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Seasonal variations in biomass, abundance and composition of zooplankton in the subarctic waters north of Iceland

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Abstract The seasonal variations in biomass, abundance and species composition of zooplankton in relation to hydrography and chlorophyll *a* were studied in the subarctic waters north of Iceland. The sampling was carried out at approximately monthly intervals from February 1993 to February 1994 at eight stations arranged along a transect extending from 66°16′N–18°50′W to 68°00′N–18°50′W. The mean temperature at 50 m depth showed a clear seasonal pattern, with lowest water temperatures in February (~1.1°C) and the highest in July (~5.4°C). The spring growth of the phytoplankton began in late March and culminated during mid-April (~7.0 mg Chl *a* m^{-3}). Both the biomass and the abundance of total zooplankton were low during the winter and peaked once during the summer in late May (~4 g m^{-2} and ~38,000 individuals m^{-2}). A total of 42 species and taxonomic groups were identified in the samples. Eight taxa contributed ~90% of the total zooplankton number. Of these *Calanus finmarchicus* was by far the most abundant species (~60% of the total zooplankton). Less important groups were ophiuroid larvae (~9%), *Pseudocalanus* spp. (~8%), *Metridia longa* (~4%), *C. hyperboreus* (~3%), *Acartia longiremis* (~2%), chaetognaths (~2%) and euphausiid larvae (~2%). The dominant copepods showed two main patterns in seasonal abundance: *C. finmarchicus*, *C. hyperboreus* and *C. glacialis* had one annual peak in numbers in late May, while *Pseudocalanus* spp., *M. longa* and *A. longiremis* showed two maxima during the summer (July) and autumn (October/November). Ophiuroid larvae and chaetognaths (mainly *Sagitta elegans*) peaked during the middle of July, while the number of euphausiid eggs and larvae was greatest from May to July. The succession in population structure of *C. finmarchicus* indicated its main spawning to be in April and May, coincident with the phytoplankton spring bloom. A minor spawning was also observed sometime between August and October. However, the offspring from this second spawning contributed only insignificantly to the overwintering stock of *C. finmarchicus*.

Introduction

The sea area north of Iceland is very important for the commercial fisheries around the island. This region serves as nursery grounds or feeding grounds for several commercially important fish stocks [e.g. cod (*Gadus morhua*), Greenland halibut (*Reinhardtius hippoglossoides*) and capelin (*Mallotus villosus*)]. Further, the area supports a large stock of deep-water prawn (*Pandalus borealis*) which is also commercially exploited. Zooplankton is an important component of the food of these species (Hopkins et al. 1989; Magnússon and Pálsson 1989; Sigurdsson and Astthorsson 1991; Astthorsson and Gislason 1997b; Pálsson 1997; Sólmundsson 1997) and given the role of zooplankton in transferring matter and energy from phytoplankton to higher trophic levels in marine food chains it is clearly of interest to study the productivity and seasonal dynamics of zooplankton in this area.

Earlier investigations on the seasonal abundance of zooplankton off the north coast of Iceland are restricted to one fjord study (Kaasa and Gudmundsson 1994) and no information is available on the seasonal dynamics of zooplankton in the oceanic waters north of Iceland. Other investigations on the seasonal abundance of zooplankton in Icelandic waters are confined to the southwest, west and northwest coasts (Hallgrímsson 1954; Astthorsson and Gislason 1992; Gislason et al. 1994; Gislason and Astthorsson 1995, 1996).

The aim of the present investigation is to describe the average annual cycle of zooplankton in the subarctic waters north of Iceland and to relate this to

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hydrography and chlorophyll *a*. The investigation forms a part of a research effort, which started in the late 1980s, with the aim of comparing and getting a better understanding of the seasonal changes and population dynamics of plankton communities in the different environments around Iceland (see e.g. Astthorsson 1990; Astthorsson and Gislason 1992; Gislason and Astthorsson 1995, 1996).

Materials and methods

The sampling was undertaken at approximately monthly intervals, from February 1993 to February 1994, at eight stations arranged along a transect extending 104 nm from the coast between 66°16′N–18°50′W and 68°00′N–18°50′W (Fig. 1). At the shallowest station the bottom depth was 80 m while at the outermost one it was 1,045 m.

The zooplankton was collected using a 60-cm-diameter Bongo net with 335-μm-mesh nets. The Bongo net was towed obliquely from the surface to 100 m depth (or ~5 m above the bottom at the shallowest station) and back to the surface, while the ship cruised at 2.5 knots. Payout and retrieval rates were ~10 m min^{-1}. The volume of water filtered by the net was measured with a HydroBios flowmeter and the depth was monitored with a Scanmar acoustic depth recorder. The zooplankton samples were preserved in 4% neutralized formalin after collection. In the laboratory, the displacement volume of total zooplankton and euphausiids was measured after large gelatinous zooplankton had been removed. The samples were then analysed in the following way: euphausiids and fish larvae were initially counted from whole samples. Except on a few occasions when the sample was very small, the remainder was subsampled with a Motoda splitter (Motoda 1959) and an aliquot containing at least 500 individuals analysed for species composition.

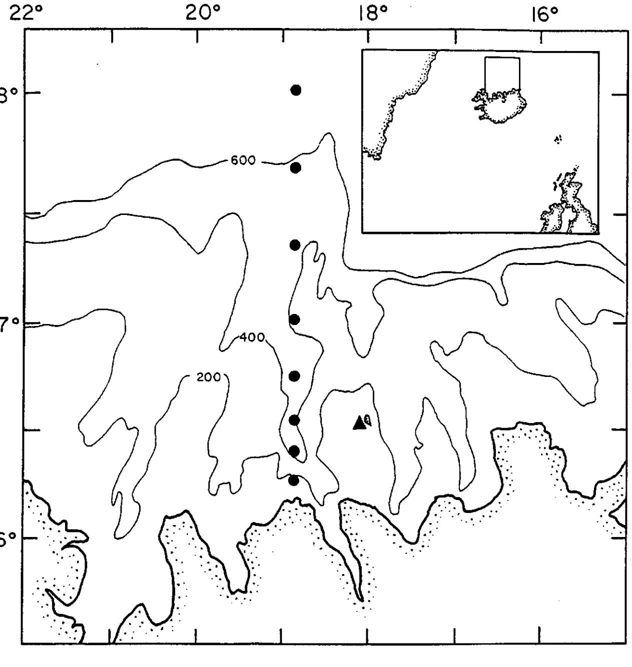

Fig. 1 Map of the study area north of Iceland showing the sampling stations. The *triangle* indicates the station from which the data on chlorophyll *a* are presented

Three species of the genus *Calanus* (*C. finmarchicus*, *C. glacialis* and *C. hyperboreus*) co-occurred in the samples. These were staged and then assigned to species by measuring their prosome lengths and using the length criteria given by Unstad and Tande (1991).

In the present paper, the displacement volume data have been converted to dry weight biomass using information from Matthews and Heimdal (1980). Data on biomass and abundance were standardized per 1 m^{-2} and presented as geometric means from all eight stations. For all the most abundant species and groups the general trend in the seasonal abundance was similar at all stations, with no evident onshore-offshore trend in the temporal development of any of the groups.

The zooplankton data have some important limitations: as discussed by Gislason and Astthorsson (1995), the rather coarse Bongo net (335 μm) will underestimate the abundance of the smaller zooplankton components. Further, the fact that the zooplankton is only sampled from the uppermost 100 m will inevitably lead to underestimates of zooplankton abundances, especially during winter due to the ontogenic migration of the zooplankton to deep waters for overwintering. In spite of these limitations, we nevertheless believe that the present material demonstrates the main seasonal changes in the meso- and macroplankton community in the subarctic waters north of Iceland.

On most cruises temperature and salinity were recorded with a Sea Bird Electronics SBE-9 CTD. The measurements of temperature and salinity are submitted as means from 0, 10, 15, 20, 30, 40 and 50 m depth from all eight stations.

Results

Environmental conditions

The seawater on the shelf area north of Iceland is a mixture of relatively warm Atlantic water, carried from the south by a branch of the North Icelandic Irminger Current, and cold low-salinity polar and Arctic water which enter the area with the East Greenland Current and East Icelandic Current respectively (Stefánsson 1962; Stefánsson and Jakobsson 1989). The contribution of Atlantic, Arctic and polar water in this mixture is highly variable between years (Malmberg and Kristmannsson 1992). Thus, in warm years relatively warm and saline Atlantic water dominates in the area, while in cold ones the water is mainly of Arctic origin. The year 1993 has been characterized as a warm year with Atlantic water predominating in the area during spring and summer (Anonymous 1993; Malmberg and Jónsson 1997).

The mean temperature of the upper 50 m of the water column showed a clear seasonal pattern (Fig. 2A). The lowest temperatures were recorded in February (~1.1°C). Warming of the water began in March/April and the temperature gradually increased to a maximum in July (~5.4°C). After that the temperature decreased again and when the investigations ended (February 1994) the temperature was about one degree higher than at the start (February 1993). The mean annual temperature range was approximately 4.3°C.

The salinity variations of the upper 50 m are shown in Fig. 2B. The salinity changed relatively little from February to May 1993 (from ~34.7 to 34.9 psu), but at midsummer it dropped suddenly, by as much as 0.7 psu,

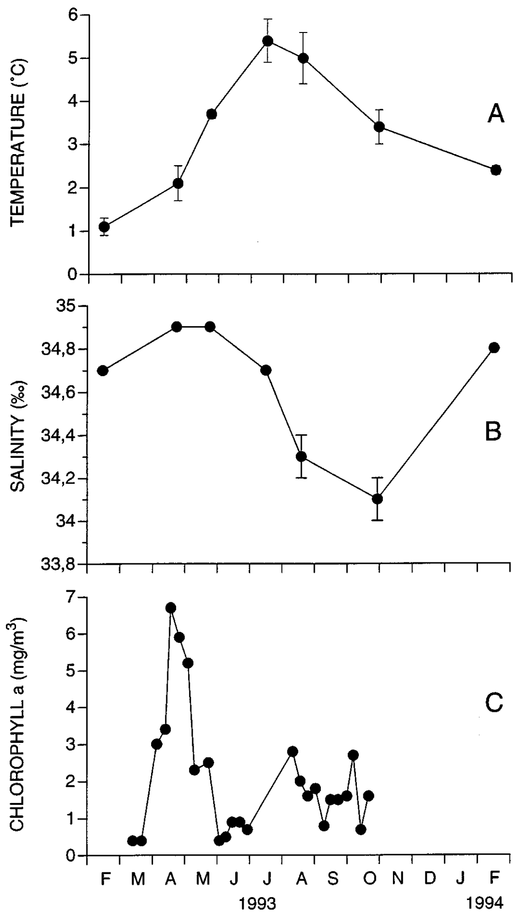

Fig. 2A–C Seasonal changes in temperature (**A**), salinity (**B**) and concentration of chlorophyll *a* (**C**) north of Iceland. The temperature and salinity values (February 1993 to February 1994) are means of measurements from 0, 10, 15, 20, 30, 40 and 50 m depth from eight stations, while the chlorophyll *a* values (March to October 1993) are measurements made at the surface at one station. *Vertical lines* in **A** and **B** denote standard error. **C** redrawn from Astthorsson and Gislason (1997a)

to reach a minimum of about 34.1 psu in October. It then rose again to a value of 34.8 psu in February 1994. These changes reflect seasonal variations in the relative magnitude of Atlantic water in the area north of Iceland, which in turn are related to seasonal variations in the strength of the North Icelandic Irminger Current (Stefánsson 1962). Thus, in late spring and early summer the relative quantity of Atlantic water is greatest, while during autumn and winter the salinity decreases due to the mixing of the Atlantic water with Arctic water at the more offshore stations and coastal water at the nearshore ones.

The seasonal fluctuations in the mean temperature and mean salinity of the upper 50 m of the water column were similar along the transect. However, the actual temperature was generally 1–2°C lower at the outermost station when compared to the other stations while the salinity was similar at all stations.

In order to give a rough estimate of the phytoplankton development in the area we present in Fig. 2C the seasonal variation in chlorophyll *a* based on weekly measurements made in the surface at a single station near the study transect (66°32′N–18°00′W, Fig. 1) (Astthorsson and Gislason (1997a). The chlorophyll *a* content was low in early to middle March ($<$ 1.0 mg Chl *a* m^{-3}), started to increase in late March and culminated during mid-April (~7.0 mg Chl *a* m^{-3}). After that the biomass of phytoplankton decreased to a minimum at the end of May ($<$ 0.5 mg Chl *a* m^{-3}). The concentration of chlorophyll *a* remained fairly low in June (~0.5 mg Chl *a* m^{-3}), but a small autumn increase was observed in early August (~3.0 mg Chl *a* m^{-3}). The concentration of chlorophyll *a* then fluctuated somewhat, while generally showing a decreasing trend (Fig. 2C).

Biomass and abundance of total zooplankton

The seasonal variation in total zooplankton biomass was characterized by low winter values and one maximum during the summer (Fig. 3A). From February to April the biomass remained low (~1 g m^{-2}). It started to increase at the end of April and a maximum occurred in late May (~4 g m^{-2}). Thereafter the biomass of total zooplankton remained high ($>$ 3 g m^{-2}) till the middle of August when it decreased rapidly, and by November it had again reached low winter values ($<$ 1 g m^{-2}). The annual mean biomass of total zooplankton was ~2 g m^{-2}.

The seasonal cycle of zooplankton abundance was generally similar to that of the biomass with low winter values and one peak during the summer coinciding with that of the biomass (Fig. 3). The numbers were low in

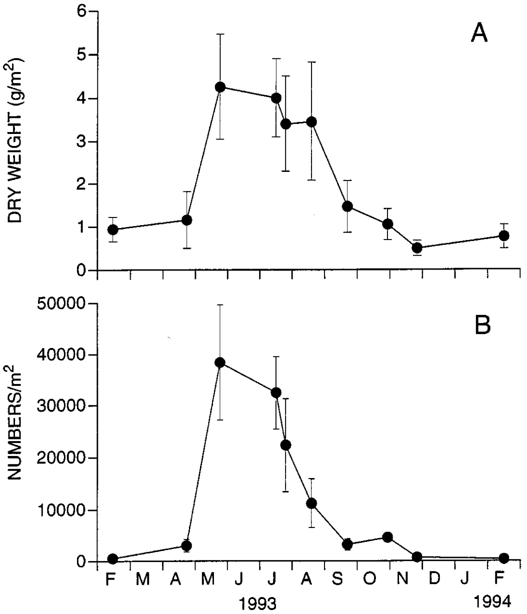

Fig. 3A,B Dry weight of total zooplankton (**A**) and number of total zooplankton (**B**) north of Iceland from February 1993 to February 1994. The values are means from eight stations and *vertical lines* denote standard error

February (~500 individuals m^{-2}) and April (~3,000 individuals m^{-2}), started to increase significantly by the end of April and peaked in late May (~38,000 individuals m^{-2}). In the middle of July the abundance was still high (~32,000 individuals m^{-2}), but then the numbers decreased rapidly to a minimum in mid-September (~3,000 individuals m^{-2}). A small increase was again observed in late October (~5,000 individuals m^{-2}), but by late November low winter values were again observed (< 1,000 individuals m^{-2}). The annual mean zooplankton abundance was ~11,000 individuals m^{-2}.

Taxonomic composition

The seasonal changes in the relative abundance of the major taxonomic groups are illustrated in Fig. 4. Copepods dominated the zooplankton during the whole year, composing 80–90% of the plankton at most sampling dates. In July, however, ophiuroid larvae made up a significant fraction of the catch (~22%).

A total of 42 species and taxonomic groups were identified in the samples (Table 1). Together, eight taxa constituted ~90% of the total zooplankton: *Calanus finmarchicus* (~60%), ophiuroid larvae (~9%), *Pseudocalanus* spp. (~8%), *Metridia longa* (~4%), *C. hyperboreus* (~3%), *Acartia longiremis* (~2%), chaetognaths (~2%) and euphausiid larvae (~2%). The most abundant groups are discussed in more detail below.

Copepods

Figure 5 illustrates the seasonal abundance of the six most numerous copepod species in the samples. In Fig. 6 we present information on the seasonal abundance of the different developmental stages of the most abundant copepod, *C. finmarchicus*.

Three species of the genus *Calanus* were found in the samples, (*C. finmarchicus*, *C. hyperboreus* and *C. glacialis*), all of which showed similar variations in their seasonal abundance (Fig. 5). Thus, for all three species the numbers remained low during the winter months and peaked once during the summer in late May (~32,000, ~1,500 and ~1,300 individuals m^{-2} for *C. finmarchicus, C. hyperboreus* and *C. glacialis*, respectively). Although only found sporadically during the winter, the three *Calanus* species never completely disappeared from the samples.

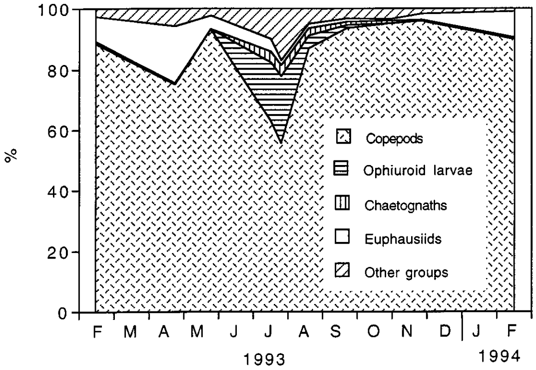

Fig. 4 Relative frequency of most numerous zooplankton taxa north of Iceland from February 1993 to February 1994. The values are means from eight stations

The abundance of early copepodite stages (CI, CII and CIII) of the new spring generation of *C. finmarchicus* (G1) was greatest in late May, while the numbers of adults of the overwintered generation (G0) were highest in April and May, with the males appearing first (Fig. 6). This indicates that the spring spawning of *C. finmarchicus* in the subarctic waters north of Iceland occurred in April and May, i.e. coinciding with the spring bloom of the phytoplankton (cf. Figs. 2C, 6). No sampling was carried out in June and therefore the progression in stage composition could not be followed from May to June. However, it is evident that the offspring from the spring spawning (G1) had developed to the overwintering stage (CV) by July and August (Fig. 6). While the majority developed no further, a small fraction had developed to the adult stages (CVIs) in August (Fig. 6). An increase in the number of stages CI, CII and CIII followed in October, indicating that a second spawning occurred sometime between the samplings in August and October. However, the offspring from this second spawning (G2) were few and did not contribute much, if anything, to the overwintering stock of *C. finmarchicus* (Fig. 6).

The seasonal succession in the abundance of the different developmental stages of *C. hyperboreus* and *C. glacialis* during spring and summer (A. Gislason, unpublished data) was generally similar to that of *C. finmarchicus*. Thus, for both species the number of adults (CVIs) reached a maximum in April and May, followed by peaks in the number of young stages (CI–CIII) in late May. However, unlike *C. finmarchicus* the numbers of stages CI–CIII of *C. hyperboreus* and *C. glacialis* did not show a second maximum in the autumn. This shows that both species have one breeding period confined to late winter and spring. Only very few individuals of *C. hyperboreus* and *C. glacialis* were caught during autumn and winter and therefore it is not possible to resolve their life-cycle in detail. Nevertheless it can be stated that stages CIII and CIV were probbaly the main overwintering stages of *C. hyperboreus* (A. *Gislason*, unpublished data), which indicates a life-cycle of more than 1 year for this species.

The seasonal changes in abundance of the three other most abundant copepods (*Pseudocalanus* spp., *M. longa* and *A. longiremis*) showed some similarities while they differed somewhat from those of the *Calanus* species (Fig. 5): unlike the *Calanus* species the numbers of *Pseudocalanus* spp., *Metridia longa* and *A. longiremis* peaked twice during the summer and autumn. The first maximum was observed in middle to late July (~2,700,

Table 1 Species or taxa identified at a transect north of Iceland, February 1993 to February 1994 (*VC* very common species, annual mean abundance > 500 individuals m^{-2}; *C* common species, annual mean abundance 200–500 individuals m^{-2}; *R* rare species, annual mean abundance < 200 individuals m^{-2})

Taxon	Category
Foraminifera	
Unidentified	R
Coelenterata	
Unidentified	R
Polychaeta	
Unidentified	R
Gastropoda	
Unidentified	R
Limacina spp.	R
Cladocera	
Podon leuckarti G. O. Sars	R
Evadne nordmanni Lovén	R
Copepoda	
Calanus finmarchicus (Gunnerus)	VC
Calanus hyperboreus (Krøyer)	C
Calanus glacialis (Jaschnov)	R
Pseudocalanus spp.	VC
Paracalanus parvus (Claus)	R
Euchaeta norvegica Boeck	R
Scolecithricella minor (Brady)	R
Temora longicornis (Müller)	R
Metridia longa (Lubbock)	C
Metridia lucens Boeck	R
Centropages hamatus (Lilljeborg)	R
Acartia longiremis (Lilljeborg)	C
Acartia clausi Giesbrecht	R
Unidentified Calanoida	R
Oithona similis Claus	R
Oithona spinirostris Claus	R
Cirripedia	
Unidentified	R
Isopoda	
Unidentified	R
Amphipoda	
Themisto spp.	R
Unidentified	R
Euphausiacea	
Euphausiid eggs	R
Euphausiid larvae	C
Meganychtiphanes norvegica (M. Sars)	R
Thysanoessa longicaudata (Krøyer)	R
Thysanoessa inermis (Krøyer)	R
Decapoda	
Brachyura	R
Natantia	R
Anomura	R
Chaetognatha	
Sagitta elegans Verrill	C
Unidentified	R
Ophiuroidea	
Unidentified	VC
Larvacea	
Unidentified	R
Fish eggs	
Unidentified	R
Fish larvae	
Mallotus villosus (Müller)	R
Ammodytes sp.	R

~1,300 and ~700 individuals m^{-2} for *Pseudocalanus* spp, *Metridia longa* and *A. longiremis*, respectively) and the second in October/November (~1,000, ~350 and ~650 individuals m^{-2} for *Pseudocalanus* spp, *Metridia longa* and *A. longiremis*, respectively). All three species were present throughout the year, being found in very low numbers during the winter.

Several other copepods were found in the samples but only in quite low numbers. These rarer copepods are listed in Table 1.

Ophiuroid larvae

The seasonal change in the abundance of ophiuroid larvae is shown in Fig. 7A. Ophiuroid larvae were absent from the winter samples and showed one clear abundance peak during the middle of summer. They first appeared in the samples during the latter part of May, reached a definite maximum in the middle of July (~6,000 individuals m^{-2}) and were last recorded in the September samples.

Chaetognaths

The chaetognaths, generally considered as one of the main predators of the planktonic community, were caught in significant numbers during midsummer (Fig. 7B). They were not routinely identified to species but judged by careful examination of many individuals from several samples; by far the majority of the chaetognaths belonged to *Sagitta elegans*. The seasonal variation in abundance of the chaetognaths (Fig. 7B) was very similar to that of the ophiuroid larvae (Fig. 7A); as with the ophiuroid larvae, the numbers of chaetognaths began to increase in June and reached a maximum in the middle of July (~1,000 individuals m^{-2}). After this, the number of chaetognaths fell drastically and they were not recorded in samples taken after September.

Euphausiids

As Astthorsson and Gislason (1997a) recently reported on the biology of euphausiids in the subarctic waters

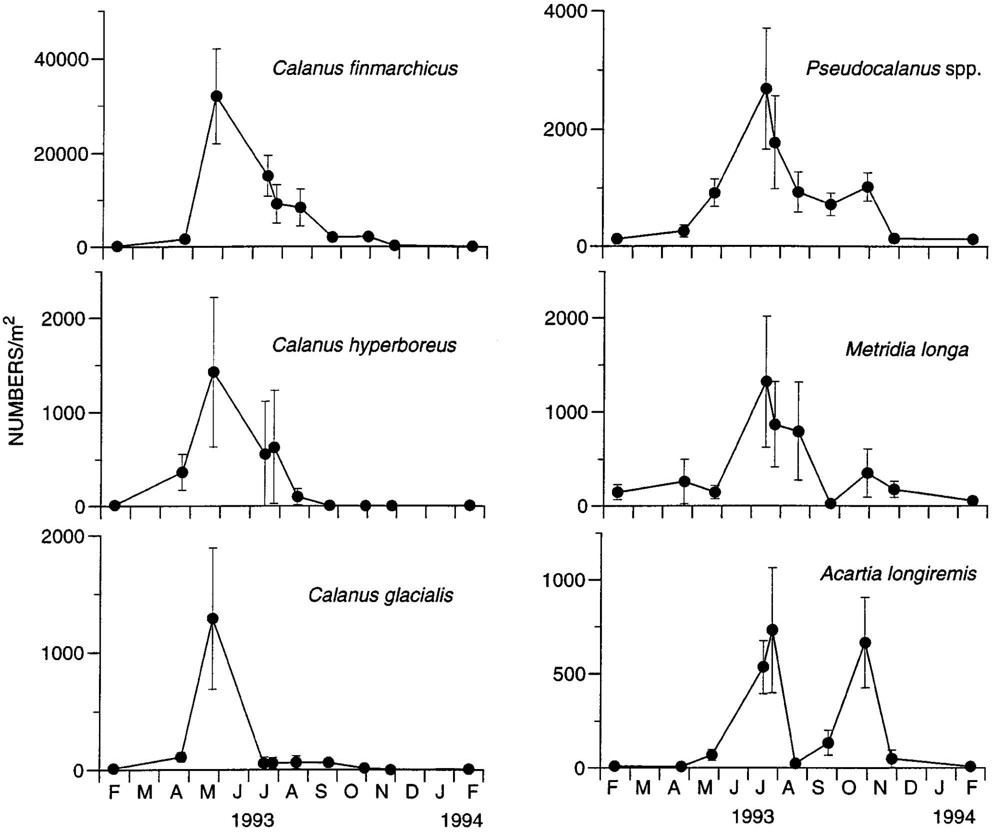

Fig. 5 The abundance of most numerous copepods north of Iceland from February 1993 to February 1994. The values are means from eight stations and *vertical lines* denote standard error. Note different scales

north of Iceland, using the same material given here, we only submit the most important findings in the present paper. Three euphausiid species, *Thysanoessa inermis*, *T. longicaudata* and *Meganyctiphanes norvegica*, were found in the samples. Of the immature and adult euphausiids, *T. inermis* was by far the most abundant one (~76%), followed by *T. longicaudata* (~14%) and *Meganyctiphanes norvegica* (~9%).

The seasonal occurrence of the eggs and larvae in the samples (Fig. 8), together with information on the maturity of the animals (Astthorsson and Gislason 1997a), suggests that the main spawning took place from late April to late May, and that the bulk of the nauplii had developed to the furciliae stages by the middle of July. Thus the spawning of the euphausiids in the subarctic waters north of Iceland occurred during the phytoplankton spring bloom and at a similar time to the spring spawning of the most abundant copepod, *C. finmarchicus*. (cf. Figs. 2C, 8).

Discussion

In the subarctic waters north of Iceland the spring bloom of the phytoplankton began in late March, reached a maximum in late April and terminated at the beginning of June (Fig. 2C). In late May, when the spring bloom was coming to an end, the biomass and abundance of total zooplankton (especially *C. finmarchicus*) were approaching their maximum. Since the concentration of nutrients in May/June was still high in the sea area north of Iceland (Anonymous 1993), it seems unlikely that nutrient deficiency was hampering the growth of the phytoplankton at that time. It is more likely that the reduction in the phytoplankton standing stock during May was caused by increased grazing pressure from the zooplankton. However, the autumn bloom in August, observed at about the time when the zooplankton stocks were rapidly declining (Fig. 3), probably occurred as a combination of reduced grazing pressure and renewal of nutrients into the euphotic layer.

While the seasonal development of temperature and salinity was similar at all stations, the coldest water was generally found at the outermost station (A. Gislason, unpublished data). In spite of this the general trend in the seasonal abundance of all the most abundant species and groups was similar at all stations. In the context of the present paper in giving a general and broad overview of the seasonal dynamics of zooplankton in the area, we therefore feel justified in combining the zooplankton data from all the stations in the present analysis.

From February 1993 to February 1994 the biomass and numbers of total zooplankton peaked once in late May in the subarctic waters north of Iceland (Fig. 3). Likewise, in Isafjord-deep, a fjord on the northwest coast of Iceland (Astthorsson and Gislason 1992), and Eyjafjördur, a fjord on the north coast (Kaasa and Gudmundsson 1994), there is basically only one maxi-

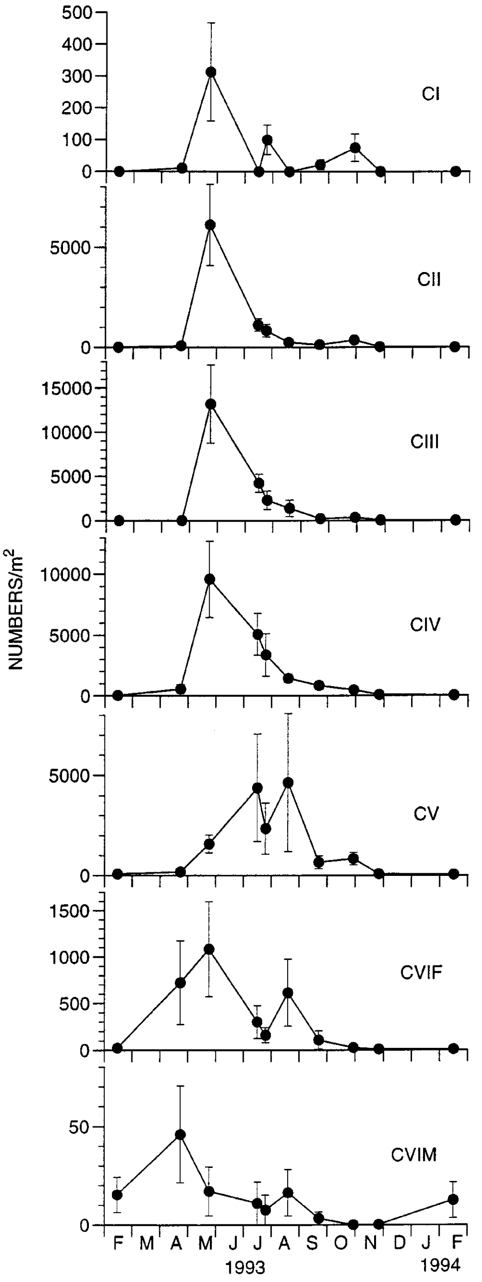

Fig. 6 The abundance of different developmental stages of *Calanus finmarchicus* north of Iceland from February 1993 to February 1994. The values are means from eight stations and *vertical lines* denote standard error. Note different scales

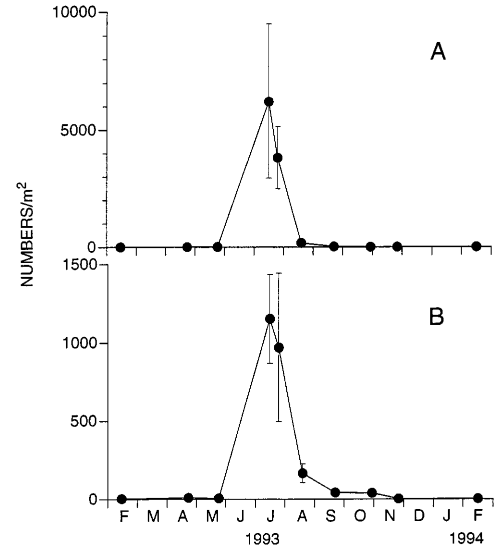

Fig. 7A,B The abundance of ophiuroid larvae (**A**) and chaetognaths (**B**) north of Iceland from February 1993 to February 1994. The values are means from eight stations and *vertical lines* denote standard error. Note different scales

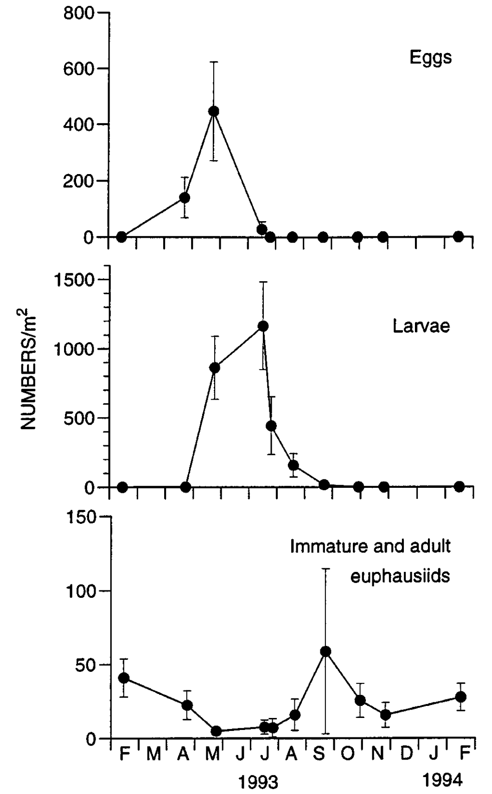

Fig. 8 The abundance of euphausiid eggs, larvae and immature and adult euphausiids north of Iceland from February 1993 to February 1994. The values are means from eight stations and *vertical lines* denote standard error. Note different scales

mum in abundance in late summer and autumn. However, in the relatively warm Atlantic water off the southwest and south coasts, Hallgrímsson (1954) and Gislason and Astthorsson (1995) observed two peaks in both biomass and total numbers during the summer and early autumn. This can probably be attributed to higher temperatures and higher primary production off the southwest and west coasts of Iceland compared to those in the waters off the northwest and north coasts.

The lower biological production in the waters north of Iceland compared to that of the south coast is further demonstrated by the annual mean biomass of zooplankton, which in the waters north (present study) and northwest (Astthorsson and Gislason 1992) of Iceland is approximately twice as low as that of the southwest coast (Gislason and Astthorsson 1995) (Table 2). Moreover, the annual mean abundance of zooplankton is approximately 5 times lower in the waters north (present study) and northwest (Astthorsson and Gislason 1992) of Iceland compared to the waters off the southwest coast (Gislason and Astthorsson 1995). Presumably, this reflects the much lower production of zooplankton in the colder waters off the northwest and north coasts of Iceland compared to the relatively warmer waters off the southwest coast. In this context, it should be mentioned that, according to Thórdardóttir (1995), the annual primary production in the waters north of Iceland is on average only about two-thirds of that south of the island, indicating that the subarctic waters north of Iceland may generally sustain lower zooplankton production than the Atlantic water south of the country. The annual mean zooplankton biomass of Icelandic waters is 2–5 g dw m^{-2} (Table 2) and is generally comparable with other high latitude ecosystems of the North Atlantic, such as the Barents Sea (Sakshaug et al. 1994) and the Nova Scotia Shelf (Sameoto and Herman 1992), indicating the similar magnitude of the secondary production of these systems.

The maxima in both biomass and numbers of total zooplankton in late May in the subarctic waters north of Iceland mainly reflect the increasing numbers of the most abundant zooplankter, *C. finmarchicus*, after spring spawning (cf. Figs. 3, 5). The decrease in both total biomass and especially in total abundance after the middle of July (Fig. 3) is probably mainly caused by predation from capelin. With average stock size of ~1,900 thousand tonnes (Vilhjálmsson 1994), this is by far the largest plantivorous fish stock in Icelandic waters and during its summer feeding period in the subarctic waters north of Iceland, it mainly feeds on copepods and euphausiids (Sigurdsson and Astthorsson 1991; Astthorsson and Gislason 1997b). However, factors such as food limitation and ontogenic migration to deeper waters for overwintering may also be causing the observed decline in zooplankton biomass and numbers in the upper 100 m during late summer and autumn. Thus, in the neighbouring Norwegian Sea (Østvedt 1955) and Greenland Sea (Richter 1995), several species including *C. finmarchicus* begin their seasonal downward migration from June onwards. It is also worth pointing out that the decrease in zooplankton abundance after the middle of July coincided with the abundance peak of the carnivorous chaetognath *S. elegans* (cf. Figs. 3A, 7B), suggesting that predation by the chaetognaths may have contributed to the decline of the zooplankton stocks. Finally, it should be noted that the decline after mid-July occurred at a time when the relative quantity of water of Arctic origin north of Iceland was rapidly increasing (Fig. 2B). This may have diluted the concentrations of zooplankton in the area, and also the low temperatures associated with it may have negatively affected the growth of the zooplankton.

In the present material copepods dominated the zooplankton, usually accounting for 80% or more of the plankton, which is in accordance with earlier zooplankton investigations around Iceland (Astthorsson and Gislason 1992, 1995; Gislason and Astthorsson 1995). Similarly, from the western Iceland Sea (between Jan Mayen, East Greenland and Iceland) Astthorsson et al. (1995) reported the zooplankton to be dominated by copepods, with *C. finmarchicus* as the single most abundant species. In the Barents Sea (Hassel 1986), the NEW Polynya off east Greenland and in the Fram Strait (Hirche et al. 1994) copepods are also the dominating group.

The species composition of the zooplankton fauna in the subarctic open waters north of Iceland, as observed in the present investigation, shows some similarities to that which has been reported from fjords on the northwest and north coasts of Iceland (Astthorsson and Gislason 1992; Kaasa and Gudmundsson 1994). Thus, *C. finmarchicus, Pseudocalanus* spp. and *A. longiremis* are common in both habitats. However, the neritic species *Verruca stroemia*, *Balanus balanoides*, *Temora longicornis, Evadne nordmanni* and *Podon leuckarti*, together with *Oithona* spp., are abundant in the fjords and not in the open waters north of Iceland, whereas the reverse is true for the ophiuroid larvae and the arctic copepods *Metridia longa*, C. hyperboreus and *C. glacialis*. However, from the southwest coast of Iceland, Gislason and Astthorsson (1995) reported *C. finmarchicus, T. longicornis* and *E. nordmanni* to be the most numerous species.

In 1993 the main spawning of *C. finmarchicus* in the subarctic waters north of Iceland occurred in April and May, closely following the spring bloom of the phytoplankton (cf. Figs. 2C, 6). The close association between the spawning of *C. finmarchicus* and phytoplankton growth has previously been shown by a number of workers (see Hirche 1996 for a review). Later in the year (August to October) a small part of the spring generation took part in another spawning. However, the offspring from this second spawning hardly contributed anything to the overwintering stock (Fig. 6). The biomass of phytoplankton was low at this time (Fig. 2C) and the decreased survival of the copepodids may have been caused by lack of suitable food. Conversely, in the

Table 2 Annual means of total numbers and total biomass in different areas around Iceland. The sampling was carried out with a 335 μm Bongo net and the values are for the uppermost 100 m of the water column

Area	Biomass (g dry weight m^{-2})	Abundance (numbers m^{-2})	Reference
North	2	11,000	This study
Northwest	2.6	18,000	Astthorsson and Gislason (1992)
Southwest	5	76,000	Gislason and Astthorsson (1995)

warmer waters off the southwest coast of Iceland two generations of *C. finmarchicus* are recruited to the overwintering population during the summer (Hallgrímsson 1954; Gislason and Astthorsson 1996). This is in agreement with studies from the west coast of Norway where one generation per year develops off the north coast while there are two or even more generations per year off the south coast (Wiborg 1954; Lie 1965; Matthews et al. 1978). As pointed out by Hirche (1996), both temperature and/or food may be operating as controlling factors in this respect.

The copepods *C. hyperboreus* and *C. glacialis* are both known to be associated with water of Arctic origin, with their main distribution in the northern North Atlantic, the Greenland Sea and the Arctic Ocean (Grainger 1961; Jaschnov 1972; Hirche 1991). They are probably expatriates in the shelf waters north of Iceland, being transported to the area from the north by the East Greenland Current. However, the seasonal variation of young copepodite stages (CI–CIII) and adult females of these species in the samples (A. Gislason unpublished data) suggests that they are both reproducing successfully in the region. For *C. hyperboreus* the limited data on stage composition indicate that this species has at least a 2-year life-cycle in the subarctic waters north of Iceland. Information on the seasonal development of *C. hyperboreus* and *C. glacialis* in other areas suggests a south-north gradient in the length of the life-cycle for these species. Both species have been reported to have an annual life-cycle in the southern parts of their distribution range (Conover 1967; Matthews et al. 1978; Runge et al. 1985; Sameoto and Herman 1992), whereas a 2- to 4-year life-cycle has been proposed for the northern parts (Dawson 1978; Tande et al. 1985; Hirche 1991, 1997).

The copepods *Pseudocalanus* spp., *Metridia longa* and *A. longiremis* all showed two peaks in abundance during the year (Fig. 5). However, as the developmental stages of these were not separated it is impossible to evaluate to what extent the abundance peaks reflect reproduction of these animals or if they are an effect of advective processes. It is, however, important to note that the second peak for these species occurred after the influx of Arctic water masses to the area had taken place (Fig. 2B) and, atleast for the Arctic species *Metridia longa,* the second peak may therefore be related to advection to the area of study.

The large year-to-year fluctuations in the inflow of Atlantic water to the sea area north of Iceland have profound effects on the biological production in the region (Thórdardóttir 1977, 1984; Astthorsson et al. 1983; Stefánsson and Jakobsson 1989; Stefánsson and Ólafsson 1991; Astthorsson and Gislason 1995). Thus, increased stratification in cold years may lead to an early depletion of nutrients in the surface layers and reduced primary production and, ultimately, reduced growth of zooplankton. Conversely, by maintaining mixing and renewal of nutrients to the surface layers in warm years, the Atlantic influx may prolong the growth season of the phytoplankton, which in turn may positively affect the growth of zooplankton. The year 1993 has been characterized as a warm year with great influx of Atlantic water to the shelf area north of Iceland (Anonymous 1993; Malmberg and Jónsson 1997). The results of the present study indicate that during such conditions the season of primary and secondary production in the subarctic waters north of Iceland lasts about 5–6 months (Figs. 2C, 3).

As stated in the Introduction, the aim of this study was to present a general overview of the seasonal dynamics of the zooplankton in the subarctic waters north of Iceland. Further studies should aim at getting a better understanding of the spatial variability in the different water masses. In that context the area northeast of Iceland is of particular interest because there the arctic influences in Icelandic waters are most prominent.

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