9 Climate variability and possible effects on arctic food chains: The role of *Calanus*

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9.1 Introduction

The large oscillations of abiotic factors in the Arctic is critical in structuring its marine biota and the biodiversity of its indigenous populations and communities. The seasonal light cycle is modified by the sea ice cover, creating a situation dominated by phytoplankton blooms, that follow the receding ice edge, and in leads as the sea ice opens during the Arctic summer (Sakshaug 1997, 2003; Hegseth 1998; Falk-Petersen et al. 2000a; Engelsen et al. 2002). Blooms of phytoplankton propagate through Arctic waters (Zenkevich 1963) and carbon fixed through photosynthesis is rapidly converted into large, specialised lipid (marine fat) stores by the herbivorous *Calanus* species (Lee 1975; Sargent and Henderson 1986). These high-energy lipids are then rapidly transferred upwards through the food chain in large amounts (Falk-Petersen et al. 1990). The increase in lipid level from 10-20% of dry mass in phytoplankton to 50 - 70% in herbivorous zooplankton is probably one of the most fundamental specialisations in polar bioproduction. The lipid – based energy flux is one of the primary reasons for the large stocks of fish and mammals in Arctic waters.

The importance of the diatom => *Calanus* food chain in the Arctic pelagic food has been demonstrated by Falk-Petersen et al. (1986; 2002) and Scott et al. (2002). A wide spectrum of predators from zooplankton to fish and sea birds has also been analysed by using fatty acid trophic markers in Arctic waters. In all of these studies the *Calanus* C20 and C22 lipid trophic markers were strikingly dominant, demonstrating the importance of the

Calanus species in the Arctic pelagic ecosystem (Falk-Petersen et al. 2001, 2002, 2004; Dahl et al. 2003.

The population size spectrum and energy content of the key *Calanus* species, being potential prey for zooplankton-eating fish and sea birds, is therefore instrumental in structuring the biodiversity of Arctic ecosystems. We believe that understanding the climate variability is a key to under-stand the biology of Arctic animals and the biodiversity of Arctic systems. In this paper we discuss how different climate regimes in the Nordic Seas can influence *Calanus*- based Arctic food chains**.**

9.2 Climate variability and species distribution

9.2.1 The distribution of the *Calanus* species and the current system.

The circulation of water in the Nordic Seas, the modification of water masses and changes of ice conditions are important for a) the local climate and b) the larger-scale systems of oceanic and atmospheric circulation af-fecting the climate of northern Europe and c) the marine food resources.

The distribution of the three main *Calanus* species in the Nordic Seas and the Eurasian Basin of the Arctic Ocean is strongly influenced by two large, interconnected current systems (Fig. 9.1). The current system is mainly governed by the topography (Rudels et al. 1999; Hansen and Østerhus 2000). In the south the North Atlantic Current enters the Norwe-gian Sea on both sides of the Faroe Islands and flows northwards parallel to the Norwegian Coast (Hansen and Østerhus 2000). North of the Lofoten Islands at approx. 72 ^{o}N one branch turns northwest and flows along the Barents Sea margin as the West Spitsbergen Current. Northwest of Spits-bergen, a part of the current branch westward and southwards and meets the East Greenland Currents flowing southwards before part of the current turns eastwards first into the Iceland Sea and then into the Norwegian Sea north of Iceland.

In the north the Atlantic water enters the Arctic north of Spitsbergen, Svalbard where it submerges under the Arctic water masses (Nansen 1902). It then circulates the Eurasian basin and returns into the Fram Strait on the Greenland side as Arctic Intermediate Waters at depths of 500-900 m. This deep and cold-water mass turns east north of Jan Mayen, and fol-lows the same circulation system as surface water along the Spitsbergen
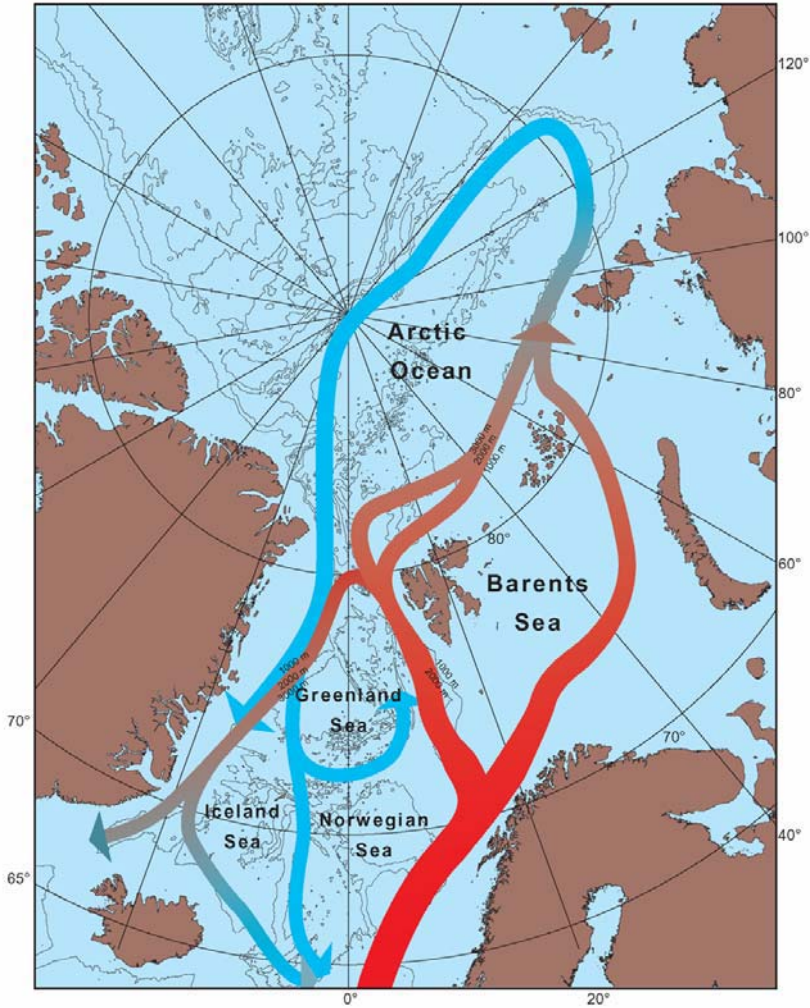
Fig. 9.1. The current system in the European Arctic. The red arrow showing the North Atlantic current entering the Arctic and the blue indicating gradually cooling and sinking (modified after Hansen and Østerhus 2000, Jones et al. 1995).

Shelf slope. In the Fram Strait, therefore, there is an exchange of the waters between the Polar Ocean and the Nordic Seas, with a southward flow on the western side and a northward flow on the eastern side (Jones et al. 1995). The North Cape Branch of the North Atlantic Current enters Barents Sea through the Bear Island Trough (The Barents sea opening) before it flows into the eastern Barents Sea. It then flows northwards along No-
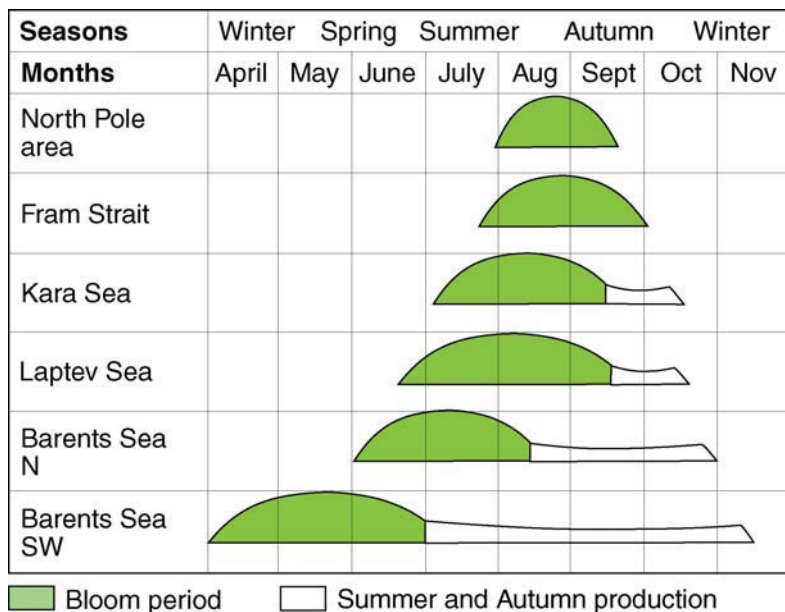
vaya Zemla before it enters the Arctic Ocean between Franz Josef Land and Novaya Zemlya, flowing parallel to the northern branch around the Eurasian basin (Rudels et al. 1999).

The two interconnected current systems in the Atlantic and Arctic (Fig. 9.1) transports *Calanus finmarchicus, C. glacialis* and *C. hyperboreus* long distances and they are found distributed all over the Arctic, including the Norwegian Sea, the Barents Sea, the White Sea, the Arctic Ocean, the Greenland Sea and coastal waters bordering Siberia, East Canada and Alaska. The different species do, however, originate from different centres of distribution and are used as indicator species for the different water masses (Van Aken et al. 1991). The three *Calanus* species also have different core areas for over-wintering, the Norwegian Sea being central for *Calanus finmarchicus,* the Arctic shelf area for *C. glacialis* and the Greenland Sea and the Arctic Ocean for *C. hyperboreus* (Jaschnov 1970; Runge et al. 1986; Conover 1988; Tande 1991; Hirche and Mumm 1992; Hirche and Kwasniewski 1997; Hirche 1997).

9.2.2 Climate variability.

Arctic systems are characterised by pronounced seasonal oscillations in incident solar radiation such that the light regime changes dramatically during the year, from a period of darkness lasting approximately 4.5 month at 80°N to a period of midnight sun during summer. The ice cover and sea water temperature also changes dramatically, both on very short time scales from hours to days and on long time scales from years to decades (Polyakov 1999, Falk-Petersen et al. 2000a; Vinje 2001; Engelsen et al. 2002). The extent to which ice cover can vary is emphasised by the fact that the North Pole can be largely ice - free during summer in some years while it is totally ice covered in others (Polyakov et al. 1999) and phytoplankton blooms are regularly registered in North Pole waters (Zenkevich 1963). Starting and continuation of the bloom in the different parts of the Arctic Ocean corresponds to features of the annual cycle of the ice concentration (Fig. 9.2).

Analysis of the inter-annual water temperature variations along a section across the Atlantic water inflow in the Norwegian, Barents and Greenland seas (Tereshchenko 1997; Furevik 2001) have shown several cold and warm periods during last five decades, varying in periods of 2 to 7 years. Inter-annual and decadal variability of the summer water temperature (Fig. 9.3) was studied between 1950 and 2000 in the core Atlantic inflow in the West Spitsbergen Current (data extracted from a box delineated by 78-79N, 8-10E) and the Barents Sea Opening (box delineated by 72.5-73.5N,

Seasons	Winter	Spring	Summer		Autumn		Winter	
Months	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

Modified after Zenkevich 1963

Fig. 9.2. Time related plankton blooms in the Arctic Oceans (modified after Zen-kevitch 1963).

19.5-21.5E). For this study all available data from the National Oceano-graphic Data Center archive (NODC-02, period 1900-1990), Greenland Sea Project dataset (period 1987-1993), ESOP project I and II dataset (period 1993-1998), VEINS project dataset (period 1997-2000), NPI dataset (period 1959-2003), Russian data collected at the NPI (period 1959-1992) and Climatic atlas of the Barents Sea (Matishov et al. 1998) were used. The temperature decrease in the 50's, 60's and 70's and increased in the 80's and 90's in both areas. The regime shift, between the two periods took place between 1978 and 1979. The surface water of the West Spitsbergen Current had a maximum values at the start of the 50s and the end of the 90s of 4 to 6.5°C and a minimum at the end of the 70s of 1.5 to 3 °C. The Barents Sea Opening had higher temperatures with a maximum at the start of the 50ties and the end of the 90s of 6 to 7 °C and a minimum at the end of the 80s of 4.5 to 5.5°C at 50 m. Periods with warming is related to high North Atlantic Oscillation (NAO) modus and increased Atlantic water in-flow (Furevik et al. 2005).

Analysis of historical data of sea ice (Vinje 2001) shows that the ice ex-tent has been reduced monotonically over a period 135 years (Fig. 9.4).

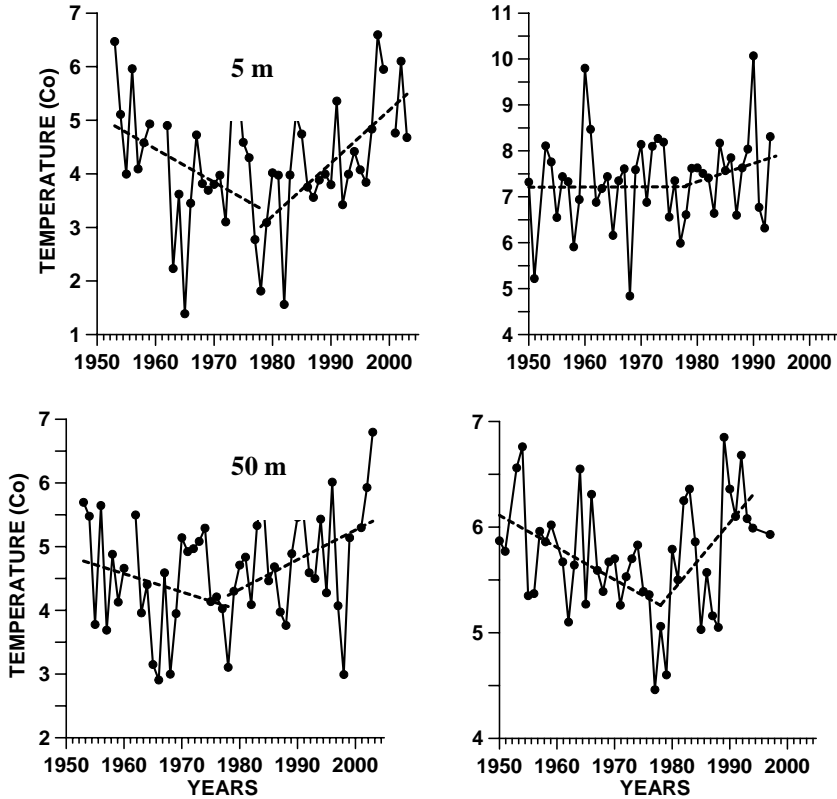April ice extent has decreased by ~33% over the past 135 years and reached

Fig. 9.3. The time series of the summer (July-September) water temperature (solid line and points) along the path of Atlantic water in the West Spitsbergen current for box: 78-79N, 8-10E (left panels) and in the Barents Sea Opening for box: 72.5-73.5N, 19.5-21.5E (right panels) at the depths 5 and 50 m. Linear trends (dashed lines) are shown for two periods 1953-1978 and 1978 – 2003 in West Spitsbergen current and 1950-1978 and 1978-1995 in the Barents Sea Opening.

minima in the 1990s. A strong negative correlation is found between NAO winter index and the Nordic Seas April ice extent (Fig. 9.4, Vinje 2001). For example most of the Barents Sea, parts of the Greenland Sea and the Norwegian Sea were ice covered in the spring of 1966 when NAO index was low while in 1995 (high NAO) most of the same areas were ice free.

9.2.3 Phytoplankton bloom.

The large and spatial changes in ice concentration directly influence the light available for primary production. Blooms of phytoplankton develop as the ice opens (Engelsen et al. 2002) and Zenkevich (1963) described the
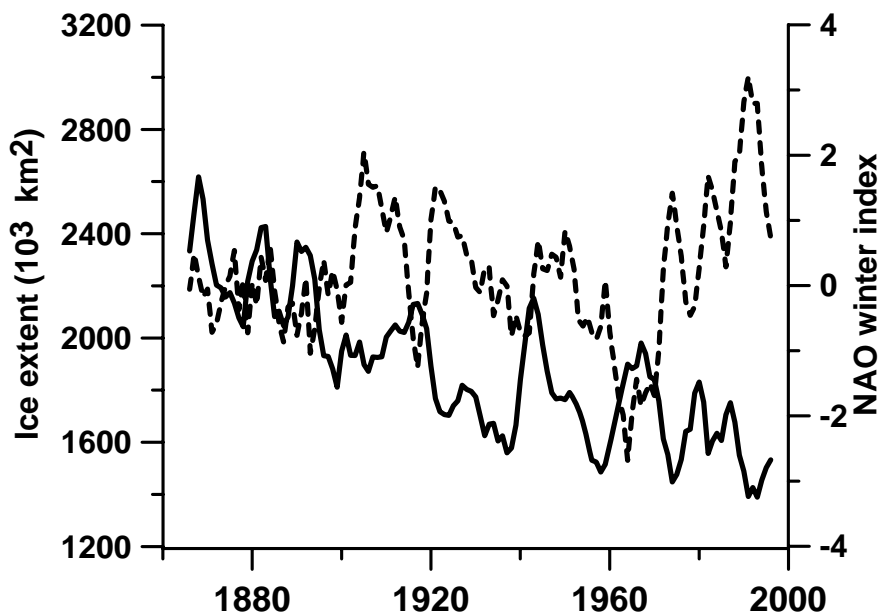

Fig. 9.4. 5-yr running means April ice extent in the Nordic Seas (solid line) and NAO winter index (dashed line). Modified after Vinje (2001).

propagation of the algal bloom along a latitudinal gradient from the southern Barents Sea to the North Pole (Fig. 9.2). The algal bloom is often found in the southern Barents Sea as early as March – April, during the summer in the northern Barents Sea and in August – September in the Fram Strait and in the Arctic Ocean. Thus, herbivorous zooplankton in high latitude, ice-covered seas is exposed to large variations in food availability, not only between seasons (Lee and Hirota 1973; Falk-Petersen et al. 2000b) but also between years, decades and longer periods. The pelagic *Calanus* species being one of the major components of the Arctic marine ecosystem must, therefore, be 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.

9.3 The *Calanus* species

Table 9.1 shows the impressive plasticity of the Arctic *Calanus* species. In the North Sea, *C. finmarchicus* can have a life span of less than a year (Wiborg 1954; Marshall and 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 (MacLellan 1967, Lie 1968, Sekerak et al. 1976, Tande 1991, Falk-Petersen et al. 1999). *C. glacialis* has a life span of 1 to 3 years but for most areas a life span of 2 years is reported (Conover and Huntly 1991, Kosobokova 1999). *C. hyperboreus* shows the most impressive plasticity, with a life span from two to five years (Dawsen 1978, Conover and Huntly 1991, Hirche 1997, Falk-Petersen et al. 1999). Such plasticity in the different species reflects differences in their environments. The central Arctic Ocean has the highest variability in sea climate and, therefore, the lowest predictability of food available for herbivorous zooplankton. The ability of the different developmental stages of calanoids to over-winter depends on their abilities to store energy. It is interesting to note that all three species have similar energy content (dry weight 0.14, lipid 0.05 mg pr individual), at their first main over-wintering stage (Fig. 9.5). The similarity of the energy content of the first over - wintering copepodite stages, V, IV and III for *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, respectively, is consistent with the energy demand of the first over - wintering being the same for the three species.

Table 9.1. The Arctic *Calanus* complex. Life span (years), maximum size (mm), lipid weight (LW) as mg • ind-1, and % total lipid (TL) of DW, % wax ester (WE) of TL. IV and V = copepodite stages, F = females.

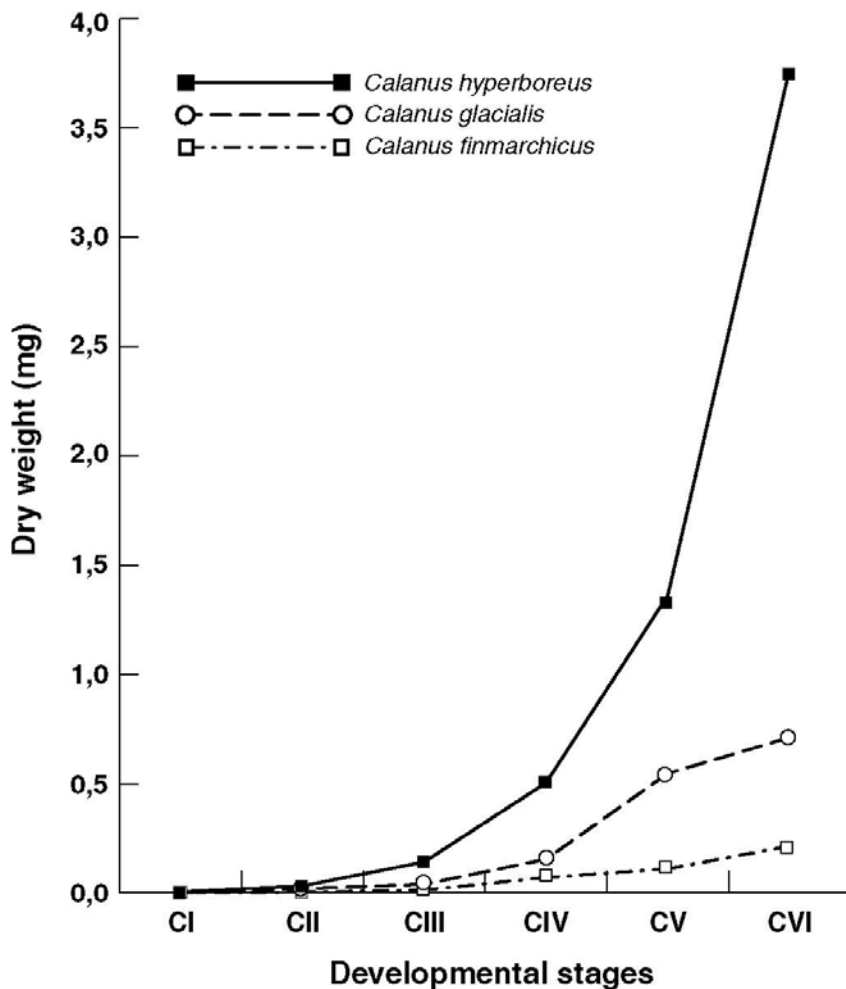| Species	Life span	Stage	Max. size	LW	% TL	% WE
C.finmarchicus. .	1	IV	2.2	0.02	53	63
		V	3.0	0.04	34	68
		F	3.2	0.08	31	62
C. glacialis	2-3	IV	2.8	0.05	56	68
		V	4.0	0.38	61	72
		F	4.6	0.45	70	68
C.hyperboreus.	2-5	IV	4.0	0.28	54	72
		V	6.0	1.03	65	75
		F	7.0	1.81	62	75

Fig. 9.5. Growth in terms of dry weights of the different copepodite stages (I to VI) of Calanus finmarchicus, Calanus glacialis and Calanus hyperboreus. Data from Mauchline 1998.

9.3.1 *Calanus hyperboreus*

C. hyperboreus, the most polar species, has its centre of distribution in the current system connecting the deep-sea areas such as the Greenland Sea, the Fram Strait and the Arctic Ocean (Fig. 9.1). These are areas with marked annual and inter-annual 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 scarce. *C. hyperboreus* has adapted to this condition by developing a large plasticity in its life strategy (Table 9.1). It is a large copepod and can over - winter, as early as stage III, after accumulating large energy reserves in the form of high - energy wax esters (Hirche 1997; Scott et al. 2000). Under favourable conditions when primary production is high, the animal has a life span of 2 years, while under extensive ice cover it has a life span from 3 to 5 years. *C. hyperboreus* females store large quantities of wax esters which are consumed in the spawning process during winter. Spawning takes place independent of the algal bloom and the fertilised eggs will normally develop rapidly via the naupliar stages to stage III or IV copepodites during the short bloom in the following summer/ autumn. When *C. hyperboreus* has accumulated sufficient lipid reserves it migrates down to deep waters (500-2000 m) and enters diapause (Vinogradov 1997). 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 variation in ice cover and especially the greater the likelihood of prolonged ice cover, the greater the advantage for an 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.

9.3.2 *Calanus glacialis*

C. glacialis is a typical shelf species which spawns in waters all around the Arctic shelf and in the White Sea. Although the shelf areas experience large variations in ice cover, the ice nearly always opens up for shorter or longer periods during the summer or autumn allowing an annual algal bloom to occur. *C. glacialis* has a life span of 1-3 years. It spawns before or during the yearly spring bloom (Niehoff et al. 2002) and it grows rapidly in the same year to reach its over-wintering stage IV, with large energy-rich wax ester reserves (Table 9.1). It then descends to deep areas on the shelf (200 to 300 m) to enter diapause and over-winter. Scott et al. (2000) suggested that this species is well capable of developing from eggs via the naupliar stages to wax ester-rich stage III and stage IV copepodites within a single year. However, the large increment in body mass and lipid reserves as it develops further from stage IV to stage 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 cope-

podites then over-winter and spawn immediately prior to or during the spring bloom in their subsequent third year of life.

9.3.3 *Calanus finmarchicus*

C. *finmarchicus*, the smallest of the three *Calanus* species, is an Atlantic boreal deep-water species. It has two main centres of distribution, one connected to the large gyre in the Norwegian Sea (Fig. 9.1) and the other in the Subarctic Gyre south of the Labrador Sea and east of Newfoundland. In addition there is a small sub-population south of Newfoundland (Matthews 1969; Aksnes and Blindheim 1996; Planque et al. 1997; Bucklin et al 2000). Breeding populations are also found along the Norwegian coast and in the southern Barents Sea. These are areas where a predictable annual spring bloom occurs between March and May. North of the Arctic Circle, *C. finmarchicus* develops from eggs, via 6 naupliar and several copepodite stages to their major over-wintering stage V within 6 to 10 weeks in favourable years (Sargent and Falk-Petersen 1988). They also accumulated high-energy wax esters as reserves and over-winter in diapause at depths of 500 to more than 2000m (Gislason and Astthorson 2000). The onset of reproductive maturity and egg production occur before the onset of the phytoplankton bloom and are mainly fuelled by internal reserves of wax esters (Ohman and Hirche 2001). The per capita egg production rate increases at the time of the bloom (Niehoff et al. 1999) and final gonad maturation followed by successful spawning depends on timing of the spring bloom (Niehoff et al. 2002).

9.4 Ecosystem effects of Arctic warming

According to our present understanding there are two possible scenarios of climate change in the region. The first is based on the hypotheses that the Arctic climate varies in cycles (Proshutinsky et al. 1999) and that we now are at the beginning of a cold period, leading to heavy ice conditions in the Barents, Greenland and parts of the Norwegian Seas (Vinje 2001). The second scenario is based on a hypothesis of a continuation of the present trend, resulting in a permanent warming of the Arctic climate (IPPC 2001) and a decrease of the ice extent of the Barents Sea and the Southern Arctic Ocean. The extent of the ice cover in the Nordic Seas in spring has decreased since 1860 due to the net thermal effect of the north-bound currents in the area (Vinje 2001). A warming of the water masses in the central Arctic Ocean has been observed in the 1990s, explained by increased
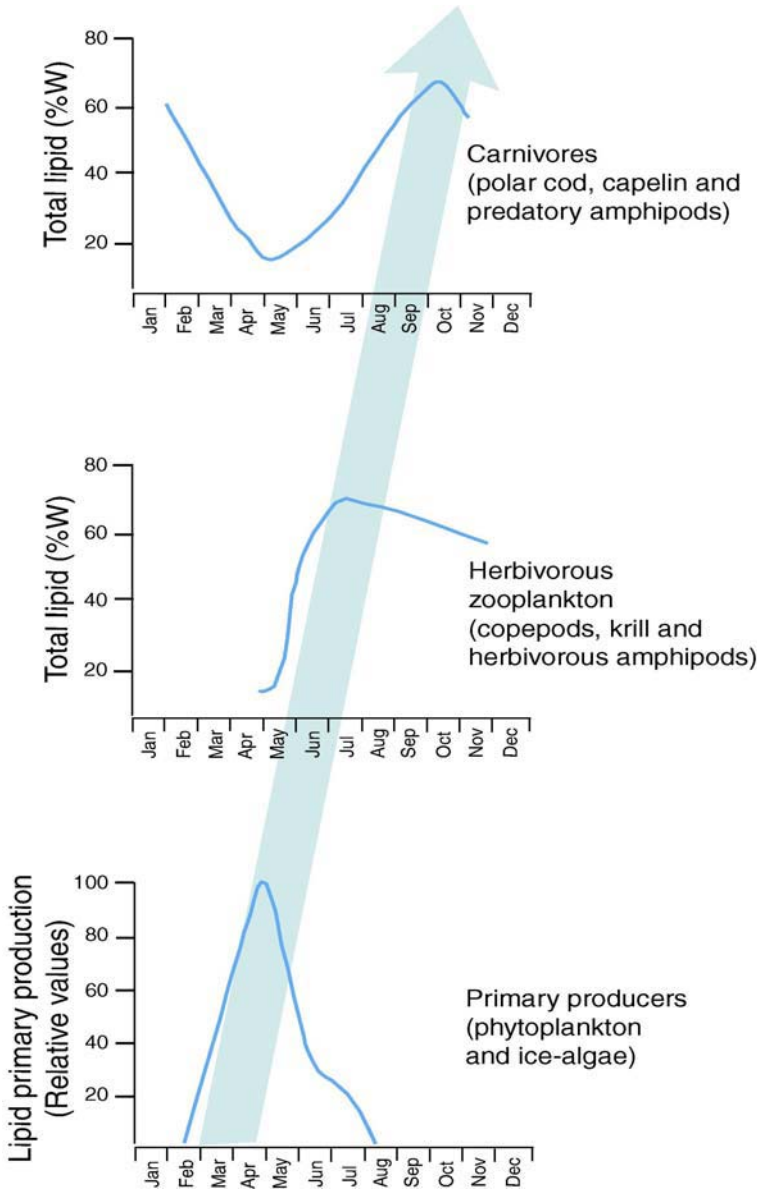
Fig. 9.6. The transfer of lipid from the spring bloom via Calanus and krill to capelin within six months (modified after Falk-Petersen et al. 1990).

Atlantic water influx in periods with high NAO modus (Furevik et al. 2005). Should Arctic warming be a long-term trend, as suggested by IPPC, and much of the southern part of the Arctic Ocean become ice - free during

spring and summer, a yearly spring algal bloom will occur in this area, resulting in a large increase in "new" primary production. This will probably create an environment favourable to *C. finmarchicus* and detrimental to *C. glacialis* and especially to *C. hyperboreus.*

Polar pelagic systems are notoriously instable (Sakshaug 1997) and herbivorous zooplankton exposed to marked variations in food available has adapted by storing lipids as energy reserves. The lipid accumulated in large amounts by calanoid copepods is exploited as an energy source by large-stocks of fishes like herring (*Clupea harengus*) and the capelin (*Mallotus villosus*), which themselves can store large quantities of oil derived from zooplankton (Fig. 9.6). These energy rich fishes, together with *Calanus*, krill and amphipods species, occurring in dense schools and swarms, constitute large energy-packed food items for sea birds and marine mammals enabling them to sustain over-wintering populations (Welch et al. 1992). This lipid-based energy flux, from algae to marine mammals (Fig. 9.6), is likely to be a key determinant of the biodiversity and productivity of this environment.

The size spectrum and energy content of the major zooplankton species in Arctic ecosystems determine their value as food sources for the upper trophic levels. Both vary substantially among the three *Calanus* species. For example, *C. glacialis* and *C. hyperboreus* are considerably larger and adults contain approx. 10 and 25 times more energy (lipids), respectively, than *C. finmarchicus*. Fig. 9.5 and Table 9.1 summarise the important characteristics of the individual *Calanus* CV. Taken together this tells us that in the Arctic basin *C. hyperboreus* is the most highly adapted of the three species in accumulating large, energy-rich lipid reserves, followed by the Arctic shelf *C. glacialis* and the north Atlantic *C. finmarchicus* (Sargent & Falk-Petersen 1988; Scott et al. 2000). Perhaps more important for a zooplankton predator, is the difference in the food size spectrum between the three *Calanus* species, decreasing from the large energy-rich quanta provided by *C. hyperboreus* to the smaller less energy-rich quanta provided by *C. finmarchicus*.

9.5 Conclusions

From the above we conclude that *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 the timing and length of the annual bloom, as found in the northern Barents Sea and the Arctic
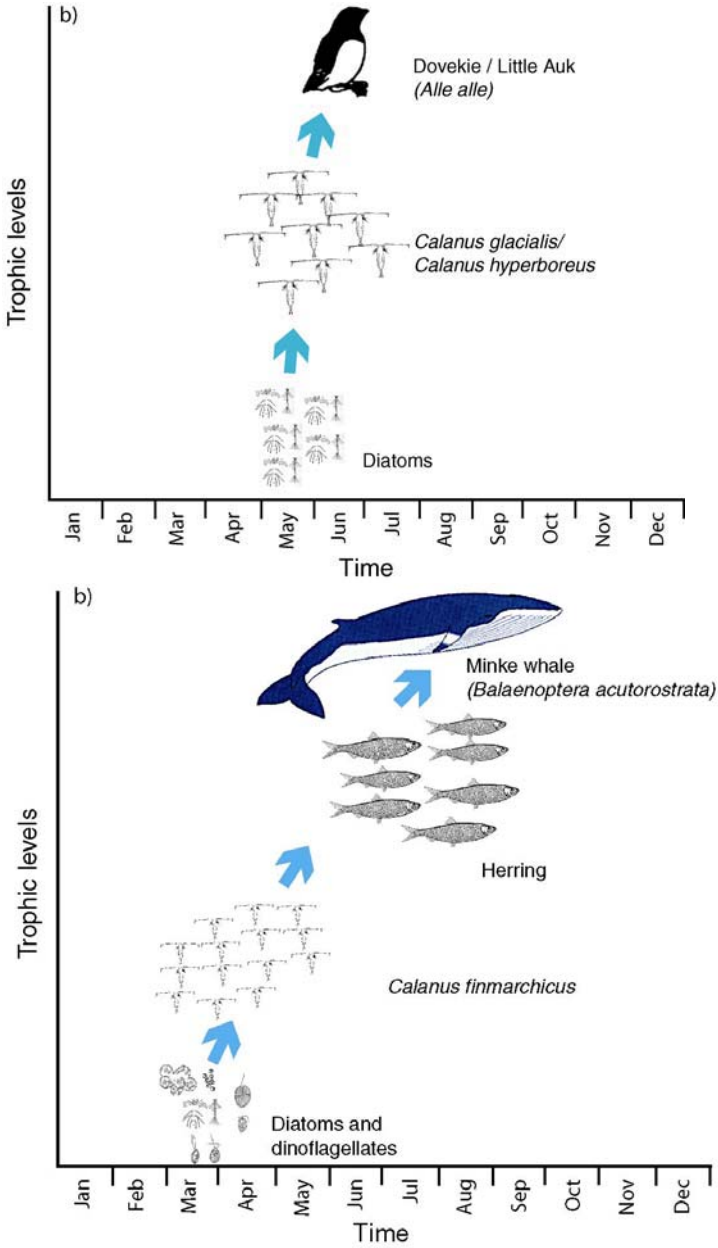
Fig. 9.7. *Calanus* based food web in the Nordic Seas. a) *C. glacialis / C. hyperboreus* based food web b) *C. finmarchicus* based food web.

shelves. *Calanus hyperboreus* is a deep-water species adapted to an environment with large inter-annual variations in ice cover and algal blooms, as found in the central Arctic Ocean and the Fram Strait.

We postulate that a warmer climate with reduced ice cover and new phytoplankton bloom regimes will shift zooplankton community structure towards a smaller zooplankton size spectrum (*C. finmarchicus*), with lower energy content per individual. The changes in zooplankton communities will be reflected in the diet composition and affect the general ecology of specialised seabirds. The little auk (*Alle alle*) requires access large energy-rich zooplankton (*C. glacialis and C. hyperboreus*) to successfully raise their chicks (Fig. 9.7a, Weslawski et al. 1994; Pedersen and Falk 2001). In Iceland, colonies of this high - arctic seabird were heavily reduced during the first half of the last century associated with the rapid warming in the Icelandic climate during the same period (Gudmundsson 1952). The rise in temperature probably triggered a shift in the zooplankton distribution favouring *C. finmarchicus* instead of *C. hyperboreus*, a situation having fatal impact on the little auk. It is more difficult to deduce consequences for generalised sea birds and sea mammals. However, Kitaysky and Golubova (2000) concluded, after 8 years of observation in the Okhotsk Sea, that internal oceanographic change impacted alcid reproduction performances by affecting food accessibility to planktivorous auklets and piscivorous puffins in opposite ways. A northward expansion of *C. finmarchicus* to the northern Barents Sea and into the Arctic Ocean north of Svalbard, due to a continuous warming of the water masses and new phytoplankton bloom regime, will create a prey base in the area that will favour the development of herring stocks. From this we postulate that Arctic warming will cause a ecosystem shift, from today's *C. glacialis* / *C. hyperboreus* based energy transfer favouring little auk (Fig. 9.7a) to a *C. finmarchicus* based food chain leading to minke whale (*Balaenoptera acutorostata*) via herring (Fig. 9.5b).

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