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Lipids and life strategy of Arctic *Calanus*

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Abstract
The three Arctic *Calanus* species, *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, are the most important herbivores in Arctic seas in terms of species biomass. They play a key role in the lipid-based energy flux in the Arctic, converting low-energy carbohydrates and proteins in ice algae and phytoplankton into high-energy wax esters. In this paper we review the over-wintering strategy, seasonal migration, stage development, life span, feeding strategy, body size, lipid biochemistry and the geographic distribution of the three dominant *Calanus* species in Arctic waters. We then relate these parameters to other biotic and abiotic factors, such as the timing of the Arctic phytoplankton and ice algae bloom, sea ice cover and climate variability. We also present new data on fatty acid and fatty alcohol content in the three *Calanus* species in addition to reviewing the available literature on these topics. These data are analysed for species homogeneity and geographic grouping. The dominance of diatom fatty acid trophic markers in the lipids of *Calanus* underpins the importance of diatoms as Arctic primary producers, even if dinoflagellates and *Phaeocystis pouchetii* can also be important food sources for the calanoid copepods. We conclude that the Arctic *Calanus* species are herbivores, engineered to feed on the Arctic bloom, and that the timing of the bloom is the most important factor in determining the life strategies of the individual species.

Key words: *Arctic,* Calanus, *fatty acids, life strategy, lipids, trophic markers*

Introduction

The *Calanus* species, *C. finmarchicus* (Gunnerus, 1765), *C. glacialis* Jaschov, 1955, and *C. hyperboreus* Krøyer, 1838, constitute a key role in the pelagic food web of the Arctic and northern seas. They are the most important biomass species and the prime herbivores in these waters (Conover & Huntley 1991; Mauchline 1998; Ringuette et al. 2002; Nielsen et al. 2007; Søreide et al. 2008). As light intensity increases in spring in high-latitude marine systems, ice melts and stratification of nutrient-rich water masses facilitate a short and intense Arctic bloom of phytoplankton and ice algae that propagate through Arctic waters producing a luxury of high-quality food available for zooplankton grazers. The carbon fixed through photosynthesis during the Arctic bloom is rapidly converted into large, specia-lized lipid (oil) stores by the *Calanus* herbivores (Lee 1975; Sargent & Henderson 1986; Falk-Petersen et al. 1987, 2000a; Lee et al. 2006), and the high-energy lipid compounds are transferred through the food chain in large amounts, being the major source of energy for the large stocks of fish, birds and marine mammals in the Arctic (Falk-Petersen et al. 1990, 2004; Dahl et al. 2003). These two factors (the timing of the Arctic bloom of ice algae and phytoplankton, and the lipid-driven energy flow through Arctic food webs) are the most prominent features of Arctic ecosystems that determine the structure of communities and populations in high-latitude ecosystems.

Towards higher latitudes, the amplitude of the primary production cycle becomes shorter due to the seasonality of light and ice conditions (Falk-Petersen et al. 2000b; Madsen et al. 2001; Ringuette

Season	Winter	Spring		Summer		Autumn		Winter	
Month	April	May	June	July	Aug	Sept	Oct	Nov
North Pole area								
Fram Strait								
Kara Sea								
Laptev Sea								
Barents Sea N								
Barents Sea SW								

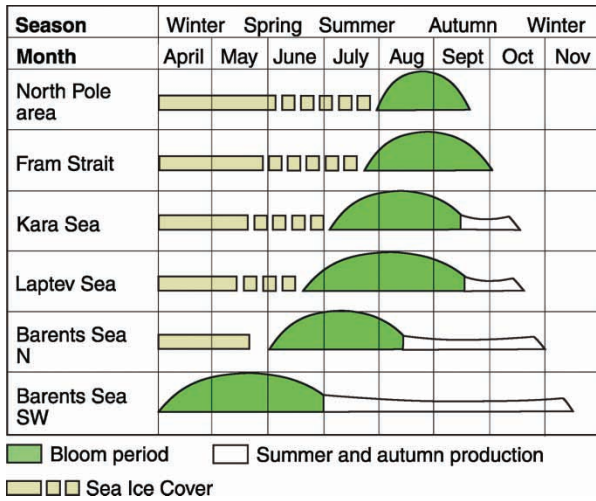■ Bloom period   □ Summer and autumn production
▭▢▢ Sea Ice Cover

Figure 1. Time-related plankton blooms in the Arctic Oceans (modified after Zenkevitch 1963).

et al. 2002; Hansen et al. 2003; Nilelsen et al. 2007). In the European Arctic the yearly ice melt starts in south west and blooms of phytoplankton propagate through the area (Figure 1), starting in the southern Barents Sea in April–May, continuing in the seasonal ice covered seas as the northern Barents Sea and the Laptev Sea in July–August, culminating at the North Pole in August–September and eastern Fram Strait in September–October (Zenkevich 1963; Falk-Petersen et al. 2008). A similar situation exists in the American Arctic where the polynya opens up in early spring and the bloom propagate through the polynya as the ice is melting and the polynya increases in size. In the Canadian archipelago as well as in fjords on northeast Greenland the bloom starts as late as July–August (Welch et al. 1992; Rysgaard et al. 1999; Mei et al. 2002; Mundy et al. 2005). We suggest that the timing of the phytoplankton bloom, related to the dynamics of the sea ice cover and the sea climate, is a key in structuring the Arctic *Calanus* complex and the biodiversity of Arctic ecosystems (Ringuette et al. 2002; Blachowiak-Samolyk et al. 2008a; Madsen et al. 2008).

The three *Calanus* species are all widely distributed in the Arctic Ocean and the northern seas (Mauchline 1998). They also have some other common characteristics in that they are all herbivores, over-winter at depths in diapauses with reduced metabolic activity (Hirche 1997), have high total lipid contents of partially more than 50%, are rich in high energy wax esters (70–90%) and long-chain fatty alcohols and fatty acids (Lee 1975; Sargent & Henderson 1986; Falk-Petersen et al. 1987; Kattner et al. 1989; Scott et al. 2000, 2002; Lee et al. 2006).

The question still is: how and why do the three *Calanus* species co-exist in the Arctic? In this paper we discuss this question by relating the physical forcing of the Arctic marine system to distribution, over-wintering strategy, seasonal migration, stage development, life span, feeding strategy, size, lipid dynamics and lipid composition of the three *Calanus* species.

Distribution and seasonal migration

The distribution of the three *Calanus* species is strongly influenced by two large, interconnected gyres or current systems in the Nordic Seas and the Arctic Ocean (Rudels et al. 1999; Hansen & Østerhus 2000; Figure 2) and the cyclonic circulation in Baffin Bay (Melling et al. 2001).

Calanus finmarchicus, C. glacialis and *C. hyperboreus* are all found distributed in Arctic waters, including the Norwegian Sea, the Barents Sea, the White Sea, the Arctic Ocean, the Greenland Sea and the coastal waters bordering Siberia, East Canada and Alaska. However, the three species have different and distinct centres for over-wintering (Jaschnov 1970; Runge et al. 1986; Conover 1988; Hirche & Mumm 1992; Hirche 1997; Hirche & Kwasniewski 1997).

Calanus finmarchicus has its centre of distribution in the Norwegian Sea and the Labrador Sea, but it is also the dominant biomass zooplankton species south of Newfoundland, in the Barents Sea south of the Polar Front as well as along the Norwegian coast (Aksnes & Blindheim 1996; Planque et al. 1997). These are areas where a predictable annual spring bloom occurs between March and May. *Calanus finmarchicus* have also been recorded in low numbers all around the Arctic Ocean and East Greenland in connection with submerged Atlantic water that flow along the shelf margin (Figure 2; Ringuette et al. 2002; Hirche & Kosobokova 2007; Nielsen et al. 2007; Madsen et al. 2008). Due to the Correolis Force the Atlantic flow is deflected into the Barents Sea north of Svalbard, the Kara Sea, the Siberian Shelf, the Canadian Arctic shelf as well as into the fjords on east Greenland (Rudels et al. 1999), transporting *C. finmarchicus* in low numbers into these areas. During winter the larger part of the population migrates down to deep water (Figure 3). In the Norwegian Sea the over-wintering stages start migrating to depths of 500 m to more than 2000 m at the end of the vernal bloom (Østvedt 1955; Kaartvedt 1996; Visser & Jonasdottir 1999; Gislason & Astthorson 2000) while, in fjords and shelf seas, the over-wintering populations are found in deep trenches and basins (Kaartvedt 1996). During late winter (February–April) the population, now ready to spawn, migrates to surface waters, and the animals are transported by surface currents from

Figure 2. The current system of the Arctic Seas.

their centre of distribution in the Norwegian Sea to all bordering seas (Sundby 2000).

Calanus glacialis is a typical shelf species distributed along the Arctic shelf seas including the Barents Sea shelf north of the Polar Front, along the east Greenland shelf, through the Canadian islands, in Baffin Bay, along the north west coast of North America, in the White Sea as well as on the Siberian shelf and as far east as the northern part of the Sea of Okhotsk. It spawns on the shelf, along the slope and in fjords (Figure 3; Conover 1988). These areas are often ice-covered until summer or autumn and the Arctic blooms occur late depending on the local ice conditions.

Calanus hyperboreus has its centre of distribution associated with deep-water areas such as the Greenland Sea, the Fram Strait, the Labrador Sea, the Baffin Sea and the Arctic Ocean Basin. However, it is transported with the major currents and can be found in low numbers over most of the shelf seas, the Nordic Seas, along the Norwegian coast and even in the North Sea. The over-wintering stages of *C. hyperboreus* migrate down to deep waters (500–

2000 m) during winter (Figure 3; Vinogradov 1997). The centres of distribution are associated with areas of high ice cover, where the light available for phytoplankton and ice algae blooms are dependent on both seasonal and large scale climate forces.

Life cycle strategies

Calanus finmarchicus has a one-year life cycle in Baffin Bay, the Barents and the Norwegian Seas, and it spawns in coincidence with the period of maximum phytoplankton bloom (Tables I and II and Figures 3 and 4). *Calanus finmarchicus* mainly spawns in April–May during or just after the bloom peak (Tande 1982; Tande et al. 1985; Niehoff et al. 2002; Madsen et al. 2008). The stage I copepodites (1–2.2 µg dry mass (DM)) develop to the lipid-rich over-wintering stage IV (40–70 µg DM) and stage V copepodites (130–240 µg DM) by June–July (Table III; Mauchline 1988; Kattner et al. 1989). The lipid-rich over-wintering stages then descend to deep water in June-July to undergo diapause (Kaartvedt 1996). The over-wintering stage, mainly stage V

copepodites, develops into males and females in January, and the subsequent energy-intensive development of ovaries in females between January and March is reflected in large decreases in dry mass and in the energy-rich wax ester deposits (Tande 1982; Falk-Petersen et al. 1987).

Calanus glacialis often has a two-year life cycle (Tande et al. 1985; Eilertsen et al. 1989; Michel et al. 2006) and spawns during the spring of its third year (Tables I and II and Figures 3 and 4; Smith 1990; Hirche & Kwasniewski 1997). MacLellan (1967) observed a one-year cycle for *C. glacialis* in West Greenland, while Kosobokova (1999) found that part of the White Sea population can be up to 3 years old, and that the females can spawn twice. *Calanus glacialis* develops its gonads to an advanced stage on internal lipid reserves well before the phytoplankton bloom, while spawning takes place just before or during the Arctic algae bloom, and may be partly fuelled by ice algae (Smith 1990; Hirche & Kattner 1993; Hirche & Kwasniewski 1997; Niehoff et al. 2002; Hirche & Kosobokova 2003). Successful spawning probably requires an energy input either from under-ice algae or from the phytoplankton bloom during egg production (Niehoff et al. 2002). Depending on the availability of food, i.e. on the timing of the bloom, *C. glacialis* can be found spawning from April until the end of August (Diel 1989; Hirche 1989a). After months of starvation, gonads developed in only 2 weeks (Hirche 1989a). In open shelf waters, *C. glacialis* spawns at the end of April, and it then develops rapidly into lipid-rich stage III or IV copepodites (Tande & Henderson 1988). Eggs of *C. glacialis* have been found floating in large numbers under the ice, consistent with a high lipid content and pre-bloom spawning (Werner & Hirche 2001). The lipid content of the younger stages of *C. glacialis* is unknown, but the lipids increase from stage IV to stage V copepodites and then to females from approx. 55, 60 to 70% DM, respectively (Table III).

Calanus hyperboreus spawns during winter (Hirche & Niehoff 1996) between October and March (Tables I and II), the spawning being fuelled entirely by pre-existing, internal lipid reserves. After the onset of the subsequent bloom, the eggs develop rapidly via nauplii into stage II and III copepodites, which are concentrated in the surface layers during the entire summer (May–October), probably feeding actively during this period. Large numbers of lipid-rich CIV, CV and females *C. hyperboreus* has been recorded active feeding on blooms of phytoplankton late autumn in the southern Arctic Ocean (Falk-Petersen et al. 2008). Daase et al. (2008), however, found that young stages of *C. hyperboreus* were feeding in the chlorophyll maximum in the
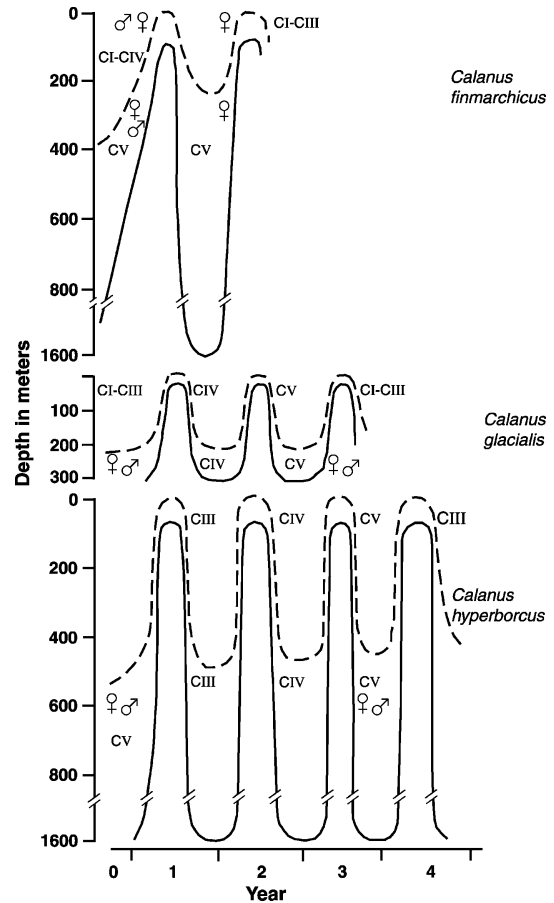

Figure 3. Generalized seasonal migration and stage development of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus*. Upper and lower line delineates the general depth of the population.

surface waters along the on the Spitsbergen shelf in mid September, while adult stages had migrated down to deep waters. In general, *C. hyperboreus* over-winter at depths of 800–1500 m, mainly as stages III, IV and V copepodites, in the Greenland Sea Gyre, Baffin Sea and the central Arctic Ocean (Figures 3 and 4; Vinogradov 1997). The first over-wintering stage is stage III, and they subsequently then develop into stage IV copepodites during their second summer, with a body mass of approximately 2 mg and a lipid content of more than 50% of their dry mass (Table III). They then descend again to deep water (800–1500 m depth) and do not ascend to surface waters until late in the following summer. During this third summer they grow rapidly, increasing their dry mass 7 times and their lipid content probably exceeds 65% of their dry mass, as they develop into stage V copepodites. The stage V copepodites finally develop to adults during winter and then reproduce in the following spring, i.e. in the fourth year of their life. Stage V copepodites and females are segregated in two depth strata, with

Table I. Life span of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in Arctic waters.

Species	Life span (years)	Area	References
Calanus finmarchicus	1	East Greenland	With 1915
		Barents Sea	Jaschnov 1939; Manteiphel 1941;
		Norwegian Sea	Kamshilov, 1955
		Foxe Basin	Ostvedt 1955; Lie 1968
		West Greenland	Grainger 1965
		Current	MacLellan 1967; Madsen et al. 2008
		Davis Strait	Sekerak et al. 1976
		Barents Sea	Falk-Petersen et al. 1999
	2	Canadian archipelago	Longhurst et al. 1984
Calanus glacialis	1	West Greenland	MacLellan 1967; Sekerak et al. 1976
		Current	Huntley et al. 1983
		Davis Strait	Runge et al. 1986
		Nova Scotia	Smith 1990
		Fram Strait	
	1–2	Barents Sea	Falk-Petersen et al. 1999
	2	Arctic Ocean	Grainger 1965
		Resolute area	Conover & Huntley 1991
		Barents Sea	Jaschnov 1961, 1970;
		White Sea	Tande et al. 1985;
			Slagstad & Tande 1990;
			Pedersen et al. 1995
			Prygunkova 1974
	2–3	Barrow Strait	Conover et al. 1991
	3	White Sea	Kosobokova 1999
Calanus hyperboreus	1	Davis Strait	Sekerak et al. 1976
	1–2	East Greenland	Ussing 1938
		Norwegian fjords	Wiborg 1954;
		Norwegian Sea	Matthews et al. 1978; Østvedt 1955
		Canadian archipelago	Grainger 1959
		Fram Strait	Smith 1990
	2 2	North of Iceland	Gislason & Astthorsson 1998
		Canadian archipelago	Longhurst et al. 1984
	2–3	Arctic Ocean	Harding 1966; Dawson 1978
		West Spitsbergen	Hirche 1997
		Current	
	3	Arctic Ocean	Harding 1966; Dawson 1978;
		Resolute area	Pavshtiks 1983
			Conover & Huntley 1991
	3–4	Canadian	Conover 1988; Conover et al. 1991;
		Greenland Sea Gyre	Conover & Siferd 1993
			Hirche 1997
	3–5	Barents Sea	Falk-Petersen et al. 1999

stage V copepodites over-wintering at 500–1000 m and females being concentrated at depths of 200–500 m, where they shed eggs (Vinogradov 1997). Life spans from 1–2 years and up to 4–6 years have been suggested for *C. hyperboreus*, depending on the geographical region and the food availability (Table I, Figure 4). This probably reflects the large plasticity developed by the species to cope with the variability in available food. Interestingly, *C. hyperboreus* over-winters in deep water at relatively high temperatures of 0–2°C, whereas it actively feeds and grows in the surface layers at temperatures of –1 to –1.8°C.

Plasticity

The impressive plasticity of the three *Calanus* species is shown in Figure 3 and Table I. In the North Sea, *C. finmarchicus* can have 1–3 generations per year (Wiborg 1954; Marshall & Orr 1955), while in the Norwegian Sea, along the coasts of north Norway, Greenland and east Canada and the Nordic Seas, the life span is mainly one year. A two-year life span is described for *C. finmarchicus* only from the Canadian archipelago (Longhurst et al. 1984). *Calanus glacialis* has a life span of 1–3 years, but for most areas a life span of 2 years is reported. *Calanus hyperboreus* shows the most impressive

Table II. Over-wintering stages and spawning periods of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in Arctic waters.

Species	Area	Stages	Spawning	References
C. finmarchicus	Canadian	CIII	April–May	Longhurst et al. 1984
	archipelago	CIV–CV	April–May	Pedersen et al. 1995
	Barents Sea	CIV–CV	August–October	Hirche et al. 1994
	Greenland Sea	CV		Hirche 1991
	(Northeast Water	CV		Hirche & Kwasniewski 1997
	Polynya)	Female		Gislason & Astthorsson 1998
	Greenland Sea			Hirche 1989b
	North of Iceland			
	Greenland Sea			
C. glacialis	Baffin Bay	CIII	May–June	Grainger 1963
	Canadian	CIII	May–June	Longhurst et al. 1984; Tande
	archipelago	CIII–CIV	February–March	et al. 1985; Pavshtiks 1977;
	Barents Sea	CIV	June	Kosobokova 1986
	Basin White Sea	CIV	March	Prygunkova 1968
	White Sea	CIV and	March–April	Kosobokova & Pertzova 1990
	Greenland Sea	CV	Late winter	Kosobokova 1999
	(Northeast Greenland	CIV	February	Hirche 1991;
	(Young Sound)	CV–CVI	March–April	Hirche et al. 1994; Nielsen
	Water Polynya)	CV–CVI	April	et al. 2007
	West Greenland	CV–CVI	May–June	MacLellan 1967
	Davis Strait		May–October	Huntley et al. 1983
	Fram Strait		May–July	Smith 1990
	North of Iceland		June–July	Gislason & Astthorsson 1998
	David Strait Barents Sea			Sekerak et al. 1976; Tande
	(central part)			1991
	Barents Sea			Pedersen et al. 1995; Falk-
	(around 78° N)			Petersen et al. 1999
	Barents Sea (central part)			Tande et al. 1985; Slagstad &
	Polar basin			Tande 1990; Johnson 1963
	Resolute area			Conover & Huntley 1991
	Laptev Sea (east part)			Michel et al. 2006
				Kosobokova & Hirche 2001
C. hyperboreus	Canadian	CIII	Winter	Longhurst et al. 1984
	archipelago	CIV, CV	October–March	Ringuette et al. 2002; Hirche
	North Water	CIII	January–February	et al. 1994
	(Canada)	CIII and	Late winter	Hirche & Niehoff 1996;
	Greenland Sea	CIV	January–May	Hirche 1997
	Greenland Sea	CIII–CIV	May–June	Wiborg 1954
	Off Norway	CIV	January–April	Gislason & Astthorsson 1998
	North of Iceland	CV		Johnson 1963
	Arctic Ocean			Grainger 1965
	Foxe Basin			Conover 1988;
	Resolute Passage			Conover et al. 1991
	Greenland Sea			Conover & Huntley 1991
				Hirche & Kwasniewski, 1997

plasticity with a life span from 1 to 5 years or even longer (Hirche pers. comm.). Such plasticity in the different species reflects differences in plasticity towards their environments. The central Arctic Ocean has the highest variability in sea climate and, therefore, the lowest predictability of food available for herbivorous zooplankton, both between years and seasons.

The abilities of the different developmental stages of calanoids to over-winter depend on their capacity to store energy as lipids, principally wax esters (Lee 1974; Sargent & Falk-Petersen 1988). Stage III copepodites of *C. hyperboreus* have dry masses 3 times higher than *C. glacialis* and 11 times higher than *C. finmarchicus* (Table III). The same is also evident for stage IV copepodites, and even more for stage V copepodites. Thus, the dry masses (and probably also the lipid contents) of the first over-wintering stages, stage III for *C. hyperboreus*, stage IV for *C. glacialis*, and stage V for *C. finmarchicus*, are approximately the same (0.09–0.15 mg dry mass per individual).

Diapause is a part of the life cycle of all *Calanus* species. The three species described here migrate down to deep water, where they over-winter as lipid-rich stages (Conover 1988). The similarity of the energy content of the first over-wintering copepodite
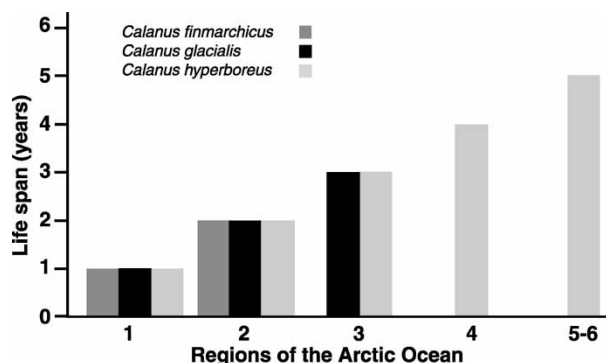
Figure 4. Life span of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in Arctic waters. The numeration generalizes a gradient of geographic regions from the southern Barents Sea to the North Pole as indicated in Figure 1.

stages, V, IV and III for *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, respectively, is consistent with the energy demand for the first over-wintering being the same for the three species. It has been shown by model studies where respiration, lipid stores and food availability were used as parameters, that *C. finmarchicus* has substantially higher probability of survival when it over-winters as stage V copepodites than as stage IV (Einane pers. comm.). By inference, therefore, stage IV *C. glacialis* and stage III *C. hyperboreus* both have more than sufficient energy stores to over-winter successfully in diapause.

Lipids and trophic markers

The role of wax esters

The three *Calanus* species build up their lipid reserves rapidly and have high total lipid and wax

ester contents. All this is associated with a herbivorous strategy well fitted to the Arctic environment with short intense blooms of phytoplankton (Sargent & Henderson 1986; Sargent & Falk-Petersen 1988; Falk-Petersen et al. 2000b, 2004, 2007; Hagen & Auel 2001; Scott et al. 2002; Varpe et al. 2007). An interesting effect of the high lipid content is that lipids and especially wax esters, being much lighter than seawater, will create a positive up thrust in the lipid-rich stages of the three *Calanus* species (Figure 5; Koegeler et al. 1987).

The biosynthesis of wax esters is a special adaptation of *Calanus* species and some other zooplankter to cope with the high seasonality of food availability. It is a very effective way to quickly produce high amounts of lipids during food plenty. The biosynthesis of fatty alcohols for the formation of wax esters is a mechanism for removing end-product inhibition in the fatty acid biosynthesis while producing a more reduced, i.e. more energy-rich, end product. Therefore, the formations of wax ester accelerate de novo biosynthesis of lipids utilizing the abundant diet (Sargent & Henderson 1986). Part of the fatty alcohol moieties of wax esters may originate from dietary fatty acids, but they are mainly produced from fatty acids, which are themselves biosynthesized de novo from protein and carbohydrate dietary precursors. The fatty acid moieties in the wax esters are derived from dietary fatty acids and are also to a smaller extent produced de novo (Sargent & Henderson 1986; Kattner & Hagen 1995). A longer chain fatty alcohol (or fatty acid) has higher energy content per unit mass than a shorter chain one. Therefore, the energy content of lipid is maximized by increasing the chain lengths of their constituent

Table III. Prosome length (mm), wet mass (WW), dry mass (DW) and lipid mass (LW) as mg ind^{-1}, and % total lipid of DW in different developmental stages of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*. Length from Hirche et al. (1994), WW, DW and % total lipid of DW from Scott et al. (2000). DM of stages I–II are calculated after Mauchlene (1989).

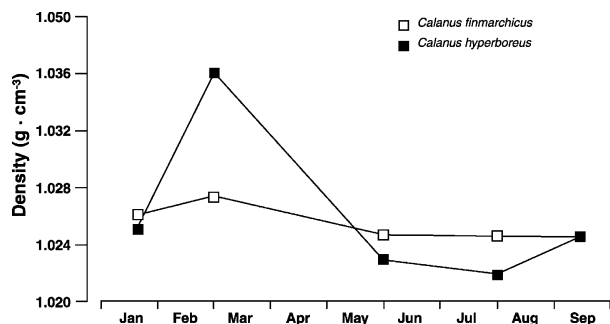| Species	Stage	Length (mm)	Wet mass (mg ind^{-1})	Dry mass (mg ind^{-1})	Lipid mass (mg ind^{-1})	% lipid
Calanus finmarchicus	I	0.68		0.0016		
	II	0.93		0.004		
	III	1.31		0.013		
	IV	1.6–2–2	0.28	0.04	0.02	53
	V	2.0–3.0	0.56	0.13	0.04	34
	F	2.4–3.2	1.08	0.26	0.08	31
Calanus glacialis	II	1.31		0.019		
	III	1.81		0.04		
	IV	2.2–2–8	0.39	0.09	0.05	56
	V	3.0–4.0	2.38	0.62	0.38	61
	F	3.2–4.6	2.60	0.64	0.45	70
Calanus hyperboreus	I	1.04		0.05		
	II	1.63		0.032		
	III	2.47		0.142		
	IV	3.4–4.0	1.91	0.51	0.28	54
	V	4.5–6.0	6.44	1.58	1.03	65
	F	6.2–7.0	12.09	2.92	1.81	62

Figure 5. Seasonal variation in the specific gravity (buoyancy) of *Calanus finmarchicus* and *Calanus hyperboreus* (after Koegeler et al. 1987).

fatty alcohols and/or fatty acids. The very high amounts of de novo synthesized 22:1 and 20:1 fatty alcohols and acids is a store of exceptional high energy value lipids (Sargent & Falk-Petersen 1988). A large amount of energy, 182 moles ATP, is generated from the catabolism of one mole of 22:1 fatty acid.

The results presented here establish that *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* have very high levels of 20:1 and 22:1 alcohols, ranging from 67 to 93%. Ratios of $22:1(n–11)/20:1(n–9)$ in females of *C. hyperboreus*, *C. glacialis* and *C. finmarchicus* of 1.74, 0.74 and 1.04, respectively, are reported from Kongsfjorden (Scott et al. 2002). The same trend can be seen in the ratios of *Calanus* from other regions (Table IV) even if there is a great variation in the ratios between season and location. Furthermore, *C. hyperboreus* has the largest lipid stores with the highest percentages of $22:1(n–11)$ alcohol and fatty acid. This species is the most active of the three species in biosynthesizing lipid de novo and accumulates wax esters with the highest energy content (Albers et al. 1996). This is consistent with *C. hyperboreus* being the most highly adapted of the three species, maximizing formation of the longest chain wax esters (Graeve & Kattner 1992), reflecting its main location in the most extreme environment, the Greenland Sea and the Arctic basin.

Fatty acids of polar lipids

The polar lipids presented in Table IV represent three different seasons. Spring data were from the Northern Barents Sea and Kongsfjorden, summer data from the western Fram Strait and from all three season from the Arctic Ocean. The polar lipids were very rich in the typical diatom fatty acid marker $20:5(n–3)$ (eicosapentanoic acid; EPA), and especially the dinoflagellate marker $22:6(n–3)$ (docosahexaenoic acid; DHA). There are, however, some interesting differences between developmental stages and geographical region and season. In *Calanus*

finmarchicus, the level of $20:5(n–3)$ increases from approximately 13 to 20% and $22:6(n–3)$ from approximately 10 to 30–40% between copepodite stage V and females. Another interesting feature is that the levels of the very important $22:6(n–3)$ fatty acid is much higher in all the three *Calanus* species in summer and autumn both in the Fram Strait and the Kongsfjorden (34–46%) than the Northern Barents Sea (Central Bank) (13–20%) in spring. $22:6(n–3)$ is a unique fatty acid, having a multifunctional role in cell membranes including functions as fluidity, elastic compressibility and permeability. It is produced by dinoflagellates and plays a role in locomotion of the flagella. For human health, for example, DHA is linked positively to the prevention of cancer and heart disease and is essential to neurological functions (Stillwell & Wassall 2003). The level of the dinoflagellate-derived DHA in phospholipids (34–46%) in *Calanus* females are much higher than in wax esters (0–10%). This shows that DHA is preferentially incorporated into copepod phospholipids and cell membranes. Although diatoms are the major food of *Calanus* copepods, and contribute much more to the animals' total lipids than flagellates, the flagellates may have a more critical and fundamental role in the successful growth and reproduction of this species by contributing DHA to the formation of cell membranes (Scott et al. 2002).

Lipid trophic markers

The use of fatty acid trophic markers (FATM) (Dalsgaard et al. 2003) is based on the observation that marine primary producers lay down certain fatty acid patterns characteristic of different taxa that may be transferred conservatively through the food chain (Sargent & Whittle 1981; Dalsgaard et al. 2003). Of the important phytoplankton species in polar waters, diatoms are rich in the fatty acids $20:5(n–3)$, $16:1(n–7)$ and C16 PUFA (polyunsaturated fatty acids) but deficient in C18 PUFA. Dinoflagellates are rich in $18:4(n–3)$, $18:5(n–3)$ and especially $22:6(n–3)$ and deficient in $16:1(n–7)$. The haptophyceae *Phaeocystis pouchetii*, which often dominates the blooms in sub-Arctic waters (Falk-Petersen & Hopkins 1981), is rich in C18 PUFA, especially $18:4(n–3)$ and $18:5(n–3)$, together with $20:5(n–3)$ and $22:6(n–3)$, while $16:1(n–7)$ is only found in very small amounts (Sargent et al. 1985; Hamm et al. 2000). The $20:1(n–9)$ and $22:1(n–11)$ units, present in very large amounts in *Calanus* copepods, are formed by de novo biosynthesis in these animals, which in our present knowledge are the major site of the formation of $20:1(n–9)$ and $22:1(n–11)$ units to the marine food web (Sargent & Whittle 1981). The FATM

Table IV. Fatty acid composition of polar lipids of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* from the Arctic.

	Calanus finmarchicus				*Calanus glacialis*					*Calanus hyperboreus*				
Location	NBS[1]		FSW[3]	HB[11]	NBS[1]	KGF[8]			FSW[3]	NBS[1]	FSW[3]	AO[9]		
Year	1986		89+90	1975	1986	2004			1989+90	1986	1989+90			
Season	spring		sum.	winter	spring	spring			sum.	spring	sum.	sum.	aut.	winter
Stage	CV	AF	AF	CV	AF	CIV	CV	AF	AF	AF	AF	CIV–V	CIV–V	CIV–V
Replicate	n=1	n=1	n=2		n=1	n=6	n=6	n=3	n=4	n=1	n=3	n=1	n=1	n=2
14:0	4.4	3.9	3.3	4.6	6.1	6.3	6.5	4.9	5.2	7.3	4.0	3.0	2.0	3.0
15:0	0.6	0.4	nd	0.8	0.4	0.4	0.4	0.4	1.8	nd	0.8	nd	nd	nd
16:0	33.2	27.0	25.8	21.5	31.8	10.9	9.5	9.3	25.8	29.1	25.5	12.0	14.0	15.0
16:1(n–9)	nd	nd	nd	0.8	1.6	0.5	0.3	0.3	nd	nd	nd	nd	nd	nd
16:1(n–7)	5.4	2.7	1.1	2.8	4.0	7.2	9.6	6.9	4.6	6.3	2.5	3.0	3.0	5.0
16:1(n–5)	1.6	0.6	0.2	1.2	0.8	0.3	0.3	0.1	0.1	1.0	0.9	nd	nd	nd
18:0	3.1	1.8	3.6	2.2	1.2	1.3	1.1	1.1	2.3	2.3	2.3	1.0	nd	4.0
18:1(n–9)	6.4	4.1	2.5	5.1	3.7	2.6	2.5	3.2	6.4	4.1	5.1	11.0	11.0	13.0
18:1(n–7)	2.4	2.2	1.0	2.2	4.4	1.1	1.0	1.3	3.7	3.5	1.4	nd	nd	nd
18PUFAs	4.4	5.6	4.6	0.0	2.6	6.7	5.4	5.2	2.2	1.5	3.1	2.0	3.0	2.0
20:1(n–9)	1.4	0.9	0.2	4.0	1.9	6.0	6.9	5.9	0.9	0.8	0.6	nd	nd	nd
20:1(n–7)	nd	nd	nd	0.3	0.2	0.1	0.1	0.3	nd	0.1	nd	nd	nd	nd
20:4(n–6)	0.2	0.3	0.2	0.1	0.2	0.2	0.3	0.2	nd	0.2	0.2	nd	nd	nd
20:4(n–3)	0.5	0.7	0.2	0.2	0.3	0.0	0.0	0.0	nd	0.5	nd	nd	nd	nd
22:1(n–11)	0.7	0.1	0.2	6.7	nd	3.3	3.9	4.2	nd	0.1	1.2	nd	nd	nd
22:1(n–9)	0.5	0.2	nd	0.9	0.2	0.4	0.5	0.6	nd	nd	nd	nd	nd	nd
20:5(n–3)	12.6	22.5	19.2	13.2	21.7	30.0	26.9	33.0	16.5	21.4	18.6	19.0	18.0	18.0
24:1(n–9)	2.7	1.4	nd	1.57	1.2	0.4	0.4	0.1	nd	2.1	nd	nd	nd	nd
22PUFAs	10.4	20.6	37.6	24.2	13.0	14.0	13.7	17.0	30.5	11.7	33.8	43.0	39.0	36.5
Saturated	41.3	33.1	32.7	29.1	39.5	18.9	17.4	15.6	35.1	38.7	32.6	16.0	16.0	22.0
Monounsat	21.1	12.2	5.2	25.5	18.0	21.8	25.6	22.9	15.7	18.0	11.7	14.0	14.0	18.0
PUFAs	28.1	49.7	61.8	37.7	37.8	50.9	46.2	55.3	49.2	35.3	55.7	64.0	60.0	56.5
20:5(n–3) + 16:1(n–7)	18.0	25.2	20.3	16.0	25.7	37.2	36.5	39.9	21.1	27.7	21.1	22.0	21.0	23.0
16:1(n–7)/16:0	0.2	0.1	0.0	0.1	0.1	0.7	1.0	0.7	0.2	0.2	0.1	0.3	0.2	0.3

Northern Barents Sea (NBS), Kongsfjorden (KGF), Fram Strait East (FSE), Fram Strait West (FSW), Arctic Ocean (AO), Hudson Bay (HB) and North Water Polynia (NWP). The numbers from 1–11 refer to the original work: 1 = Falk-Petersen 1986 (unpublished), 2 = Kattner et al. 1989, 3 = Alberts et al. 1996, 4 = Scott et al. 2002, 5 = Falk-Petersen/Norwegian Polar Institute database (unpublished), 6 = Søreide et al. 2007, 7 = Leu (unpublished), 8 = Leu et al. 2006, 9 = Lee 1974, 10 = Stevens et al. 2004, 11 = Mayzaud (unpublished). ★ = neutral lipid, ★★ = total lipid.

Table V. Fatty alcohol composition of wax esters of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* from the Arctic.

Calanus finmarchicus

Location	NBS[1]		KGF[4]		KGF[5]		FSE[2]			FSE[6]			FSW[2]		FSW[3]	AO[6]	HB[11]
Year	1986		1997		1998		1984			2003			1984		1989+90	2003	1975
Season	spring		autumn		autumn		summer			spring	autumn	winter	summer		summer	autumn	winter
Stage	CV	AF	CV	AF	CV	AF	CIV	CV	AF	CV	CV	CV	AF	CV	AF	CV	CV
Replicates	$n=1$	$n=1$	$n=13$	$n=12$	$n=6$	$n=6$	$n=4$	$n=3$	$n=3$	$n=3$	$n=3$	$n=6$	$n=1$	$n=1$	$n=2$	$n=3$	
14:0	0.2	0.1	1.9	2.1	3.1	1.7	3.0	1.9	1.2	2.9	2.1	2.1	0.4	1.1	3.9	1.5	2.0
14:1	0.9	0.6	nd	nd	0.1	0.1	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.1
15:0	nd	nd	0.3	0.3	0.2	0.2	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.4
16:0	7.5	6.0	8.4	8.0	9.6	7.3	12.4	8.8	7.5	8.4	8.1	11.3	3.0	6.6	14.6	4.4	11.8
16:1(n–7)	3.3	2.7	6.2	6.8	6.2	6.8	2.5	1.6	1.4	5.1	2.4	2.1	0.7	1.8	3.4	1.9	1.9
18 total	8.4	7.2	5.9	5.6	4.8	5.4	5.2	4.1	3.4	1.5	2.7	3.4	1.9	4.0	0.0	1.1	7.5
20:1(n–9)	42.2	48.5	35.3	35.6	39.9	41.5	28.2	42.1	40.6	38.9	41.0	43.7	39.8	41.0	39.3	36.8	33.4
20:1(n–7)	nd	nd	0.7	2.3	0.5	1.4	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.6
22:1(n–11)	24.6	25.0	39.0	36.5	33.1	31.6	38.4	41.4	45.7	39.6	38.9	33.0	54.3	45.2	38.8	50.0	32.4
22:1(n–9)	nd	nd	0.3	0.8	0.6	2.8	nd	nd	nd	3.6	4.8	4.4	nd	nd	nd	4.3	1.7
20:1+22:1	66.8	73.5	75.4	75.2	74.1	77.4	66.5	83.5	86.3	82.1	84.6	81.0	94.1	86.2	78.1	91.0	68.1

Calanus glacialis

Location	NBS[1]	NBS[6]*		KGF[4]		KGF[5]		KGF[8]		FSE[6]*		FSW[3]	AO[6]*
Year	1986	2004	2003	1997		1998		2004		2003		1989+90	2003
Season	spring	spring	autumn	autumn		autumn		spring		autumn	winter	summer	autumn
Stage	AF	CV	CV	CV	AF	CV	AF	CV	AF	CV	CV	AF	CV
Replicates	$n=1$	$n=3$	$n=9$	$n=9$	$n=8$	$n=5$	$n=6$	$n=6$	$n=3$	$n=7$	$n=6$	$n=4$	$n=3$
14:0	0.7	5.7	3.2	2.1	1.5	3.4	2.6	4.3	2.8	3.1	3.5	2.1	3.3
14:1	1.3	nd	nd	0.2	0.2	nd	nd	nd	nd	nd	nd	nd	nd
15:0	nd	nd	nd	0.3	0.3	0.3	0.2	nd	nd	nd	nd	nd	nd
16:0	5.1	13.1	10.3	9.4	7.7	9.6	8.2	12.7	12.1	8.8	13.2	9.3	9.2
16:1(n–7)	3.0	5.4	4.4	4.2	3.8	5.8	4.3	8.6	8.6	4.1	4.7	5.3	2.7
18 total	4.6	2.1	1.8	5.9	5.2	4.0	3.8	1.7	2.3	1.6	2.6	0.0	1.8
20:1(n–9)	63.4	47.4	46.4	41.3	45.2	38.7	36.5	45.5	45.1	47.3	48.5	58.4	45.6
20:1(n–7)	1.0	nd	nd	0.7	1.9	2.3	1.3	nd	nd	nd	nd	nd	nd
22:1(n–11)	16.1	21.8	24.4	31.1	28.4	32.7	41.4	24.7	23.2	29.8	22.5	25.0	31.6
22:1 n–9	1.3	4.4	5.2	2.5	3.3	1.9	1.4	4.0	6.0	5.2	4.9	nd	5.8
20:1+22:1	81.8	73.7	76.0	75.6	78.8	75.6	80.7	74.1	74.2	82.3	75.9	83.4	83.0

	Calanus hyperboreus																				
Location	NBS[1]	NBS[6]*		KGF[4]		KGF[5]		FSE[2]**			FSE[6]*		FSW[2]**			FSW[3]	AO[6]*		AO[10]		
Year	1986	2004	2003	1997		1998		1984			2003		1984			1989+90	2003				
Season	spr.	spr.	aut.	autumn		autumn		summer			spr.	wint.	summer			summer	autumn		sum.	aut.	wint.
Stage	AF	CV	CV	CV	AF	CV	AF	CIV	CV	AF	CV	AF	CIV	CV	AF	AF	CV	AF	CIV–V	CIV–V	CIV–V
Replicates	n=1	n=3	n=9	n=12	n=14	n=6	n=3	n=5	n=3	n=3	n=6	n=3	n=2	n=2	n=3	n=3	n=6	n=6	n=1	n=1	n=2
14:0	0.5	8.1	5.2	3.3	2.6	4.6	5.2	6.4	4.4	2.0	4.9	2.1	3.4	3.1	2.1	4.4	4.1	2.0	1.0	2.0	3.0
14:1	4.0	nd	nd	nd	nd	0.0	0.0	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
15:0	10.7	nd	nd	0.3	0.3	0.2	1.2	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
16:0	1.6	13.0	10.2	8.8	6.5	9.4	4.2	7.8	7.5	4.1	7.5	4.7	11.1	7.9	5.7	11.2	8.0	3.6	5.0	8.0	33.5
16:1(n–7)	nd	1.4	2.6	3.5	2.0	3.3	2.2	0.5	0.3	0.1	1.7	0.6	2.2	1.1	1.2	1.6	1.3	0.6	2.0	4.0	5.0
18 total	1.8	0.5	0.5	3.3	2.3	2.5	1.4	1.3	1.2	0.4	0.7	0.7	0.7	0.8	0.7	0.0	0.6	0.4	5.0	8.0	2.0
20:1(n–9)	33.6	33.1	29.5	28.1	27.7	26.4	28.7	28.8	32.0	31.3	29.4	24.5	27.4	27.4	34.3	27.8	29.0	27.6	35.0	41.0	23.0
20:1(n–7)	3.5	nd	nd	2.4	3.1	0.0	4.9	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
22:1(n–11)	29.3	34.1	39.8	47.3	52.8	53.5	47.1	55.0	54.7	61.6	44.5	50.7	55.0	59.8	55.9	55.0	44.0	49.2	48.0	34.0	30.5
22:1 n–	8.4	6.0	8.4	1.5	1.3	0.1	5.1	nd	nd	nd	8.3	10.6	nd	nd	nd	nd	9.3	13.2	nd	nd	nd
20:1+22:1	74.8	73.2	77.7	79.3	84.9	80.0	85.9	83.7	86.7	92.9	82.2	85.8	82.4	87.2	90.2	82.8	82.3	90.0	83.0	75.0	53.5
22:1(n–11)/ 20:1(n–9)	0.9	1.0	1.4	1.7	1.9	2.0	1.6	1.9	1.7	2.0	1.5	2.1	2.0	2.2	1.6	2.0	1.5	1.8	1.4	0.8	1.3

Northern Barents Sea (NBS), Kongsfjorden (KGF), Fram Strait East (FSE), Fram Strait West (FSW), Arctic Ocean (AO), Hudson Bay (HB) and North Water Polynia (NWP). The numbers from 1–11 refer to the original work: 1 = Falk-Petersen 1986 (unpublished), 2 = Kattner et al. 1989, 3 = Alberts et al. 1996, 4 = Scott et al. 2002, 5 = Falk-Petersen/Norwegian Polar Institute database (unpublished), 6 = Søreide et al. 2007, 7 = Leu (unpublished), 8 = Leu et al. 2006, 9 = Lee 1974, 10 = Stevens et al. 2004, 11 = Mayzaud (unpublished). * = neutral lipid, ** = total lipid.

produced by microalgae together with the specific markers produced by *Calanus* species de novo can be followed through the ecosystem to predators such as fish, mammals and seabirds (Falk-Petersen et al. 1986a,b, 1990, 2004; Dahl et al. 2003).

Fatty acids and alcohols of wax esters

The composition of wax ester fatty acids and fatty alcohols are presented in Table V and VI. *Calanus* from the northern Barents Sea and Kongsfjorden were collected in spring and autumn. The dominance FATM of diatoms, $20:5(n–3)$ and $16:1(n–7)$, up to 70%, in the wax ester underpins the importance of diatoms among the Arctic marine primary producers and its importance as the base of the Arctic food chain. Also striking are low levels of the dinoflagellate marker $22:6(n–3)$ (0 and 10%), which is in contrast to findings from the Norwegian fjords and the southern Barents Sea, where dinoflagellates and especially *Phaeocystis pouchetii* can be a dominating food source (Sargent & Falk-Petersen 1981; Falk-Petersen et al. 1987).

The diatom FATM $16:1(n–7)$, 16PUFAs and $20:5(n–3)$ were very low (10–15%) in *C. finmarchicus* and *C. glacialis* during early spring at the northern Barents Sea (Central Bank) in 1986, while it increased in late spring at the same location (39%) and during summer and especially autumn, up to about 30% for both *C. finmarchicus* and *C. glacialis*. This indicates a clear seasonality of food available. The animals from early spring in the northern Barents Sea were collected before or at the beginning of the spring bloom (Melle & Skjoldal 1998) and had low levels of diatom FATM compared to animals collected later in spring at the same location, and from summer and autumn in Kongsfjorden and the Fram Strait East and West.

Calanus hyperboreus had moderate level of diatom FATM (14–28%) in the Fram Strait and northern Barents Sea during summer, while the summer data from the Arctic Ocean and autumn data from the western Fram Strait and the Arctic Ocean (North Water polynya) had very high levels of diatom FATM (up to 65%). This can be associated with late diatom blooms as the pack ice brakes up (Figure 1; Falk-Petersen et al. 2004). High values of $18:4(n–3)$ were recorded in summer in the eastern Fram Strait, indicating that the animals feed on dinoflagellates and possibly also on *Phaeosystis pouchetii* (Kattner et al. 1989). The exchange of fatty acids due to changes in phytoplankton composition is provided by feeding experiments. The assimilation of dietary fatty acids and the de novo biosynthesis are rapid processes (Graeve et al. 1994, 2005).

The very high level of $20:1(n–9)$ and $22:1(n–11)$ fatty acids and alcohols, recorded in females of *C. glacialis* and *C. hyperboreus* from the northern Barents Sea (Central Bank) in early spring, indicate active de novo biosyntheses and feeding in this area at the start of the spring bloom. It is well known that *Calanus* has a flexible feeding strategy and is able to switch to alternative prey when fresh phytoplankton are scarce, including nauplii (Bonnet et al. 2004; Basedow & Tande 2006) and protozooplankton (Mauchline 1998; Levinsen et al. 2000). However, based on the fatty acid composition and life strategy, we conclude that the three Arctic *Calanus* species are herbivores heavily utilizing the Arctic phytoplankton bloom (Søreide et al. 2008).

Discrimination of Calanus species as preys based on fatty acids and fatty alcohols

The central position of the three major species of *Calanus* in the Arctic and sub-Arctic pelagic food web makes it important to define those fatty acid trophic markers and alcohols which could be used to discriminate between the three species. The wax ester composition is used because it integrates relatively long time scales (days to weeks) and represents the main lipid class. It also yields a dual definition based on both fatty acids and fatty alcohols. The approach used here is based on the one hand on a hierarchical cluster analysis to ascertain the degree of homogeneity or heterogeneity between wax esters and species at all locations, and on the other hand on a PLS discriminant analysis (PLS-DA; Wold et al. 1984), which is a principal component analysis of the averages of the three species, weighted by their respective sample sizes. All data were normalized to constant sum, and observations were standardized by dividing each variable by the square root of its standard deviation.

The initial cluster analysis, based on the Ward's hierarchical clustering model (reciprocal neighbour; Ward 1963), was performed on both fatty acid and fatty alcohol data sets. As expected from the influence of dietary fatty acids, a large variability was recorded for the analysis based on the wax ester fatty acid fraction (cluster not shown) associated to a large part to sampling location. On the contrary, when hierarchical clustering was based on fatty alcohols, species homogeneity was the dominant feature (Figure 6) as anticipated from components resulting from de novo synthesis. A PLS-DA (not shown) suggested that *Calanus hyperboreus* can be best discriminated by higher percentages of $22:1(n–11)$ alcohols, whereas *C. glacialis* and *C. finmarchicus* can be best discriminated by higher values of $22:1 + 20:1$ and $16:1(n–7)$. This further strengthens the

Table VI. Fatty acid composition of wax esters of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* from the Arctic.

													Calanus finmarchicus											
Location	NBS[1]	NBS[1]	NBS[6]*	KGF[5]	KGF[5]	KGF[5]	KGF[5]	FSE[2]**	FSE[2]**	FSE[2]**	FSE[5]	FSE[5]	FSE[6]*	FSE[6]*	FSE[6]*	FSW[3]	FSW[2]**	FSW[2]**	FSW[5]	FSW[5]	AO[5]	AO[5]	AO[6]*	HB[11]
Year	1986	1986	2004	1998	1998	1997	1997	1984	1984	1984	1998	1998	2003	2003	2003	89+90	1984	1984	1998	1998	1998	1998	2003	1975
Season	spring	spring	spring	autumn	autumn	autumn	autumn	summer	summer	summer	autumn	autumn	spr.	aut.	wint.	summer	summer	summer	autumn	autumn	autumn	autumn	autumn	winter
Stage	CV	AF	CV	CV	AF	CV	AF	CIV	CV	AF	CV	AF	CV	CV	CV	AF	CV	AF	CV	AF	CV	AF	CV	CV
Replicates	n=1	n=1	n=3	n=6	n=6	n=11	n=11	n=3	n=3	n=4	n=2	n=3	n=3	n=3	n=6	n=2	n=1	n=1	n=3	n=3	n=6	n=6	n=3	
14:0	25.2	36.0	16.8	15.6	13.6	9.4	8.8	12.1	14.7	12.7	9.5	9.4	12.0	18.5	23.4	26.3	18.0	21.2	23.3	14.4	17.9	11.4	18.6	10.0
15:0	1.5	1.3	0.6	1.3	2.0	0.7	0.6	nd	nd	nd	2.2	1.3	0.4	0.9	1.2	0.7	nd	nd	0.9	0.7	1.1	0.8	0.9	0.8
16:0	11.2	8.6	7.8	9.8	9.4	7.8	6.3	8.6	8.2	10.1	5.3	7.1	6.2	10.0	11.9	9.8	9.3	8.8	10.7	8.2	9.3	6.7	8.6	11.9
16:1(n–9)	nd	nd	0.6	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.4	0.7	0.5	nd	nd	nd	nd	nd	nd	nd	0.4	1.1
16:1(n–7)	9.9	8.9	10.1	18.7	21.1	20.9	25.2	4.3	4.4	5.2	19.2	12.1	7.5	6.5	8.2	6.7	6.5	7.3	12.3	18.4	18.9	28.2	8.8	9.7
16:1(n–5)	1.7	1.5	0.1	nd	nd	0.1	0.2	nd	nd	nd	nd	nd	0.5	0.7	0.1	0.9	nd	nd	nd	nd	nd	nd	0.8	2.1
16PUFA	1.3	0.7	13.1	2.7	2.9	4.9	4.3	1.8	2.3	1.7	5.1	4.1	9.0	2.5	2.1	2.0	2.3	1.2	2.6	5.6	3.5	3.2	2.3	1.1
18:0	0.6	0.6	0.8	0.6	0.6	0.3	0.5	nd	nd	nd	0.2	0.7	0.5	0.7	0.7	0.9	nd	nd	0.6	0.3	0.5	0.3	0.6	0.8
18:1(n–9)	6.4	4.3	2.8	4.3	5.3	2.1	3.2	4.3	4.4	5.3	2.7	3.7	2.5	4.5	6.4	5.3	5.3	5.7	4.1	3.7	5.0	3.5	5.3	7.6
18:1(n–7)	0.7	0.5	0.5	1.1	2.4	1.5	1.6	nd	nd	nd	1.3	0.7	0.6	0.4	0.5	0.3	nd	nd	0.5	1.2	0.8	1.3	0.5	1.5
18:4(n–3)	0.8	0.0	7.0	8.2	5.1	1.8	3.7	16.7	16.2	9.0	5.5	4.2	9.2	12.6	11.1	13.7	9.3	1.6	1.6	4.6	1.4	1.8	5.6	3.2
18PUFA (other)	3.3	1.0	1.0	2.8	1.8	2.7	1.9	0.0	0.0	0.0	1.9	0.4	0.9	3.1	3.7	2.7	0.0	0.0	2.3	3.1	2.3	1.0	2.2	3.9
20:0	0.1	0.2	0.2	nd	nd	0.0	0.1	nd	nd	nd	nd	nd	0.6	0.2	0.2	nd	nd	nd	nd	nd	nd	nd	0.4	0.3
20:1(n–11)	nd	nd	0.5	nd	nd	0.3	0.3	nd	nd	nd	nd	nd	1.1	0.4	0.7	nd	nd	nd	nd	nd	nd	nd	1.2	0.3
20:1(n–9)	10.1	13.3	9.3	10.4	11.9	15.3	13.8	5.2	7.6	8.3	17.8	17.7	10.0	9.3	8.5	7.8	9.6	13.4	14.1	13.9	13.5	19.4	9.5	13.6
20:1(n–7)	0.3	0.3	0.1	0.0	0.8	2.6	1.2	nd	nd	nd	0.6	0.2	1.3	0.1	0.1	0.9	nd	nd	0.0	0.0	0.0	1.1	0.1	0.7
20:4(n–6)	0.2	0.1	0.1	nd	nd	0.9	0.4	nd	nd	nd	nd	nd	1.2	0.4	0.3	0.4	nd	nd	nd	nd	nd	nd	1.6	0.2
20:4(n–3)	nd	0.1	0.0	0.9	0.6	0.6	0.9	nd	nd	nd	0.8	0.1	3.2	0.0	0.0	0.5	nd	nd	0.7	0.6	0.5	0.7	4.0	0.5
22:1(n–11)	12.1	15.3	6.5	10.4	9.5	8.6	10.9	6.7	9.2	8.2	11.6	11.0	13.5	10.4	7.4	7.0	12.0	15.7	15.4	10.9	14.9	11.2	15.4	15.7
22:1(n–9)	1.1	1.7	0.7	0.4	1.4	1.9	0.9	nd	nd	nd	1.1	0.0	1.2	0.9	0.6	0.2	nd	nd	0.0	0.0	0.2	1.2	1.4	1.3
22:1(n–7)	nd	nd	0.1	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.3	0.1	0.1	nd	nd	nd	nd	nd	nd	nd	0.4	0.2
20:5(n–3)	0.9	nd	16.0	8.7	8.0	11.3	11.5	16.2	12.9	14.6	10.8	15.5	12.3	9.9	6.7	11.4	9.8	7.4	8.0	11.8	6.8	5.5	5.9	6.5
24:1(n–9)	0.2	1.0	0.3	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.4	0.4	0.3	nd	nd	nd	nd	nd	nd	nd	0.6	0.3
22:6(n–3)	0.0	0.0	1.4	1.3	1.2	1.2	1.7	13.0	9.4	13.8	2.3	1.6	1.9	3.2	1.5	2.2	7.7	9.8	0.8	0.5	0.8	0.8	1.1	2.6
22PUFAs (other)	0.0	0.0	0.3	0.7	0.6	0.6	0.7	0.0	0.0	0.0	0.7	9.7	0.1	0.6	0.3	0.2	0.0	0.0	0.4	0.6	0.4	0.8	0.0	0.1
Saturated	38.6	46.7	26.2	27.2	25.5	18.3	16.2	20.7	22.9	22.8	17.2	18.5	19.6	30.2	37.4	37.7	27.3	30.0	35.5	23.7	28.8	19.2	29.2	23.9
Monounsat	42.5	46.8	31.5	45.2	52.3	53.1	57.2	20.5	25.7	27.0	54.3	45.5	39.3	34.5	33.4	29.1	33.4	42.1	46.3	48.1	53.4	65.9	44.5	54.0
PUFAs	6.5	1.9	39.0	25.3	20.2	24.0	25.0	47.7	40.8	39.1	27.1	35.6	37.9	32.1	25.8	33.1	29.1	20.0	16.4	26.9	15.8	13.8	22.8	18.1
20:5(n–3)+16PUFA+16:1(n–7)	12.1	9.6	39.2	30.0	32.0	37.1	40.9	22.3	19.6	21.5	35.1	31.7	28.9	18.9	17.0	20.1	18.6	15.9	23.0	35.8	29.2	36.9	17.1	17.3
16:1(n–7)/16:0	0.9	1.0	1.3	1.9	2.3	2.7	4.0	0.5	0.5	0.5	3.6	1.7	1.2	0.7	0.7	0.7	0.7	0.8	1.2	2.2	2.0	4.2	1.0	0.8

Calanus glacialis

Location	NBS[1]	NBS[6*]	KGF[7**]		KGF[8*]		KGF[4]		KGF[5]		FSE[5]		FSE[6*]		FSW[3]	FSW[5]		AO[5]		AO[6*]
Year	1986	2003	2003		2004		1997		1998		1998		2003		89+90	1998	1998	1998		2003
Season	spring	autumn	spring		spring		autumn		autumn		autumn		aut.	win.	summer	autumn		autumn		autumn
Stage	AF	CV	AF	CIV	AF	CV	AF	CV	AF	CV	AF	CV	CV	CV	AF	AF	CV	AF	CV	CV
Replicates	$n=1$	$n=9$	$n=3$	$n=6$	$n=3$	$n=6$	$n=7$	$n=8$	$n=6$	$n=6$	$n=1$	$n=3$	$n=7$	$n=6$	$n=4$	$n=3$	$n=1$	$n=6$	$n=6$	$n=3$
14:0	14.0	9.9	4.8	5.8	8.1	8.9	5.6	7.9	10.5	8.4	9.3	14.4	8.7	16.4	13.1	11.9	11.1	8.6	8.1	8.0
15:0	0.3	0.6	0.7	0.5	0.3	0.5	0.3	0.6	1.6	1.2	0.0	0.5	0.4	0.9	0.3	0.7	0.5	0.4	0.4	0.4
16:0	2.2	6.5	17.3	8.8	5.7	8.4	4.2	6.6	5.4	5.3	4.3	7.4	5.5	9.1	6.1	5.4	5.6	4.0	4.7	5.1
16:1(n–9)	nd	0.6	0.2	0.3	0.8	0.4	nd	nd	nd	nd	nd	nd	0.5	0.6	nd	nd	nd	nd	nd	0.6
16:1(n–7)	13.5	14.5	1.5	10.9	19.6	16.3	23.2	17.8	25.0	25.0	18.6	20.0	12.1	16.5	32.9	23.8	21.4	34.7	26.0	8.5
16:1(n–5)	2.0	0.7	0.8	1.0	0.9	0.5	nd	nd	nd	nd	nd	nd	0.6	0.1	0.3	nd	nd	nd	nd	0.7
16PUFA	1.2	5.9	1.1	10.0	2.6	4.0	3.6	2.4	5.0	4.7	6.8	5.1	8.0	3.0	1.2	3.7	5.2	3.5	4.4	4.2
18:0	0.4	0.5	1.5	1.7	1.1	1.0	0.3	0.5	0.3	0.2	0.0	0.0	0.5	0.7	nd	0.1	0.2	0.4	0.2	0.3
18:1(n–9)	2.4	4.0	2.2	3.1	4.6	3.4	3.6	5.6	3.6	3.9	3.3	3.5	3.5	6.1	5.5	4.8	4.1	3.0	3.6	3.8
18:1(n–7)	0.7	0.8	0.2	1.2	1.4	1.1	1.2	0.9	1.1	0.9	1.3	1.3	0.7	0.9	1.1	0.8	0.7	1.5	1.0	0.8
18:4(n–3)	0.0	7.1	1.7	4.6	7.0	5.8	3.5	6.5	4.3	5.8	7.6	5.8	8.2	8.3	0.5	3.4	4.3	2.0	4.2	7.8
18PUFAs (other)	0.6	2.5	2.2	2.4	2.2	1.5	1.3	2.6	2.9	1.6	2.0	1.9	1.3	3.1	1.3	2.2	1.6	1.5	1.8	6.9
20:0	0.1	0.1	0.2	0.5	0.3	0.2	nd	nd	nd	nd	nd	nd	0.3	0.2	0.1	nd	nd	nd	nd	0.6
20:1(n–11)	nd	0.1	0.3	0.9	0.4	0.2	nd	nd	nd	nd	nd	nd	0.6	0.4	nd	nd	nd	nd	nd	0.9
20:1(n–9)	34.5	15.8	8.0	14.4	18.7	13.2	20.5	16.6	15.6	16.9	18.7	13.0	14.8	13.2	23.0	18.0	17.9	20.3	19.5	13.8
20:1(n–7)	1.0	0.2	0.4	1.1	1.0	0.3	1.0	0.3	0.2	0.0	0.0	0.0	0.2	0.2	1.0	0.0	0.0	1.0	0.0	1.5
20:4(n–6)	0.3	0.2	0.4	0.2	0.2	0.2	0.2	0.3	nd	nd	nd	nd	1.2	0.2	nd	nd	nd	nd	nd	1.7
20:4(n–3)	nd	0.0	0.7	1.7	nd	nd	0.7	0.9	0.6	0.6	0.7	0.7	1.5	0.0	nd	0.6	0.6	0.6	0.6	2.7
22:1(n–11)	16.8	8.0	3.6	5.7	6.5	6.4	10.3	10.7	8.9	10.4	12.5	12.1	9.7	6.7	8.3	10.0	11.0	8.0	11.0	9.8
22:1(n–9)	4.9	1.2	1.1	1.1	1.8	0.8	1.8	0.9	1.0	0.2	0.0	0.0	1.3	0.9	2.0	0.0	0.0	1.8	1.3	1.4
22:1(n–7)	nd	0.1	0.2	0.5	0.4	0.1	0.4	0.1	nd	nd	nd	nd	0.3	0.1	nd	nd	nd	nd	nd	0.5
20:5(n–3)	0.6	13.9	21.7	12.2	5.8	16.3	12.9	11.7	10.4	11.6	11.4	11.2	14.0	6.9	2.7	12.3	13.2	6.4	9.4	12.6
24:1(n–9)	1.0	0.3	nd	nd	0.7	0.4	nd	nd	nd	nd	nd	nd	0.3	0.3	nd	nd	nd	nd	nd	0.4
22:6(n–3)	0.0	1.4	19.3	5.1	2.4	6.7	1.5	2.4	1.1	1.5	1.7	1.7	2.2	1.1	0.8	0.9	0.9	0.6	1.7	2.7
22PUFAs (other)	0.0	2.1	0.9	0.6	0.7	0.9	0.8	1.0	0.9	0.9	0.7	0.6	0.3	0.3	0.0	0.5	0.5	0.5	0.9	1.2
Saturated	17.0	17.7	24.6	17.3	15.5	18.9	10.4	15.5	17.8	15.0	13.6	22.3	15.3	27.3	19.6	18.1	17.3	13.4	13.4	14.4
Monounsat	76.8	46.4	18.5	40.2	56.8	43.0	62.2	52.8	55.4	57.3	54.5	49.9	44.7	46.1	74.1	57.2	55.2	70.3	62.3	42.6
PUFAs	2.7	33.1	48.0	36.9	21.0	35.4	24.5	27.8	25.2	26.6	31.0	27.0	36.6	23.0	6.5	23.5	26.2	15.0	23.0	39.8
20:5(n–3)+ 16PUFA+ 16:1(n–7)	15.3	34.3	24.2	33.1	28.1	36.6	39.7	31.9	40.4	41.3	36.9	36.3	34.1	26.5	36.8	39.7	39.8	44.6	39.8	25.3
16:1(n–7)/16:0	6.1	2.2	0.1	1.2	3.4	1.9	5.5	2.7	4.6	4.7	4.3	2.7	2.2	1.8	5.4	4.4	3.8	8.7	5.5	1.7

Calanus hyperboreus

	NBS[1]	NBS[6]*	NBS[6]*	KGF[5]		KGF[4]		FSE[2]**			FSE[5]		FSE[6]*	FSW[3]	FSW[2]**			FSW[5]		AO[9]			AO[5]		AO[6]*			NWP[10]
Year	1986	2004	2003	1998		1997		1988			1998		2003	89+90	1984			1998					1998		2003	2003		1999
Season	spr.	spr.	aut.	autumn		autumn		summer			autumn		winter	summer	summer			autumn		sum.	aut.	win.	autumn		spring	autumn		autumn
Stage	AF	CV	CV	CV	AF	CV	AF	CIV	CV	AF	CV	AF	AF	AF	CIV	CV	AF	CV	AF	CIV-V	CIV-V	CIV-V	CV	AF	CV	CV	AF	CV
Replicates	*n*=1	*n*=3	*n*=9	*n*=6	*n*=4	*n*=14	*n*=13	*n*=3	*n*=3	*n*=3	*n*=3	*n*=4	*n*=3	*n*=3	*n*=2	*n*=2	*n*=3	*n*=2	*n*=4	*n*=1	*n*=1	*n*=2	*n*=1	*n*=1	*n*=6	*n*=7	*n*=7	*n*=27
14:0	4.6	4.9	3.6	4.6	4.2	3.3	3.3	3.4	2.6	2.9	2.9	3.6	4.5	6.4	6.6	6.7	3.6	0.9	3.1	2.0	5.0	6.0	6.1	3.9	2.2	2,9	3,0	3,1
15:0	0.2	0.1	0.2	0.4	0.7	0.2	0.2	nd	nd	nd	2.0	0.1	0.3	nd	nd	nd	nd	0.3	0.2	nd	nd	nd	0.6	0.0	0.0	0,1	0,2	0,1
16:0	2.5	2.7	2.8	3.4	2.8	2.3	2.8	3.3	2.6	3.1	2.0	2.7	3.4	5.8	8.0	5.4	3.9	3.2	2.3	3.0	4.0	5.0	2.2	8.3	1.5	2,0	2,2	3,1
16:1(n–9)	nd	0.2	0.6	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.8	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.4	0,6	0,1	nd
16:1(n–7)	20.9	7.2	12.6	nd	nd	21.7	19.3	2.6	2.8	3.7	nd	nd	12.1	11.7	12.8	14.2	16.9	nd	nd	24.0	22.0	30.0	nd	nd	6.1	6,7	7,1	17,9
16:1(n–5)	1.2	0.0	0.4	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.3	0.7	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.3	0,4	0,1	0,3
16PUFA	3.0	5.2	6.4	4.2	4.9	4.8	3.1	1.7	1.6	2.1	3.4	3.0	1.9	3.5	3.1	1.5	2.6	7.5	6.0	6.0	5.0	0.0	3.5	0.0	5.4	3,4	2,6	7,4
18:0	0.6	0.4	0.5	0.4	0.1	0.3	2.1	nd	nd	nd	0.6	0.6	0.6	nd	0.0	1.1	2.0	nd	nd	1.0	nd	nd	0.6	0.0	0.6	0,2	0,3	0,2
18:1(n–9)	4.1	3.4	2.7	3.6	2.6	2.6	0.3	4.0	4.1	3.8	3.9	3.7	3.7	5.8	6.7	6.8	5.0	1.7	2.2	3.0	8.0	7.5	6.7	45.5	2.5	3,1	2,2	2,0
18:1(n–7)	1.0	1.0	1.2	1.4	1.4	1.5	2.2	nd	nd	nd	1.3	1.4	1.3	1.6	nd	nd	nd	1.1	1.2	nd	nd	nd	1.4	1.4	0.8	0,9	0,9	1,3
18:4(n–3)	1.3	31.6	12.8	4.7	10.8	6.9	0.7	19.5	23.3	4.4	11.1	16.1	4.3	6.2	3.1	1.8	2.9	3.2	3.8	0.0	6.0	0.0	1.1	7.1	22.5	9,4	10,6	3,2
18PUFAs (other)	0.3	30.6	11.6	3.3	9.4	2.0	0.9	0.0	0.0	15.1	9.8	0.0	2.7	5.2	0.0	0.0	0.2	2.0	0.3	14.0	0.0	2.0	13.4	0.0	2.3	5,1	1,8	1,7
20:0	nd	0.1	0.1	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.7	0.8	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.5	0,4	0,5	nd
20:1(n–11)	nd	1.0	0.4	nd	nd	nd	4.9	nd	nd	nd	nd	nd	1.8	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	2.1	1,4	1,7	nd
20:1(n–9)	27.4	11.3	13.7	14.1	18.3	15.3	nd	25.9	15.7	15.2	12.9	16.8	14.9	19.0	4.1	18.0	19.5	7.0	12.2	2.0	22.0	19.0	15.7	10.0	11.5	13,9	13,4	7,1
20:1(n–7)	1.6	0.6	1.1	1.0	2.7	1.8	17.4	nd	nd	nd	0.2	1.2	1.4	1.5	nd	nd	nd	1.1	1.9	nd	nd	nd	0.0	0.0	0.7	1,0	1,5	1,2
20:4(n–6)	0.5	0.1	0.2	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.0	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.3	1.5	1.4	nd	nd	nd
20:4(n–3)	0.2	0.0	0.0	1.1	0.8	0.9	nd	nd	nd	nd	1.1	1.4	5.9	0.7	nd	nd	nd	0.6	0.7	5.0	nd	13.0	1.1	0.0	3.9	3,7	5,3	nd
22:1(n–11)	11.1	7.8	10.9	11.9	11.6	15.6	12.0	8.3	16.7	18.2	10.0	11.7	18.1	17.3	12.8	18.4	17.7	5.4	7.1	nd	15.0	7.5	23.5	11.3	12.7	15,2	15,0	6,8
22:1(n–9)	7.6	1.4	2.8	1.9	3.1	0.7	14.1	nd	nd	nd	0.7	2.7	5.0	3.2	nd	nd	nd	0.0	1.5	nd	nd	nd	0.0	2.6	2.6	3,9	6,2	1,3
22:1(n–7)	nd	0.1	0.2	nd	nd	nd	3.7	nd	nd	nd	nd	nd	1.3	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.7	0,8	1,3	0,2
20:5(n–3)	4.1	8.0	14.5	9.6	10.8	13.1	0.8	12.6	9.2	10.4	15.9	14.6	5.6	7.0	10.4	8.2	12.6	24.5	19.4	35.0	12.0	23.0	5.6	4.0	9.5	13,0	11,5	27,1
24:1(n–9)	0.6	0.1	0.3	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.7	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	0.1	0,3	0,4	nd
22:6(n–3)	0.0	3.7	5.2	2.1	4.8	3.2	0.1	11.0	10.9	6.4	7.2	9.6	3.0	2.4	7.5	10.7	3.4	1.9	2.6	3.0	1.0	4.0	2.5	3.1	5.8	5,6	6,1	5,0
22PUFAs (other)	0.0	0.4	1.3	3.8	0.0	1.2	0.9	0.0	0.0	4.6	5.1	0.0	0.0	0.5	0.0	0.0	4.1	2.1	0.7	0.0	3.0	0.0	1.6	0.0	0.3	0,7	0,0	1,8
Saturated	7.9	8.2	7.2	8.7	7.8	6.1	8.4	6.7	5.3	6.1	6.9	6.9	9.4	13.6	14.5	12.1	7.5	4.4	5.7	7.0	9.0	11.0	8.9	12.2	4.8	5,6	6,1	6,6
Monounsat	75.5	34.1	47.0	33.9	39.7	59.2	73.8	40.7	39.3	40.9	29.2	37.5	61.6	60.8	36.3	57.4	59.2	16.4	26.2	29.0	67.0	64.0	47.3	70.8	40.5	48,1	50,0	38,0
PUFAs	10.4	52.5	42.4	35.9	26.1	32.1	6.5	25.1	45.0	43.0	53.7	43.2	24.4	25.5	19.7	22.2	25.8	41.9	33.5	61.0	23.0	41.0	28.9	7.6	51.0	42,4	39,2	46,3
20:5(n–3)+16PUFA+16:1(n–7)	28.0	20.4	33.5	13.8	15.6	39.6	23.2	16.9	13.6	16.2	19.4	17.6	19.6	22.2	26.2	23.9	32.1	32.1	25.4	65.0	39.0	53.0	9.1	4.0	21.0	23,1	21,1	52,4
16:1(n–7)/16:0	8.4	2.7	4.6	0.0	0.0	9.4	7.0	0.8	1.1	1.2	0.0	0.0	3.6	2.0	1.6	2.7	4.4	0.0	0.0	8.0	5.5	6.0	0.0	0.0	4.0	3,4	3,3	5,8

Northern Barents Sea (NBS), Kongsfjorden (KGF), Fram Strait East (FSE), Fram Strait West (FSW), Arctic Ocean (AO), Hudson Bay (HB) and North Water Polynia (NWP). The numbers from 1–11 refer to the original work: 1 = Falk-Petersen 1986 (unpublished), 2 =Kattner et al. 1989, 3 =Alberts et al. 1996, 4 = Scott et al. 2002, 5 =Falk-Petersen/Norwegian Polar Institute database (unpublished), 6 =Søreide et al. 2007, 7 =Leu (unpublished), 8 =Leu et al. 2006, 9 =Lee 1974, 10 =Stevens et al. 2004, 11 =Mayzaud (unpublished). *=neutral lipid, **=total lipid.
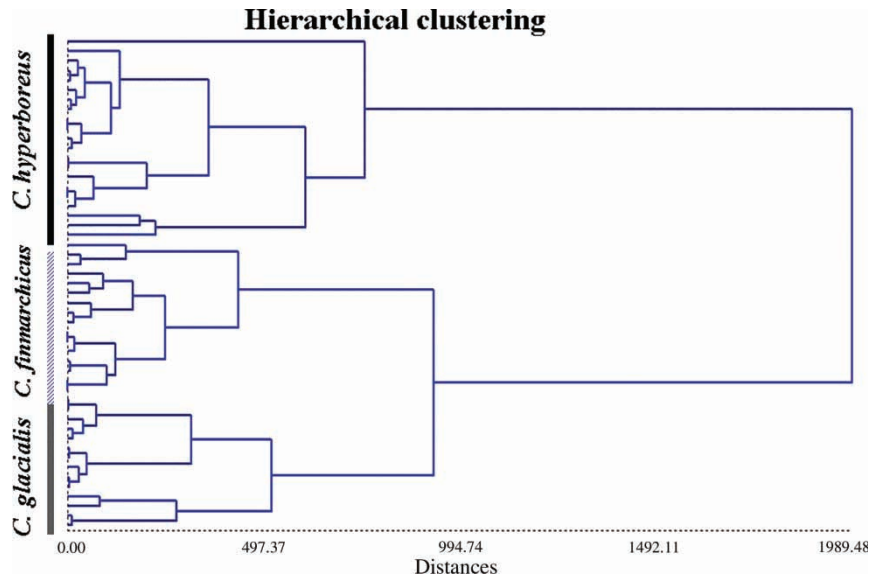
Figure 6. Hierarchical cluster analysis of fatty alcohol composition for *C. hyperboreus*, *C. glacialis* and *C. finmarchicus* collected in different sectors of the European Arctic Ocean. Symbols: Ch =*C. hyperboreus*, Cg =*C. glacialis*, Cf =*C. finmarchicus*.

understanding that fatty alcohols are mainly biosynthesized de novo from protein and carbohydrate dietary precursors, and that the biosynthesis of fatty alcohol moieties is a process that is species-specific.

The regional heterogeneity of the wax ester fatty acid composition does not exclude that, at a given location, the three species could be correctly discriminated. To test this possibility, we used PLS-DA for three groups of locations: the northern Barents Sea and Kongsfjorden, the eastern Fram Strait and Arctic Ocean, and the western Fram Strait. Three indices characteristics of each species are computed based on the results of the analysis: sum of $14:0 + 16:0$ for *C. finmarchicus*, $16:1(n-7) + 20:1(n-9)$ for *C. glacialis* and $22:1 + 16:0$ for *C. hyperboreus*. Results show that, regionally, the three species can be discriminated with 100% correct assignment, including the indices (Figures 7–9). Interestingly, the fatty acid descriptors of each species differ with the location, but the indices remain characteristic of the related species.

In two of the three sectors considered, the first discriminant function opposes *Calanus hyperboreus* to the other two species, while the second function separates *C. glacialis* from *C. finmarchicus*. In the northern Barents Sea and Kongsfjorden (Figure 7), *C. hyperboreus* is associated to the profile of C22 PUFA, while $20:1(n-9)$, $18:1(n-9)$ profiles are related to *C. glacialis* and $16:0$, $20:5(n-3)$ with *C. finmarchicus*. The fatty acid $16:1(n-7)$ and C16 PUFA are descriptors for the latter two species, suggesting that at these locations *C. glacialis* and *C. finmarchicus* fed more heavily on phytoplankton dominated by diatom. PLS-DA for East Fram Strait

and Arctic Ocean waters (Figure 8) shows slightly different descriptors with C22 PUFA, $20:4(n-3)$ for *C. hyperboreus*, $20:1(n-9)$, $18:1(n-7)$, $16:1(n-7)$ for *C. glacialis* and $16:0$ for *C. finmarchicus*. At these locations *C. glacialis* seems to be the most herbivorous species. The results for East Fram Strait are quite different since the first discriminant function opposes *C. finmarchicus* to the other two species (Figure 9). The fatty acid descriptors comprise most saturated acids and C18 PUFA, while *C. hyperboreus* was associated to changes in C22 PUFA, C16 PUFA and $20:5(n-3)$, and *C. glacialis* to $16:1(n-7)$ and $20:1(n-9)$. These last two species are clearly feeding on phytoplankton in this area.
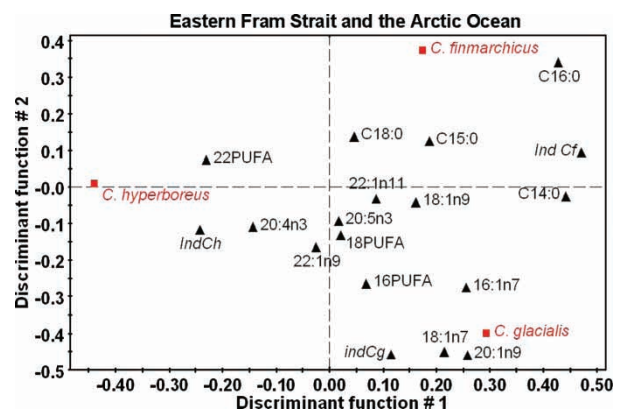
Figure 7. PLS-DA for the three main species of *Calanus* sampled in the Northern Barents Sea and Kongsfjorden based on the fatty acid composition of wax esters. Projection on the plane defines by the first two discriminant functions (DS1 =45.9% and DS2 = 33.2% total inertia). Factor loading for the fatty acid descriptors. Italic: centroid of the factorial group. Ind =indices for each *Calanus* species (see text).
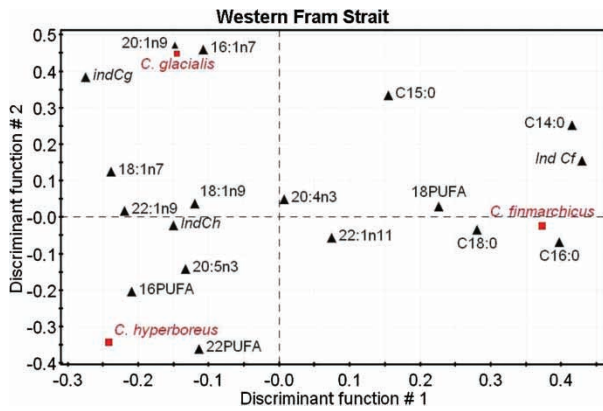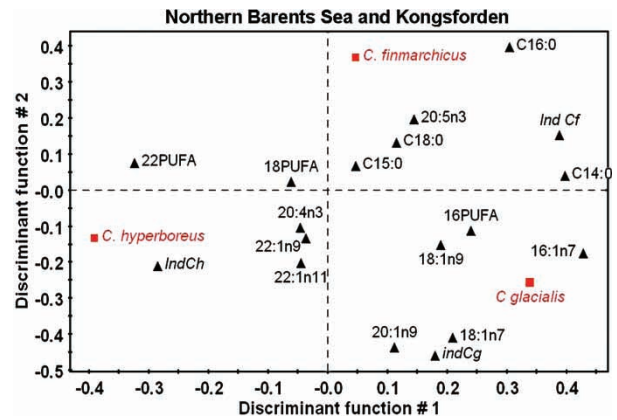
Figure 8. PLS-DA for the three main species of *Calanus* sampled in the eastern Fram Strait and Arctic Ocean based on the fatty acid composition of wax esters. Projection on the plane defines by the first two discriminant functions (DS1 =37.7% and DS2 = 32.3% total inertia). Factor loading for the fatty acid descriptors. Italic: centroid of the factorial group. Ind =indices for each *Calanus* species (see text).

Figure 9. PLS-DA for the three main species of *Calanus* sampled in the western Fram Strait based on the fatty acid composition of wax esters. Projection on the plane defines by the first two discriminant functions (DS1 =36% and DS2 =32% total inertia). Factor loading for the fatty acid descriptors. Italic: centroid of the factorial group. Ind =indices for each *Calanus* species (see text).

Biodiversity and ocean climate variability

Polar systems are characterized by pronounced seasonal oscillations in incident solar radiation. The light regime changes dramatically during the year, from a period of winter darkness to a period of midnight sun during summer north of the Arctic Circle. The ice cover also changes dramatically on very short time scales from hours to days and on long time scales from years to decades (Proshutinsky et al. 1999; Falk-Petersen et al. 2000b, 2008; Vinje 2001). These changes strongly influence the light available for primary production with little or no light penetrating to waters underlying dense ice (Hansen et al. 2003). The extent to which ice cover can vary is emphasized by the fact that the North Pole can be largely ice-free during summer in some years, while it is totally ice-covered in other years. In the North Pole region, on average more than 15% of the area is open water in late summer (Polyakov et al. 1999), and phytoplankton blooms are regularly registered in North Pole waters (Figure 1; Zenkevich 1963). Large variations in ice cover can also be seen in the marginal ice-covered seas. Large parts of the Barents Sea and the Norwegian Sea were totally ice-covered in spring of 1966, while in 1995 most of the same areas were ice free (Vinje 2001). Oscillations in ice conditions on an interannual and decadal scale are related to environmental phenomena such as the changes of the cyclonic and anticyclonic regimes over the Arctic Ocean, which occurs in periods of 10-years (Proshutinsky et al. 1999), and the North Atlantic Oscillation Index, which occurs in periods of 7 years (Dickson et al. 2000).

Plankton communities at high latitudes have developed as a result of the history of climate changes, not only the recent history, but changes that have occurred over millions of years. Diatoms and copepods have evolved during a period of global cooling, largely since the K-T extinction event 65 million years ago, when polar ice caps were formed, and marine production in high latitudes became seasonally pulsed (Rigby & Milsom 2000). Kattner et al. (2007) hypothesize that the present composition of the polar herbivore community in the Arctic, mainly consisting of the three *Calanus* species, as well as the development of highly efficient lipid synthesis of wax ester in these animals, is a consequence of the variations in climate observed over the past centuries and millennia. According to our present understanding, the Arctic *Calanus* species are engineered to feed on the Arctic bloom and convert the low-energy carbohydrates and proteins produced by phytoplankton and ice algae to high-energy wax ester lipids (Sargent & Henderson 1986; Hagen & Auel 2001; Falk-Petersen et al. 2007; Kattner et al. 2007; Varpe et al. 2007). The pelagic *Calanus* species, being one of the major members of the Arctic marine ecosystem, has adapted to an environment changing markedly on different time scales. This readily accounts for the biodiversity of the *Calanus* complex in terms of the species' different life strategies, different ecological niches and different centres of distribution.

Thus, the most polar species, *Calanus hyperboreus*, has its centre of distribution in deep-sea areas such as the central Arctic Ocean, the Fram Strait and the Greenland Sea. These are areas with marked annual and interannual variations in ice conditions. In favourable seasons, when the ice-cover opens up for longer periods, food is plenty, while in years with permanent ice cover food is effectively absent.

Calanus hyperboreus has adapted to this condition by developing a large plasticity in its life strategy. Under favourable conditions, where primary production is high, the animal has a life span of only 1–2 years (Table I), while under less favourable conditions when ice cover had been extensive it has a life span from 3 to5 years or even longer. When *C. hyperboreus* has accumulated sufficient oil reserves as high-energy wax esters, it migrates down to deep waters (500–2000 m) and enters diapause, probably neutrally buoyant. Under these conditions it has sufficient high-energy reserves to meet its minimal metabolic requirements for long periods, exceeding a single season if need be. It is logical that the greater the variations in ice cover and especially the greater the likelihood of prolonged ice cover, the greater the advantage for a herbivorous copepod to arrest development at any stage. This is more likely to occur in large copepods with large reserves of high-energy lipids in early as well as late developmental stages.

Calanus glacialis is a typical shelf species which spawns in waters all around the shelf and in the White Sea. Although the shelf areas experience large variations in ice cover, the ice mostly opens up for shorter or longer period during the summer or autumn, allowing an annual algal bloom. *Calanus glacialis* has a life span of 1–3 years. Scott et al. (2000) suggested that this species is well capable of developing from eggs to wax ester-rich stages III and IV copepodites within a single year. However, the large increment in body mass and lipid reserves as it develops further from stages IV to V copepodites is unlikely to be achieved in a single year, except under very favourable conditions. Thus, development from stage IV to stage V probably occurs in two-year-old *C. glacialis*. The resulting large, wax ester-rich stage V copepodites then over-winter and spawn immediately prior to or during the spring bloom in their subsequent third year of life.

The boreal–arctic *Calanus finmarchicus* is also a deep-water species, but its centre of distribution is further south in the Norwegian Sea and the Labrador Sea. Breeding populations are also found along the Norwegian coast, the west coast of Greenland and in the southern Barents Sea. These are areas where a predictable annual spring bloom occurs between March and May. *Calanus finmarchicus* is the smallest of the three species and develops from eggs to wax ester-rich, over-wintering stage IV and stage V copepodites, within 6–10 weeks in favourable years. Stage IV copepodites complete their development to stage V and then to females in the spring of the following year, prior to spawning. This final development depends on both internal wax ester reserves and the availability of algal food. A successful spawning depends strongly on the spring bloom.

Based on the lipid composition and the biology of the Arctic *Calanus* species we generally conclude that:

- all *Calanus* species are herbivores engineered to feed on the Arctic bloom;
- the timing of the bloom is the important factor in determining the life strategy of the individual species and biodiversity of the *Calanus* complex;
- *Calanus finmarchicus* is a deep-water species adapted to an environment with a regular yearly spring bloom, as occurs in the Norwegian Sea;
- *Calanus glacialis* is a shelf species adapted to an environment subjected to large variations in timing and length of the annual bloom, as found in the northern Barents Sea and on the Siberian and American shelves; and
- *Calanus hyperboreus* is a deepwater species adapted to an environment with large interannual variations in ice cover and algal blooms, as found in the central Arctic Ocean and the Fram Strait.

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