hispida	100	4	7	Caribbean Atlantic	Reeve et al. (1970), Lee (unpubl. data)
Group 2					
Copepoda					
C. australis	31	17	>10	Benguela Current	Attwood & Peterson (1989)
C. carinatus	131	70	12–21	Benguela Current	Borchers & Hutchings (1986)
C. finmarchicus	220	50	>21	N Atlantic	Dagg (1977), Sargent & Henderson (1986)
C. glacialis	400	56	>270	Boreal Arctic	Lee (1975), Hirche (1989), Hirche & Kattner (1993)
C. pacificus	140	45	>21	N Pacific	Lee & Hirota (1973), Runge (1984), Hassett & Landry (1990)
C. hyperboreus	1700	74	>90	High Arctic	Conover (1964), Lee (1974b)
C. plumchrus	410	59	>50	N Pacific	Benson et al. (1972)
E. norvegica	1400	46	>90	N Atlantic	Båmstedt & Matthews (1975), Sargent & Henderson (1986)
G. princeps	760	28	>60	California Current	Lee & Barnes (1975)
P. minutus	2.1	17	>14	NW, NE Atlantic shelves	Corkett & McLaren (1969), Dagg (1977), Fraser et al. (1989), Båmstedt et al. (1990)
Euphausiacea					
E. superba	98000	35	>211	Antarctic	Clarke (1980,1984a), Ikeda & Dixon (1982)
Pteropoda					
Clione limacina	4400	31	>90	N Pacific	Lee (1974a)
Clione limacina	12000	19	356	Arctic, Svalbard	Böer et al. (2005)

Lipid-rich taxa, such as copepods, euphausiids, decapods and certain pteropods from polar and temperate regions, accumulate large lipid stores during periods of high food availability followed by long starvation periods. The starvation survival times given in Table 4 for these taxa may be underestimates since bacterial infections and other factors make long laboratory starvation studies difficult to carry out. Such studies were undertaken by Ikeda & Dixon (1982) and Hirche (1989), where *Euphausia superba* and *Calanus glacialis* were starved for 211 and 270 d, respectively. Each year diapausing polar copepods have to cope with 270 or more days of starvation since they enter deep waters in summer and do not reenter surface waters until the following spring. The starvation survival times given in Table 4 are for adults or near adults, since the larval stages often cannot survive more than a few days without food (Fernandez 1979, Ikeda & Dixon 1982, Ikeda 1984, Borchers & Hutchings 1986). However, some species, e.g. *Neocalanus cristatus* and *Euchaeta japonica*, have larval forms with large lipid stores to withstand long starvation periods (Lee et al. 1974, Saito & Tsuda 2000).

Diapause

Lipid accumulation of many herbivorous copepods is closely linked to phytoplankton blooms. They feed extensively during blooms and accumulate large lipid stores. As a result of excess food these copepod species build up lipid stores and migrate to deep waters for diapause (Fig. 14, Table 5). Some species with insufficient storage lipids remain at the surface and overwinter with an omnivorous feeding strategy.

The best characterized of these copepods are species of the genera *Calanus*, *Calanoides* and *Neocalanus* from various ocean regions (Fig. 15). In polar regions, *Calanus hyperboreus* and *Calanus glacialis* exist in the Arctic and *Calanoides acutus* in the Antarctic. In boreal and temperate regions *Calanus finmarchicus* and *Calanus helgolandicus* occur in the North Atlantic, *Calanoides carinatus* in the South Atlantic/Northwest Indian and northwestern Arabian upwelling regions, *Neocalanus plumchrus/N. cristatus* in the North Pacific and *N. tonsus*

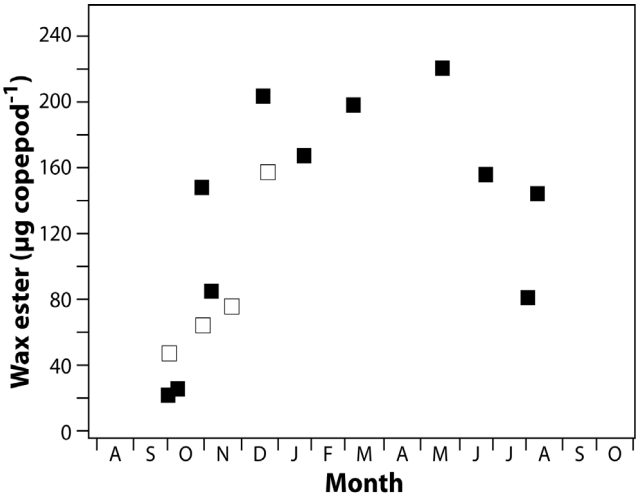

Fig. 14. *Neocalanus tonsus* (C5). Seasonal changes in wax ester levels (µg/copepod). Animals collected (□) in surface waters (0–105 m); (■) in deep waters (500–1000 m). With permission from Ohman et al. (1989)

Table 5. *Calanus* spp., *Calanoides* spp. and *Neocalanus* spp. Total lipid, storage lipid classes and related data of copepods that undergo deep-water diapause in various biomes

	Location	Diapause depth (m)	Diapause period	Spawning period	Diapause stage (C5) Lipid mass (µg ind.$^{-1}$)	Lipid (%DM)	WE (%TL)	TAG (%TL)	Source
C. hyperboreus	High Arctic	1000–2000	Sep–Mar	Jan–Apr	2800	45	91	4	a
C. glacialis	High Arctic	500–1000	Oct–Mar	Apr–Jun	631	61	76	6	b
C. finmarchicus	N Atlantic	500–1500	Oct–Mar	Mar–Jun	141	64	82	3	c
C. helgolandicus	N Atlantic	400–900	Jul–Feb	Mar–Apr	130	67	90	1	d
C. carinatus	Benguela NW Indian Ocean	300–700	Oct–May non-upwelling	Jul–Sep upwelling	70–100	42–71	86–93	4–9	e
C. acutus	Antarctic	500–1000	Feb–Oct	Nov	93	47	94	3	f
N. tonsus	S Pacific	500–1000	Jan–Sep	Aug–Sep	200–250	40	92	4	g
N. plumchrus	N Pacific	300–1000	Jul–Jan	Nov–Feb	600	67	86	4	h
N. cristatus	N Pacific	500–2000	Jul–Nov	Nov–Feb	1800	69	86	6	i
C. pacificus	N Pacific	200–500	Oct–Feb	Mar–Apr Sep–Oct	145	41	41	15	j

(a) Østvedt (1955), Lee (1974b), Dawson (1978), Head & Harris (1985), Conover (1988), Conover & Siferd (1993), Hirche (1997), Scott et al. (2000), Auel et al. (2003)
(b) Båmstedt (1984), McLaren & Corkett (1984), Corkett et al. (1986), Conover (1988), Tande & Henderson (1988), Slagstad & Tande (1990), Smith (1990), Kosobokova (1990), Tourangeau & Runge (1991), Scott et al. (2000), Pasternak et al. (2002), Ringuette et al. (2002)
(c) Østvedt (1955), Marshall & Orr (1972), Smith (1988), Pedersen et al. (1995), Hirche (1996), Heath (1999), Heath & Jónasdóttir (1999), Richardson et al. (1999), Gislason et al. (2000), Jónasdóttir et al. (2002)
(d) Gatten et al. (1979, 1980), Williams & Conway (1988)
(e) Menshah (1974), Smith (1984, 2001), Borchers & Hutchings (1986), Timonin et al. (1992), Arashkevich et al. (1996), Arashkevich & Drits (1997), Verheye et al. (2005)
(f) Schnack-Schiel et al. (1991), Kattner et al. (1994a), Schnack-Schiel & Hagen (1994, 1995)
(g) Jillett (1968), Ohman (1987), Ohman et al. (1989)
(h) Vinogradov (1968), Minoda (1971), Ikeda (1972), Fulton (1973), Lee (1974b), Miller et al. (1984), Smith & Vidal (1986), Mackas (1992), Mackas & Tsuda (1999), Evanson et al. (2000), Lee (unpubl. data)
(i) Ikeda (1972), Lee & Hirota (1973), Kayama (1982), Miller et al. (1984), Smith & Vidal (1986), Mackas & Tsuda (1999), Saito & Kotani (2000), Saito & Tsuda (2000), Lee (unpubl. data)
(j) Longhurst (1967), Lee & Hirota (1973), Aldredge et al. (1984), Smith & Vidal (1986), Ohman (1988), Osgood & Frost (1994)

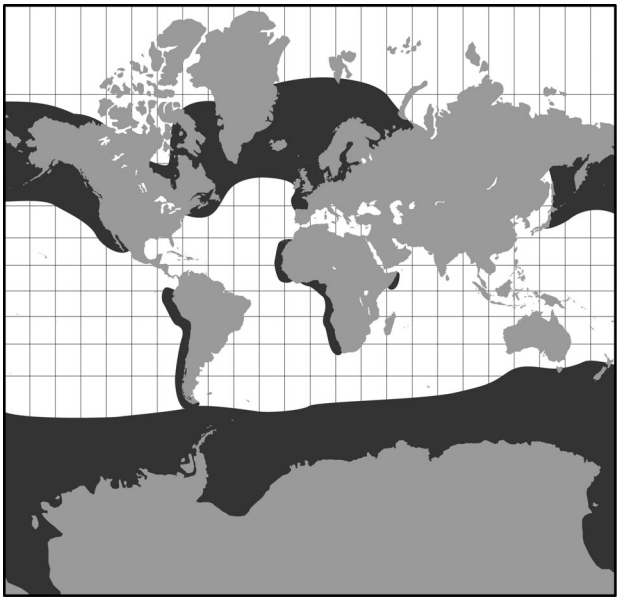

Fig. 15. Ocean regions (shaded in black), where various Calanidae (C5) undergo diapause after accumulation of large wax ester stores. The species include *Calanoides carinatus* (South Africa, Gulf of Aden), *Calanus pacificus* (California, USA), *C. marshallae* (Oregon, Washington, USA), *C. chilensis*, *C. australis* (South America), *C. finmarchicus* (north Atlantic), *C. hyperboreus*, *C. glacialis* (Arctic), *Neocalanus cristatus*, *N. plumchrus* (north Pacific), *Calanoides acutus* (Antarctic), *N. tonsus* (subantarctic)

in the subantarctic. In coastal waters *Calanus pacificus* is found in the North Pacific. Although storage lipid data are not available, it is likely that *Calanus sinicus* in the coastal China Sea builds up storage lipids since this species diapauses during summer and can withstand more than 30 d of starvation (Sun et al. 2002).

The presence of oil sacs filled with wax esters are a distinctive feature of diapausing copepods (Figs. 2 & 3a) so that more than half of the dry mass can be lipid. The reason for the use of wax esters in deep diapausing copepods is perhaps due to the fact that the thermal expansion and compressibility of wax esters is higher than that of seawater (Yayanos et al. 1978). Visser & Jónasdóttir (1999) suggested that a copepod, which is positively buoyant in warm surface waters, can become neutrally buoyant in cold deep water. As a result, even though the copepods are full of lipids, they should require minimal energy to maintain themselves in deep cold waters. Campbell & Dower (2003) discussed the difficulty of maintaining neutral buoyancy by these lipid-rich zooplankton species. In addition to diapausing copepods, most deep-water zooplankters, independent of latitude, have high amounts of wax esters (Lee et al. 1971a, Lee & Hirota 1973). The neutral buoyancy provided by wax esters in cold deep water may be advantageous to these deep-water zooplankton species.

The life cycle of high-latitude diapausing copepods has a strong linkage to the spring/summer phytoplankton blooms. Reproduction often occurs just before or during the phytoplankton bloom. At some point nauplii, after hatching, begin feeding on phytoplankton. They then undergo metamorphosis and exhibit highest lipid accumulation in C5 or adult (Figs. 11b & 16, Table 5). Many species migrate into deep waters after the accumulation of large wax ester stores. This can even occur when phytoplankton is still available; hence, maximum lipid accumulation may provide a signal for C5 to descend to deep waters (Irigoien 2004). Much larger lipid deposits are present in deeper-dwelling copepods as compared to those in upper layers (Båmstedt 1984) (Fig. 17a). Jónasdóttir (1999) found a linear relationship between the amount of storage lipid in *Calanus finmarchicus* and the depth of capture (Fig. 17b). Similarly, Pasternak et al. (2001) noted a much larger oil sac volume for deep-water *C. finmarchicus* C5 compared to the same stage in upper layers. A small percentage of *C. finmarchicus* developed into C5 late in the season. We hypothesize that these copepods do not receive the signal to descend because of insufficient lipid stores and thus spend the winter in surface waters. It seems likely that many of

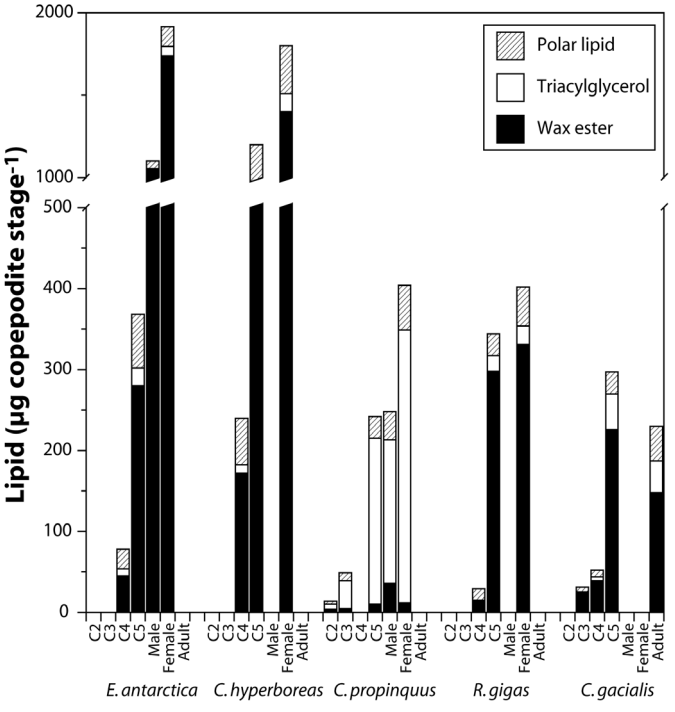

Fig. 16. Wax ester, triacylglycerol and polar lipid levels (µg per copepodid) of various copepodite stages and adults of Antarctic (*Euchaeta antarctica*, *Calanus propinquus*, *Rhincalanus gigas*) and Arctic copepods (*C. hyperboreus*, *C. glacialis*). Data from Hagen (1988), Tande & Henderson (1988), Kattner et al. (1994a), Scott et al. (2000)

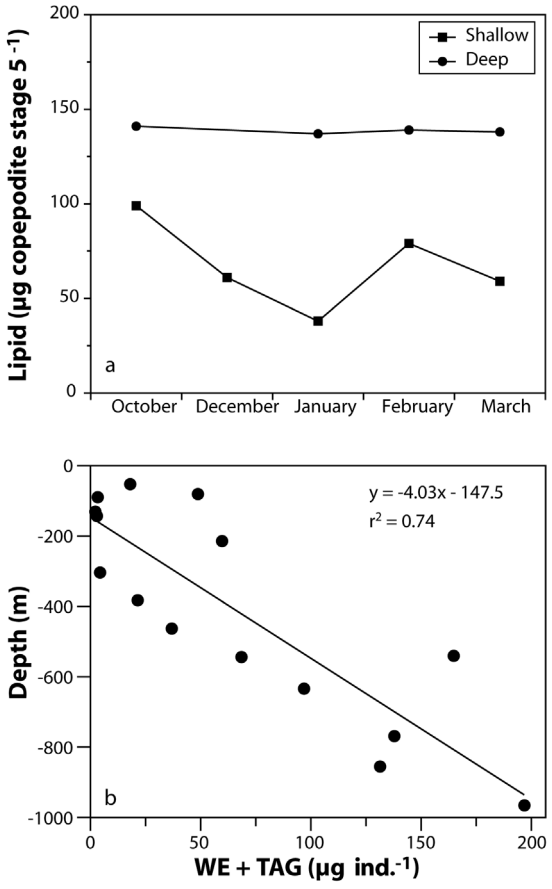

Fig. 17. *Calanus finmarchicus* (C5). (a) Lipid levels (µg ind.$^{-1}$) of specimens collected from October to March in shallower waters (<400 m) and deeper waters (>400 m). (b) Correlation of wax ester plus triacylglycerol level (µg/C5) with capture depth (specimens collected in January). Data from Jónasdóttir (1999)

these copepods will die due to poor resources for overwintering.

Another copepod, the North Pacific *Neocalanus cristatus*, reaches adulthood in deep water during winter, and its reproduction peak occurs in November. The hatched nauplii ascend to the surface utilizing lipid reserves. The late naupliar and early copepodite stages feed on the spring bloom. After extensive feeding, the summer C5 is full of wax esters and descends into deep waters from July through October, completing the life cycle (Miller et al. 1984). *N. plumchrus* C5 stages enter deep waters in July and remain in diapause from July to January, followed by deep-water reproduction in January and February, and ascend as nauplii to surface waters (Fulton 1973). Campbell et al. (2004) observed that *N. plumchrus* C5 stages, collected in the Strait of Georgia, use approx. ¼ of their wax ester stores for overwintering prior to moulting. In both *Neocalanus* species C5 stages enter deep cold water, while phytoplankton concentrations in the surface waters are still high. A somewhat different situation occurs in the Arctic copepods *Calanus hyberboreus* and *C. glacialis*, since the spring/summer phytoplankton bloom is very short, and many of the copepodids do not develop into C5 during the 1st year. C3 and C4 stages usually have sufficient wax ester stores at the end of the phytoplankton bloom to descend into deep waters for winter diapause. These C3 and C4 stages develop into C5 during the following summer (Conover 1967, Båmstedt 1984, Corkett et al. 1986, Kosobokova 1990, Conover & Huntley 1991, Hirche & Kattner 1993). *C. hyperboreus* C5 specimens can accumulate up to 2800 µg lipid per individual before descending to deep waters (Head & Harris 1985).

Wax esters vs. triacylglycerols

In herbivorous copepods with large amounts of wax esters stored in oil sacs, triacylglycerols and wax esters are utilized and accumulated at very different rates. Triacylglycerol content is generally an order of magnitude lower than wax ester content (Fig. 18). The oil sacs in these copepods contain only wax esters (Benson et al. 1972), whereas triacylglycerols are stored in other body regions, likely in the form of lipid droplets (Sargent & Henderson 1986).

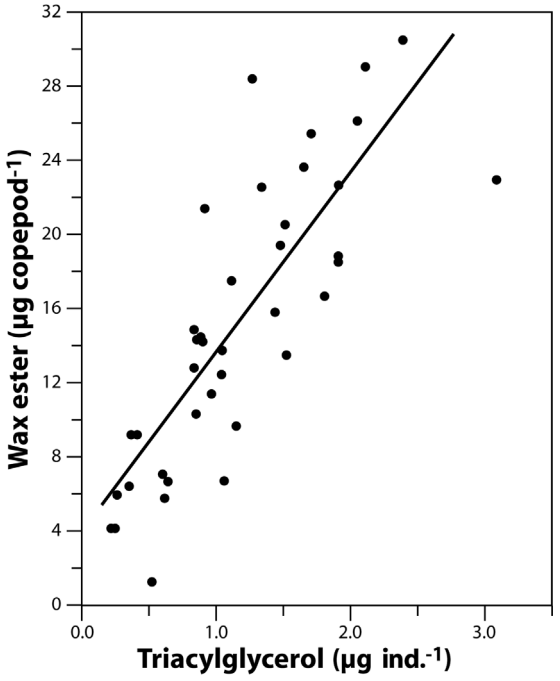

Fig. 18. *Calanus pacificus* (C5) from different stations in California Current. Mean wax ester vs. triacylglycerol levels (µg/C5). With permission from Håkanson (1987)

A pathway can be described where copepods, provided with an excess of food, assemble storage lipids in 2 phases. The initial phase is the synthesis and storage of triacylglycerol droplets; the second phase is the synthesis and storage of wax esters in an oil sac (Miller et al. 1998). Starvation of wax-ester-rich copepods (*Calanus pacificus*, *C. helgolandicus*, *Euchaeta japonica*, *Gaussia princeps*) resulted in preferential utilization of triacylglycerols, followed by a slower rate of wax ester utilization (Lee et al. 1974, Lee & Barnes 1975, Sargent et al. 1977, Håkanson 1984). Because triacylglycerols and wax esters are utilized at very different rates, 2 different lipases may be responsible for the catabolism of triacylglycerols and wax esters. Triacylglycerols can be quickly hydrolyzed to provide energy for short-term needs. In contrast, wax esters are carefully regulated by wax ester lipases, allowing for their slower utilization rates during diapause and reproduction.

Sargent & Henderson (1986) hypothesized that wax esters are mobilized by a hormone-sensitive lipase. It seems likely that hormones play an important role in the regulation of wax ester utilization, particularly during reproduction, when there is a high energy demand. Triacylglycerols can account for up to 20% of total lipid in wax-ester- rich herbivorous copepods during their active feeding period, but during diapause they become a minor lipid component. When copepods leave diapause in late winter or spring to begin reproduction, triacylglycerol content again increases, suggesting that wax esters are converted to triacylglycerols for reproductive needs (Sargent & Henderson 1986, Heath & Jónasdóttir 1999, Jónasdóttir 1999, Richardson et al. 1999).

LIPID STORAGE IN DIFFERENT OCEAN BIOMES

Since lipid storage patterns strongly differ in various regions it is important to compare lipid levels and compositions of zooplankton collected in different ocean biomes and provinces. Based on a number of ecological factors, Longhurst (1998) divided the ocean into 4 major biomes: polar, westerlies, trades/tropical and coastal biomes. These major biome categories are further subdivided into smaller units, e.g. the polar biome includes the Atlantic, Pacific and Antarctic biomes. Within each biome are a number of provinces with different biogeochemical characteristics, which led Longhurst (1998) to partition the ocean into 51 provinces. Estuaries within the coastal biome are somewhat different from other provinces of this biome since they are characterized by large numbers of meroplanktonic larvae with lipid stores (Holland & Walker 1975, Lucas et al. 1979). Sufficient studies have been carried out to allow general statements on the importance of storage lipids in the major biomes. However, zooplankton from a number of provinces has not been investigated with respect to lipid accumulation, especially within the Indian Ocean biomes.

Polar biome

Characteristic features of provinces within the polar biome are winter ice cover, seasonally migrating marginal ice zones, ice algae and a relatively short spring/summer primary production period. In general, a variety of zooplankton groups, e.g. crustaceans and pteropods, show a pronounced lipid accumulation during summer phytoplankton blooms (Hagen 1988, Hagen & Schnack-Schiel 1996, Falk-Petersen et al. 2000, Gannefors et al. 2005, Böer et al. 2005). There is some evidence of lipid accumulation in the boreal chaetognaths *Parasagitta elegans* and *Eukrohnia hamata* during the spring/summer phytoplankton blooms (Båmstedt 1978, Choe et al. 2003) and in Arctic ctenophores during feeding on copepods (Falk-Petersen et al. 2002, Lundberg 2003). While the Arctic is characterized by large populations of diapausing copepods, which overwinter in deep waters, Antarctic waters are usually inhabited by large euphausiid populations, which do not undergo diapause but remain in surface waters during winter (Falk-Petersen et al. 2000).

Antarctic euphausiids accumulate different storage lipids (Tables 3 & 8) and do not reach the very high lipid levels found in many polar copepods (Tables 5 to 7). In addition to the copepods, most Arctic planktonic crustaceans, such as the amphipods *Themisto libellula* and *T. abyssorum*, have large lipid stores, up to 42%DM, 41 to 43% of them being wax esters (Auel et al. 2002). While wax esters are the predominant storage lipid in most polar zooplankton (Conover & Huntley 1991, Albers et al. 1996), triacylglycerols are an

Table 6. Total lipid and storage lipid class data of Arctic copepods (C4 to females [f]; Svalbard, Aug-Sept) (Scott et al. 2000)

Species	Stage	Lipid mass (µg ind.$^{-1}$)	Total lipid (%DM)	WE (%TL)	TAG (%TL)
Calanus finmarchicus	C4	20	53	44	10
	C5	50	34	68	5
	f	50	24	62	6
Calanus glacialis	C4	40	56	68	2
	C5	400	62	72	6
	f	480	70	68	8
Calanus hyperboreus	C4	240	54	72	4
	C5	1200	65	75	8
	f	1800	62	75	6

Table 7. Total lipid and storage lipid class data of copepod genera from different biomes (+: trace amounts)

Species and stage	Lipid mass (µg ind.$^{-1}$)	Total lipid (%DM)	WE (%TL)	TAG (%TL)	Location	Source
Rhincalanus						
R. gigas C5	390	30	75	2	Antarctic (64°S)	Kattner et al. (1994), Schnack-Schiel & Hagen (1994)
R. gigas f	400	69	92	1	Antarctic (53°S)	Lee & Hirota (1973)
R. nasutus f	120	42	69	9	N Pacific (31°N)	Lee & Hirota (1973)
R. nasutus f	68	31	87	3	Red Sea (21–28°N)	Sommer et al. (2002), Hagen (unpubl. data)
Metridia						
M. gerlachei C5	33	16	27	19	Antarctic (72–78°S)	Graeve et al. (1994a)
M. gerlachei f	59	19	42	22	Antarctic (72–78°S)	Graeve et al. (1994a)
M. longa f	200	57	76	10	Arctic (84–88°N)	Lee (1975)
M. princeps f	100	12	41	4	N Pacific (31°N)	Lee et al. (1971a)
M. okhotensis f	367	75	91	3	N Pacific (38°N)	Saito & Kotani (2000)
Euchirella						
E. rostromagna C5	1600	45	89	7	Antarctic (72–78°N)	Hagen et al. (1995)
E. rostromagna f	1900	42	94	3	Antarctic (72–78°N)	Hagen et al. (1995)
E. rostrata f, m	140	21	0	37	N Pacific (31°N)	Lee et al. (1971a)
E. galeata f	60	4	0	14	N Pacific (31°N)	Lee et al. (1971a)
E. pulchra f	50	12	2	18	N Pacific (31°N)	Lee et al. (1971a)
E. brevis C5	70	27	7	16	S Pacific (24°S)	Lee & Hirota (1973)
E. brevis f	60	17	+	11	S Pacific (24°S)	Lee & Hirota (1973)
Euchaeta, *Paraeuchaeta*						
E. antarctica C5	1600	45	89	7	Antarctic (72–75°S)	Hagen et al. (1995)
E. antarctica f	2000	42	94	3	Antarctic (72–75°S)	Hagen et al. (1995)
E. norvegica C5	1040	43	60	15	N Atlantic (60°N)	Sargent et al. (1974)
E. norvegica f	1410	47			N Atlantic (60°N)	Båmstedt & Matthews (1975)
E. japonica C5	520	50	81	2	N Pacific (50°N)	Lee et al. (1974)
E. japonica f	600	52	60	17	N Pacific (50°N)	Lee et al. (1974)
P. barbata f	1800	48	68	9	Arctic (83–88°N)	Lee (1975)
P. glacialis f	500	43	72	9	Arctic (83–88°N)	Lee (1975)
P. rubra f	1600	57	65	11	N Pacific (31°N)	Lee et al. (1971a)
E. marina f, m	30	29	31	4	S Atlantic (24°S)	Lee & Hirota (1973)
Calanus, *Neo-*, *Eucalanus*						
C. propinquus f	720	45	3	91	Antarctic (70–75°S)	Kattner et al. (1994a), Falk-Petersen et al. (1999)
C. hyperboreus f	2100	66	91	4	Arctic (88°N)	Lee (1974b)
C. hyperboreus f	1800–2000	47–62	75	6	Arctic (78–79°N)	Scott et al. (2000), Auel et al. (2003)
C. glacialis f	480	70	68	8	Arctic (78°N)	Scott et al. (2000)
C. finmarchicus f	50	31	62	6	Arctic (78°N)	Scott et al. (2000)
C. finmarchicus f	80	40	60	10	N Atlantic (60°N)	Jónasdóttir (1999)
C. pacificus f	70	27	20	2	N Pacific (50°N)	Lee & Hirota (1973)
N. plumchrus f	410	59	86	7	N Pacific (50°N)	Lee & Hirota (1973)
N. flemingeri C5	287	53	88	6	N Pacific (38°N)	Saito & Kotani (2000)
E. bungii f	352	32	10	80	N Pacific (38°N)	Saito & Kotani (2000)
C. pacificus C5	15	20	50	5	N Pacific (33°N)	Håkanson (1984)
C. gracilis f	80	26	21	17	N Pacific (33°N)	Lee & Hirota (1973)
C. robustior f	30	8	21	3	N Pacific (33°N)	Lee & Hirota (1973)
C. gracilis f	30	11	31	8	S Pacific (24°S)	Lee & Hirota (1973)
C. minor f	1	3	+	3	S Pacific (24°S)	Lee & Hirota (1973)
N. tonsus f	162	34	90	1	S Pacific (45°S)	Ohman (1987), Ohman et al. (1989)

Table 8. Total lipid and storage lipid class data of euphausiids from different biomes

Species	Lipid mass (mg ind.$^{-1}$)	Total lipid (%DM)	WE (%TL)	TAG (%TL)	Location	Source
Euphausia						
E. superba	34.9	27	–	49	Antarctic (73°S)	Hagen (1988)
E. superba	74.0	44	–	51	Antarctic (69°S)	Atkinson et al. (2002)
E. crystallorophias	10.5	34	47	6	Antarctic (73°S)	Hagen (1988)
E. crystallorophias	8.4	34	47	6	Antarctic (70°S)	Falk-Petersen et al. (1999)
E. lucens	0.9	5	–	2	N Atlantic (15°N)	Kattner et al. (unpubl. data)
E. gibboides	1.8	10	–	8	S Atlantic (18°S)	Kattner et al. (unpubl. data)
E. pacifica	2.3	19	1	17	N Pacific (50°N)	Lee (1974a)
E. recurva	0.4	7	+	21	S Pacific (24°S)	Lee & Hirota (1973)
E. americana	0.1		–	–	Gulf of Mexico	Morris & Hopkins (1983)
Thysanoessa						
T. macrura	6.3	37	56	2	Antarctic (73°S)	Hagen (1988)
T. raschii	–	23	–	–	N Pacific (50°N)	Sargent & Lee (1975)
T. raschii	–	38	10	44	N Atlantic (70°N)	Falk-Petersen (1981)
T. inermis	–	47	40	28	N Atlantic (70°N)	Falk-Petersen (1981)

important storage lipid in Antarctic species such as *Euphausia superba*, *Calanus propinquus*, *C. simillimus*, *Stephos longipes* and *Euchirella rostromagna* (Tables 7 & 8) (Hagen 1988, Schnack-Schiel et al. 1991, Hagen et al. 1993, Ward et al. 1996).

Most ice-associated zooplankton in polar regions are high in triacylglycerols rather than wax esters. Cryopelagic amphipods (*Gammarus wilkitzkii*, *Apherusa glacialis*, *Onisimus nanseni*, *O. glacialis*) and copepods (*Jaschnovia brevis*), which live in the Arctic sea ice, have lipid contents ranging from 28 to 51% DM (Scott et al. 1999, 2001, 2002, Scott 2000). This appears to be also true for the Antarctic ice-associated copepods *Stephos longipes* and *Paralabidocera antarctica* (Schnack-Schiel et al. 1995, Swadling 2000). Species with large triacylglycerol stores do not undergo a winter diapause.

In addition to wax esters and triacylglycerols, the polar biomes have zooplankton with 2 unusual storage lipids, diacylglycerol ethers and phosphatidylcholine. Large amounts of diacylglycerol ethers have been found in the pteropod *Clione limacina* from both Arctic and Antarctic waters (Phleger et al. 1997, Kattner et al. 1998, Falk-Petersen et al. 2001, Böer et al. 2005). The Antarctic euphausiids *Euphausia superba*, *E. triacantha* and *Thysanoessa macrura* use phospholipids, primarily phosphatidylcholine, as a storage lipid (Hagen et al. 1996, Stübing 2004). Thus, *E. superba* has stores of both triacylglycerols and phosphatidylcholine. There is also some evidence that phospholipids play a storage function in the subarctic and Arctic euphausiids *Thysanoessa inermis* and *T. raschii* (Saether et al. 1986).

While most crustacean species in polar provinces have high lipid concentrations, several groups including cnidarians, ctenophores and tunicates do not accumulate significant amounts of storage lipids (Table 4). However, oil droplets have been observed in the gastrovascular system of polar medusae and ctenophores (Larson & Harbison 1989). It was suggested that these oil droplets were obtained from their prey, e.g. lipid-rich *Calanus*, since the oil droplets were absent from non-digestive tissues and rapidly disappeared during starvation. Salps grow rapidly and reproduce asexually during phytoplankton blooms but do not convert excess food into storage lipids. *Salpa thompsoni* from the Antarctic contained only 0.9%DM lipid (Hagen 1988, Phleger et al. 1998). A year with high abundance of *S. thompsoni* is generally a year with relatively low numbers of *Euphausia superba* (Loeb et al. 1997). Large salp populations are associated with winters of low ice cover, which results in an early spring bloom, and this allows an early and rapid increase of the salp population (Longhurst 1998). In contrast, large populations of *E. superba* occurred during heavy ice winters, which is associated with intensive spawning. It is interesting that these 2 zooplankton groups, both of which are primarily herbivorous, differ markedly in their different strategies with respect to lipid storage. Ohman et al. (1998) found very different seasonal dormancy patterns for 4 copepod species (*Eucalanus californicus*, *Rhincalanus nasutus*, *Calanus pacificus*, *Metridia pacifica*) in the California Current Province. *C. pacificus* in winter had dormant adults in deep water with more wax esters than actively reproducing adults in surface waters. The authors described this species as having a biphasic life history. In contrast, *M. pacifica* adult females with relatively low wax esters and triacylglycerols showed no evidence of dormancy. Adults and copepodid stage V of wax-ester-rich *R. nasutus* and triacylglycerol-rich *E. californicus* were dormant in winter but responded rapidly to changes in food availability.

Coastal boundary zone biome

It is difficult to generalize about this biome since its provinces are quite diverse. They range from coral reefs in the tropical coastal areas to the relatively shallow Baltic Sea in the North Atlantic coastal zones. Up- and downwelling is a feature of several provinces in this biome, including the Alaska Downwelling Coastal Province, the California Current Province, the Northwest Arabian Upwelling Province and the Benguela Current Coastal Province. Coastal zone province species and their lipid data are listed in Tables 4, 5, 7 & 8 and Fig. 19. Upwelling of nutrient-rich waters results in phytoplankton blooms, followed by phytoplankton decreases after depletion of nutrients. There is a buildup of storage lipids by *Calanus* spp. during upwelling followed by descent and diapause during non-upwelling periods (Table 5). Experimental evidence showed that *C. pacificus* lipid levels increased linearly as the copepod was offered increasing concentrations of the diatom *Skeletonema costatum* (Fig. 20a). A field study of wax ester accumulation by *C. pacificus* in the California Current Province gave results similar to those observed in the experimental study (Håkanson 1987). The wax ester content of the copepods at each collection site closely correlated with the different primary production rates (Fig. 20b). Wax esters are the dominant lipid class in diapausing copepods from upwelling areas, but other zooplankton in this biome often have triacylglycerols as the major storage lipid (Tables 4, 7 & 8), including lecithotrophic meroplanktonic larvae with large lipid stores (Kattner et al. 2003).

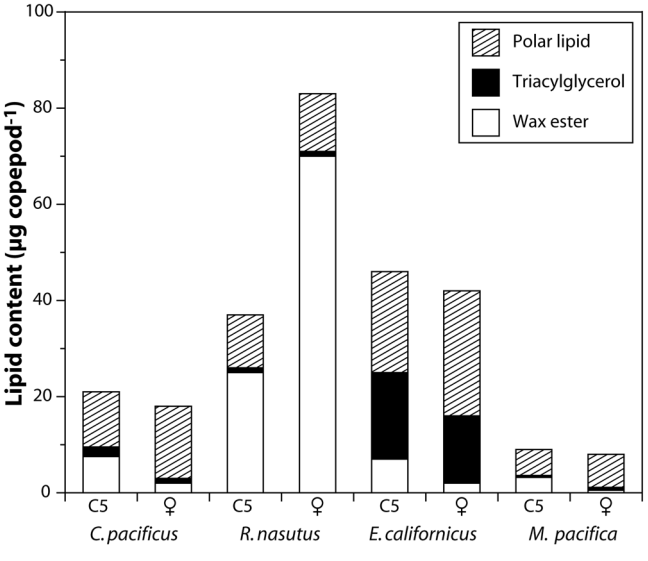

Fig. 19. Wax ester, triacylglycerol and polar lipid levels (µg per stage) of C5 and adults of different copepod species (*Calanus pacificus*, *Rhincalanus nasutus*, *Eucalanus californicus*, *Metridia pacifica*) from California Current. With permission from Ohman (1988)

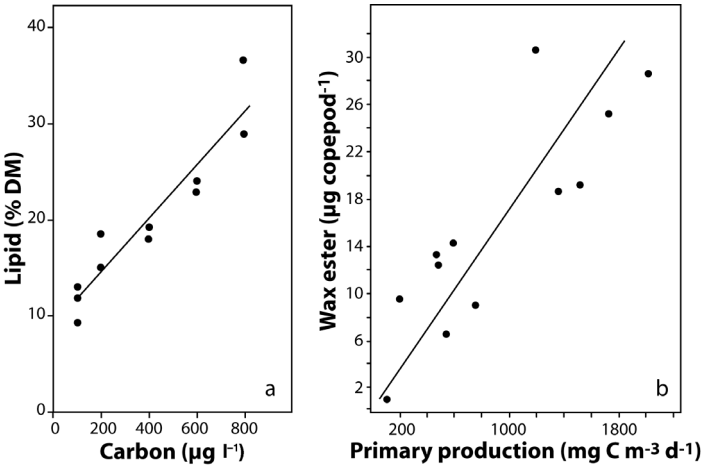

Fig. 20. *Calanus pacificus* (C5). (a) Lipid content (%DM) vs. concentration (µg C l^{-1}) of food (*Skeletonema costatum*). With permission from Lee et al. (1971b). (b) Mean wax ester levels vs. integrated primary production (mg C m^{-2} d^{-1}) in California Current. With permission from Håkanson (1987)

Estuaries fit into the coastal boundary zone biome with some unique features with respect to zooplankton and lipid. Estuaries are characterized by 2 groups of zooplankton. The first is holoplanktonic, and the entire life cycle takes place in the plankton. This group is characterized by zooplankton with low amounts of storage lipid, e.g. *Acartia* sp., *Eurytemora affinis* (Table 4) (Harris et al. 1977). However, the polar estuarine copepod *Limnocalanus macrurus* has high lipid levels composed primarily of wax esters (Hirche et al. 2003). The second zooplankton group comprises meroplanktonic larvae of benthic invertebrates. These meroplanktonic species are characterized by larvae with significant energy reserves in the form of lipid globules. They provide the energy required during the settling phase and metamorphosis. Triacylglycerols are the primary form of storage lipid for the estuarine zooplankton (Holland & Walker 1975). An exception are the lecithotrophic lipid-rich non-feeding planktonic larvae of the sea urchin *Heliocidaris erythrogramma*, which are high in wax esters (Villinski et al. 2002).

Westerlies biome

Provinces in this biome have pronounced seasonal cycles in phytoplankton productivity. All of the provinces except subarctic and subantarctic iron-limited HNLC regions (high nutrient, low chlorophyll) are characterized by a spring bloom, after nutrients from deeper waters have been transported to the surface during winter. By summer the nutrients are depleted, and in fall there can be a small autumn bloom as a

result of the vertical nutrient flux. Spring blooms are associated with zooplankton species that accumulate storage lipid, and some of the copepods descend to depths in summer and fall. These diapausing copepods accumulate wax esters as the principal storage lipid, but many of the other zooplankton groups, including a number of euphausiid and copepod species, store primarily triacylglycerols (Tables 7 & 8) (Kattner et al. 1981). During summer and winter there are resident species that do not accumulate lipid deposits such as the copepod *Centropages typicus* (Table 4).

Trade/tropical biome

This biome is associated with low nutrient concentrations and relatively low primary production rates throughout the year and thus does not have the large blooms found in the polar and westerlies biomes. While larger herbivorous species represent the characteristic feeding type in the polar biome, omnivores and carnivores are dominant in the trade/tropical biome (Longhurst 1998). Zooplankters of this biome tend to be small and lipid-poor with deposits consisting primarily of small amounts of triacylglyerols (Tables 4, 7 & 8) (Lee & Hirota 1973, Kattner et al. unpubl. data). There is a lipid gradient with maxima in polar species and minima in related tropical species. For example, the subtropical *Euchaeta marina* has a lipid content of 7.8%DM in the Gulf of Mexico (Morris & Hopkins 1983), while polar *Euchaeta* species range from 42 to 45% lipid (Table 7). The same holds true for euphausiid and pteropod species, which are lipid-rich in high latitudes but in tropical regions contain only small amounts of lipids. The low proportions of neutral lipids are triacylgycerols, whereas phospholipids, as structural membrane components, are the dominant lipid class (Kattner et al. unpubl. data). Knowledge about lipid and fatty acid compositions of tropical zooplankton is sparse. Based on some unpublished data we assume that the variability in lipid accumulation and lipid class and fatty acid compositions is small. These data must be approached with caution due to extremely high proportions of free fatty acids and sterols (Attwood & Hearshaw 1992, Yuneva et al. 1993), which point to lyses of lipids during sample preparation due to very active lipases in the animals probably related to the high ambient temperatures.

DISCUSSION AND FUTURE DIRECTIONS

Many questions remain concerning the role and importance of lipids in marine zooplankton. As noted above, many zooplankton groups, especially a number of copepod species in cold-water habitats, can convert low-lipid phytoplankton into large lipid stores. Few studies have determined the minimum amount of food required before lipid accumulation occurs. Lipid stores allow zooplankton to survive during periods of food scarcity. Copepods, undergoing diapause in cold deep water, often have very low rates of metabolism and often utilize only minor amounts of their large lipid stores during diapause. However, when reproduction takes place at depth in winter, lipid utilization increases, and the energy and materials needed for reproduction are provided by lipid stores. Other species that reproduce during phytoplankton blooms have less need for lipid, but there remains the question as to how these species cope with situations where food levels are inadequate during the reproduction period. Are these species able to interrupt gonad maturation during a period of insufficient food? Some species that reproduce during phytoplankton blooms still contain lipid stores. Perhaps these lipid stores function as a supplement when food quality or quantity is poor. Lipovitellin is an important constituent of most zooplankton eggs, and when there is inadequate food only limited amounts of this compound can be synthesized by the female. Some species can survive by body shrinkage, e.g. krill, utilizing all their biochemical constituents. Other successful zooplankton use all their food for growth and maintence rather than convert excess food into lipid stores. More knowledge about their life history may help in understanding why different zooplankton species employ very different strategies with respect to lipid accumulation.

A long history of controversy concerns the relative importance of lipids in buoyancy and storage in zooplankton. An active discussion on the use of lipids for buoyancy regulation in diapausing copepods is ongoing since both body composition and lipid compressibility may be important factors. Work needs to be carried out on the thermocompressibility of common storage lipids, i.e. triacylglycerols, diacylglycerol ethers and wax esters, to better understand density changes of these different types of lipid in various zooplankton groups and their possible role in buoyancy.

In addition to more chemical characterization of zooplankton storage lipids, more histology work needs to be carried out as well as more work on metabolic pathways involving lipids. It would be useful to isolate and culture copepod oil sac cells to determine their role in the synthesis and utilization of oil sac lipids. More ultrastructural studies of tissues with lipid stores will provide more insight into the various storage sites of zooplankton, for example, a determination of whether phosphatidylcholine in high-latitude euphausiids is stored in lipid micelles, lipoproteins or perhaps unique vesicles. Further work is warranted on the use of phospholipids as energy reserves.

Besides euphausiids do other zooplankton groups utilize phospholipids for storage? Is the structure of storage phosphatidylcholine different from that of membrane phosphatidylcholine, i.e. fatty acids of the glycerol backbone? What are the essential fatty acids of zooplankton? An unsettled issue concerns the ability of some zooplankton groups, e.g. protozoans, to perform *de novo* synthesis of the polyunsaturated n-3 fatty acids. Crustacean zooplankton do not synthesize these polyunsaturated acids, which play an important role in zooplankton membranes, but obtain them from their diet. In light of the importance of egg lipovitellin for the survival of many zooplankton embryos more work is needed on the isolation and characterization of lipovitellin from such zooplankton groups as pteropods, chaetognaths and salps.

A future topic that needs to be addressed is the impact of climate change on zooplankton communities, specifically the effects on lipid-storing species. It has been suggested that during warming periods, warm-water species with lower lipid stores invade ocean areas normally inhabited by high-lipid cold-water forms. This will not only impact the plankton community but also affect the energy flux of the entire system. The increase in solar ultraviolet radiation and its effects on surface-living zooplankton is a much discussed topic. The high content of polyunsaturated fatty acids in zooplankton suggests that an increase in ultraviolet radiation would likely lead to increases in the photo-oxidation rates of zooplankton lipids. The toxicity of oxidized polyunsaturated lipids, as well as the damage caused by free radicals produced during lipid photo-oxidation, are well known from the medical literature. Work remains to be done to show that increased ultraviolet exposure results in effects on the zooplankton community due to increased lipid photo-oxidation rates.

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