

Vertical distribution and seasonal dynamics of mesozooplankton in the Iceland Basin

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The abundance and seasonal vertical distribution of dominant zooplankters in the Iceland Basin was studied from data collected on four cruises between November 1996 and June 1997. Two species, *Calanus finmarchicus* and *Pareuchaeta norvegica*, constituted >90% of the copepod biomass. A seasonal migration pattern was evident in *C. finmarchicus*, *P. norvegica*, *Oithona* spp. and *Metridia lucens*: From December to February they inhabited the deeper layers, whereas from April to June they were most abundant in the upper layers. The vertical distribution of *Pleuromamma robusta* was rather similar year round, with highest numbers being caught above 200-400 m depth. *Oncaea* spp. stayed deep during winter, but only a limited part of the population rose to upper waters during the summer. The reproduction of *P. norvegica* occurred at depth in February and was uncoupled to the spring bloom. As judged by the incidence of adults of both sexes the reproduction of *M. lucens* took place in spring and summer. The data on *Oithona* spp. and *Oncaea* spp. indicate that the former group reproduces between April and June in the upper layers, whereas the latter appears to reproduce year-round at depth. The breeding of *P. robusta* took place in relatively shallow water and was probably not confined to a particular season of the year.

Keywords: Zooplankton, copepods, vertical distribution, seasonal dynamics, Iceland Basin

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Introduction

The oceanic region southwest of Iceland is divided by the Reykjanes Ridge into two deep basins, the Irminger Sea and the Iceland Basin. The zooplankton in both areas is characterized by low diversity and few species (Beaugrand *et al.* 2000). In both regions the zooplankton is dominated by *Calanus finmarchicus*, *Pareuchaeta norvegica*, *Oithona* spp. and *Oncaea* spp. In addition, previous studies show that *C. hyperboreus* may be important in terms of biomass west of the Ridge (Irminger Basin), whereas *Metridia lucens* and *Pleuromamma robusta* are relatively important east of it (Iceland Basin) (Gislason 2003, Williams 1988, Irigoien and Harris 2006).

Previous research activity on the life history of oceanic zooplankters in the Iceland Basin has been mainly focused on *C. finmarchicus* (Gislason and Astthorsson 2000, Gislason *et al.* 2007), and there is limited information on other species, except the works of Williams (1988) and Irigoien and Harris (2006) from the southern Iceland Basin, which, however, did not sample the whole water column. Recently, Gislason (2003) reported on the life-cycle strategies of the dominant copepods in the nearby Irminger Sea, some of which are common to the present study. Here, I describe the seasonal vertical distribution and seasonal dynamics of copepods in the Iceland Basin, as based on data sampled from near the bottom and to the surface at three stations during two cruises in winter, one in spring and one in summer.

Methods

Samples were collected during four cruises carried out from November 1996 to June 1997 (27 November-6 December 1996, 29 January-6 February 1997, 2-10 April 1997, and 18-26 June 1997). During each cruise 17 stations were undertaken, but here I only consider three of them, located in the northern part of the Iceland Basin (Fig. 1).

Temperature and salinity were recorded with a CTD (Sea Bird Electronics SBE-9). Seawater samples (1-2 l) for the measurement of chlorophyll *a* were collected from depths of 0, 10, 20, 30 and 50 m, and filtered through GF/C glass fibre filters. The filters were then homogenized in 90% aqueous acetone and the extract measured in a spectrophotometer according to the method described by Strickland and Parsons (1968). These measurements were made at all stations, but as the temporal patterns of change at all three stations were similar, I present hydrography and chlorophyll data from one station only (Fig. 1)

The zooplankton were collected using a Multi Plankton Sampler from HydroBios (0.25 m² mouth area, 200 µm mesh size) that was towed from near the bottom and to the surface with a speed of ~1 m s⁻¹. The Multi Plankton Sampler is equipped with five nets that can be opened and closed on command from the ship. By deploying the sampler three times, a total of 12 depth layers were sampled from 2200 m and to the surface. The volume of water filtered by the net was measured with HydroBios flowmeters fitted in the mouth of each net.

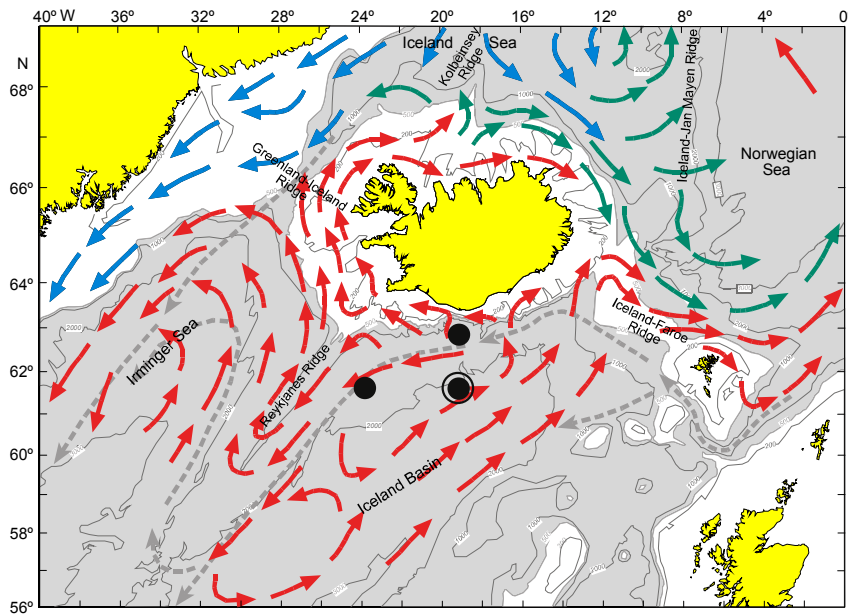


Figure 1. Map of the sea area around Iceland showing the sampling stations. The encircled station is the one from which data on hydrography and chlorophyll *a* are presented. Inserted on the figure are the main ocean currents in the upper layers, adapted from Valdimarsson and Malmberg (1997), and the main overflow paths over the Greenland-Iceland-Scotland Ridge, adapted from Hansen and Østerhus (2000). Red arrows: Atlantic Water; blue arrows: Polar Water; green arrows: mixed water; grey broken arrows: main overflow paths.

The zooplankton samples were preserved in 4% neutralized formalin until analysis in the laboratory. As a rule, the entire sample was counted for the larger plankton (euphausiids, amphipods, mysids, decapods, chaetognaths and copepods >1 mm prosome length). Except when the sample was very small the remainder was then subsampled with a Motoda splitter (Motoda 1959) and an aliquot containing at least 500 individuals analysed for species composition. Further, the copepods *C. finmarchicus*, *C. hyperboreus*, *P. norvegica*, *M. lucens* and *P. robusta* were classed to developmental stages. For *P. norvegica*, counts of males and of females with spermatophores and/or egg sacs attached to the genital segment were made. A few isolated egg sacs of *P. norvegica* were also observed in the samples. They have probably become detached from the females during sampling (Bakke 1977; Hopkins 1982). The number of isolated egg sacs in the samples was therefore taken into account when estimating the number of ovigerous females.

Data on abundance (numbers per m⁻³) were calculated for each net using the data from the flowmeters. Number per m⁻² was obtained for each net by multiplying the abundance (number per m⁻³) by the depth range for that net. Total water column abundances (number per m⁻²) were then calculated from the sum of the abundances (number per m⁻²) for all the nets in a vertically stratified tow.

The copepod numbers have been converted to biomass (dry weight) using information from various sources. For *C. finmarchicus*, *P. norvegica*, *M. lucens*, *P. robusta* data from Longhurst and Williams (1992) obtained at Ocean weather station India have been adopted. The biomass of *C. hyperboreus* and *C. glacialis* was calculated using data from Hirche (1997) and Slagstad and Tande (1990), respectively. For *M. longa*, the dry weight of the copepodite stages C5 and adults was calculated using data from Grönvik and Hopkins (1984), while the dry weight for the younger copepodite stages was estimated by assuming the same ratio between the biomass of C5 and a particular copepodite stage as for *M. lucens* (Longhurst and Williams 1992). The biomass of *Oithona* spp. was taken from Coyle *et al.*, (1990), assuming the dry weight to be 0.2% of the wet weight. *Oithona* spp. was taken to be 50% adults and 50% copepodite stages C5, since the younger copepodite stages were probably greatly undersampled by the 200 µm mesh nets (Colton *et al.* 1980; Nichols and Thompson 1991). The dry weight of *Oncaea* spp. was assumed to be the same as for *Oithona* spp. *Pseudocalanus* spp. was taken as 50% adults and 50% copepodite stages C5, and the dry weight calculated using information from Tande (1991). The dry weights of *Scolecithricella minor* and *Spinocalanus* spp. were assumed to be the same as that of the similarly sized *Pseudocalanus* spp. The

biomass of *Microcalanus* spp. was calculated using information from Davis (1984) assuming that the stock consisted of 50% adults and 50% juveniles. Other copepod species were of minor importance in terms of biomass and were excluded from the calculations. These calculations provide only crude estimates of biomass but they can at least be considered conservative values of copepod biomass. No attempt was made to estimate the biomass of other zooplankton groups.

To facilitate comparison of the depth distributions of the dominant copepods, percentile depth distributions were calculated and depicted as box plots, with each box encompassing 50% of the population and the whiskers 95% (Pennak 1943).

Results

Hydrography

Surface temperatures in the Iceland Basin ranged from $\sim 8^{\circ}\text{C}$ (December 1996) to $\sim 9^{\circ}\text{C}$ (June 1997) (Fig. 2A). A seasonal temperature signal was evident down to a depth of ~ 500 m. Below ~ 1000 m depth, temperatures remained between ~ 3 and $\sim 6^{\circ}\text{C}$ throughout the study period.

Surface salinity ranged seasonally from ~ 35.1 to ~ 35.2 (Fig. 2A). A tongue of low salinity water (~ 34.89 - 34.95) was evident between ~ 1400 and ~ 1700 m depth.

Based on salinity and temperature, different water masses may be identified (Blindheim *et al.* 1996; Mortensen *et al.* 1999). The upper layers (above ~ 1000 m depth) were dominated by Atlantic Water (AW, $T > 5^{\circ}\text{C}$, $S > 35.00$) (Fig. 2A). The so-called Labrador Sea Water (LSW, $T \sim 3$ - 4°C , $S \sim 34.8$ - 34.9), which originates by deep convection in the Labrador Sea, was found at depths of about 1400-1700 m.

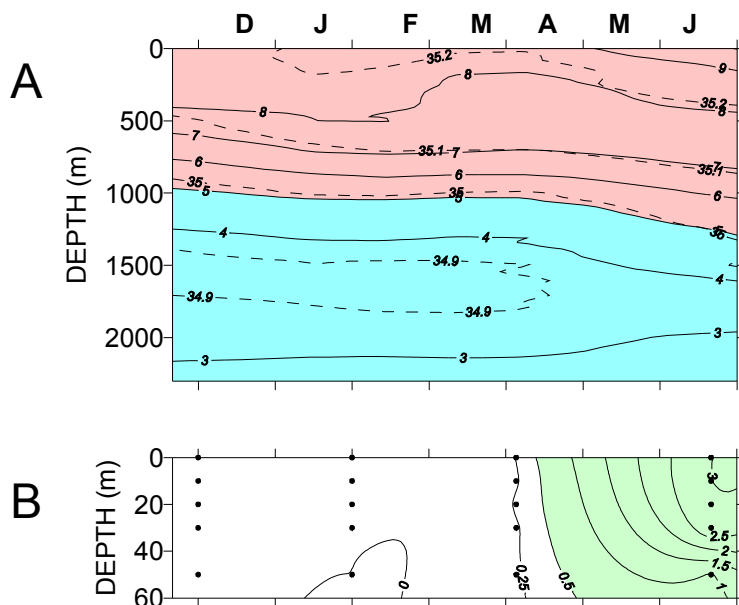


Figure 2. Seasonal variation in temperature and salinity (A), and chlorophyll a (B) at one station in the Iceland Basin December 1996 to June 1997. For location of station refer to Fig. 1. The red shading in (A) indicates Atlantic Water.

Phytoplankton

During the winter (December 1996 to February 1997) the concentration of chlorophyll a was negligible ($< 0.08 \text{ mg Chla m}^{-3}$) (Fig. 2B). In April, as the surface waters began to warm up (Fig. 2A), some very limited phytoplankton growth had begun ($> 0.25 \text{ mg Chla m}^{-3}$). In June the stratification was stronger (Fig. 2A), and the biomass of phytoplankton was also higher, with concentrations above 2 Chla m^{-3} extending down to ~ 40 m depth (Fig. 2B).

Abundance and composition of zooplankton

Copepods were by far the most important group in terms of numbers, constituting $> 90\%$ of all the animals, except in June when they contributed $\sim 70\%$ of the catch and foraminiferans made up $\sim 20\%$ (Fig. 3).

Calanus finmarchicus clearly dominated the copepod biomass ($\sim 76\%$), with *P. norvegica* also important ($\sim 14\%$) (Fig. 4, Table 1). Thus, these two species together constituted $\sim 90\%$ of the copepod biomass. *C. hyperboreus* ranked third in biomass ($\sim 3\%$) and *Oithona* spp. fourth ($\sim 2\%$). In terms of numbers, *Oithona* spp. dominated ($\sim 49\%$), with *C. finmarchicus* ranking second ($\sim 25\%$) and *Oncaea* spp. third ($\sim 14\%$).

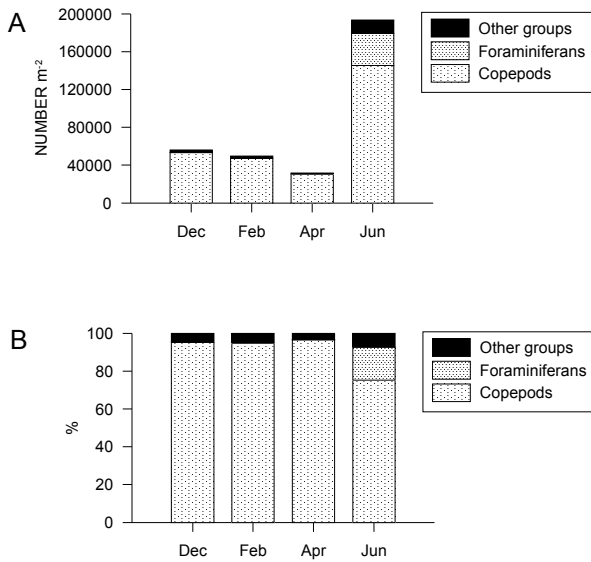


Figure 3. Total depth integrated number and percentages of zooplankton in the Iceland Basin from December 1996 to June 1997.

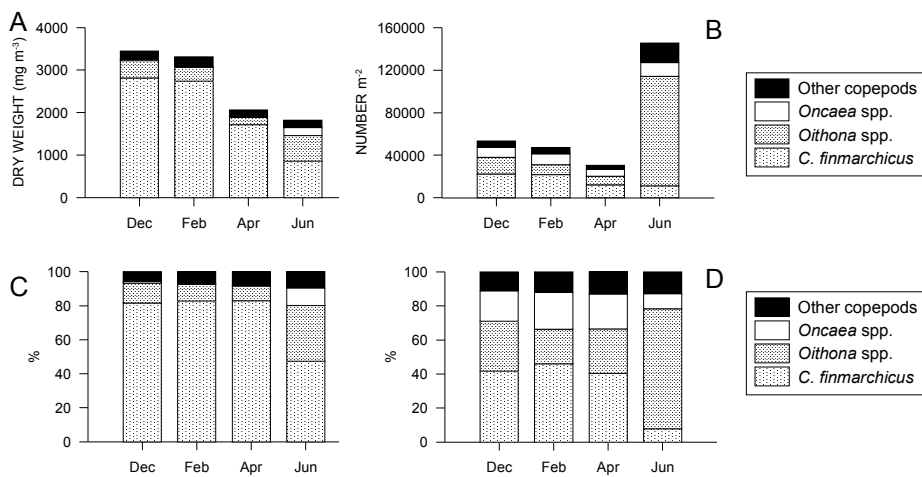


Figure 4. Total depth integrated (0-2200 m) biomass (A), number (B), relative biomass (C), and relative number (D) of copepods in the Iceland Basin from December 1996 to June 1997. The values are means from three stations

Table 1. Average depth integrated (0-2200 m) biomass (mg dry weight m⁻²) and number (m⁻²) of copepods in the Iceland Basin from December 1996 to June 1997. Relative values (%) are also shown. The values are means from 3 stations (see Fig. 1 for location of stations).

	Dry weight		Numbers	
	mg m ⁻²	%	m ⁻²	%
<i>Calanus finmarchicus</i>	2034.2	76.4	16914.6	24.5
<i>Paraeuchaeta norvegica</i>	373.3	14.0	573.9	0.8
<i>Calanus hyperboreus</i>	70.1	2.6	41.1	0.1
<i>Oithona</i> spp.	62.2	2.3	33986.9	49.2
<i>Metridia lucens</i>	30.3	1.1	391.5	0.6
<i>Pleuromamma robusta</i> .	26.6	1.0	141.4	0.2
<i>Oncaea</i> spp.	17.8	0.7	9716.2	14.1
Other copepods	116.7	4.5	7412.6	10.5
Total	2661.1	100.0	69137.1	100.0

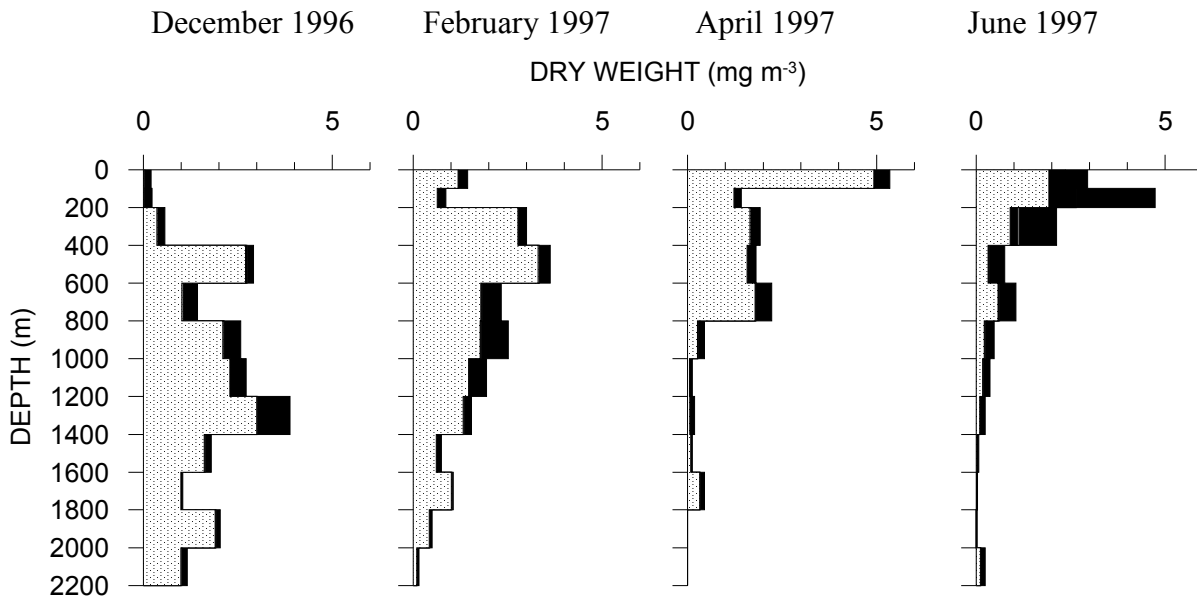


Figure 5. Vertical distribution of copepod biomass in the Iceland Basin from December 1996 to June 1997. The values are means from three stations. Gray shading: *C. finmarchicus*; black shading: Other copepods.

The vertical distribution of copepod biomass during the study period is shown in Figure 5. In December the bulk of the biomass was found between 400 and 1400 m depth, whereas in February the biomass was greatest between 200 and 1400 m depth. In spring (April) most of the biomass occurred above 800 m depth with a clear maximum in the shallowest depth layer (0-50 m). In summer (June) the biomass was highest above 400 m and there was a maximum in the 100-200 m layer.

Calanus finmarchicus

Calanus finmarchicus ranked first in terms of biomass and second in numbers (Table 1). As Gislason and Astthorsson (2000) recently reported on the ecology of *C. finmarchicus* in the oceanic area southwest of Iceland, partly based on the same material as dealt with here, I will only submit the most important findings in the present paper.

C. finmarchicus overwintered mainly between ~400 m depth and down to the bottom (>2000 m) (Gislason and Astthorsson 2000). During the winter (December-February), by far the majority of the stock was present as C5 (84-86%) with a smaller proportion as C4 (12-14%) and females (1-2%). In April adult individuals were prominent in the samples, both males (~25%) and females (~15%), whereas in June the youngest copepodite stages (C1-3) made up some 15% of the population, the remainder being mainly C5 (~80%). The ascent to the upper layers probably occurred mainly during March and April, and continued until May.

On the basis of the seasonal vertical distribution, stage composition, and daily egg reproduction rates, Gislason and Astthorsson (2000) concluded that in the oceanic areas southwest of Iceland *C. finmarchicus* reproduces mainly in the upper layers of the ocean (0-100 m), with peak reproduction taking place in May.

Pareuchaeta norvegica

Pareuchaeta norvegica ranked second in copepod biomass (~14%) and fourth in numbers (~1%) (Table 1). During winter (December-February), the main part of the population was found between 600 and 1400 m depth (Fig. 6). The ascent to the upper layers occurred sometime between February and April, when the highest concentrations were observed between 200 and 400 m depth. In June the concentrations were highest between 100 and 200 m depth.

During winter and spring (December-April), depth integrated numbers fluctuated between ~300 and ~500 individuals m⁻², but after April number increased dramatically (to ~1,200 individuals m⁻²) (Fig. 7A).

From December to February, the proportion of stages C4-5 decreased while that of the adults increased, suggesting that the juveniles were developing to become adults during this time (Fig. 7B). A high proportion

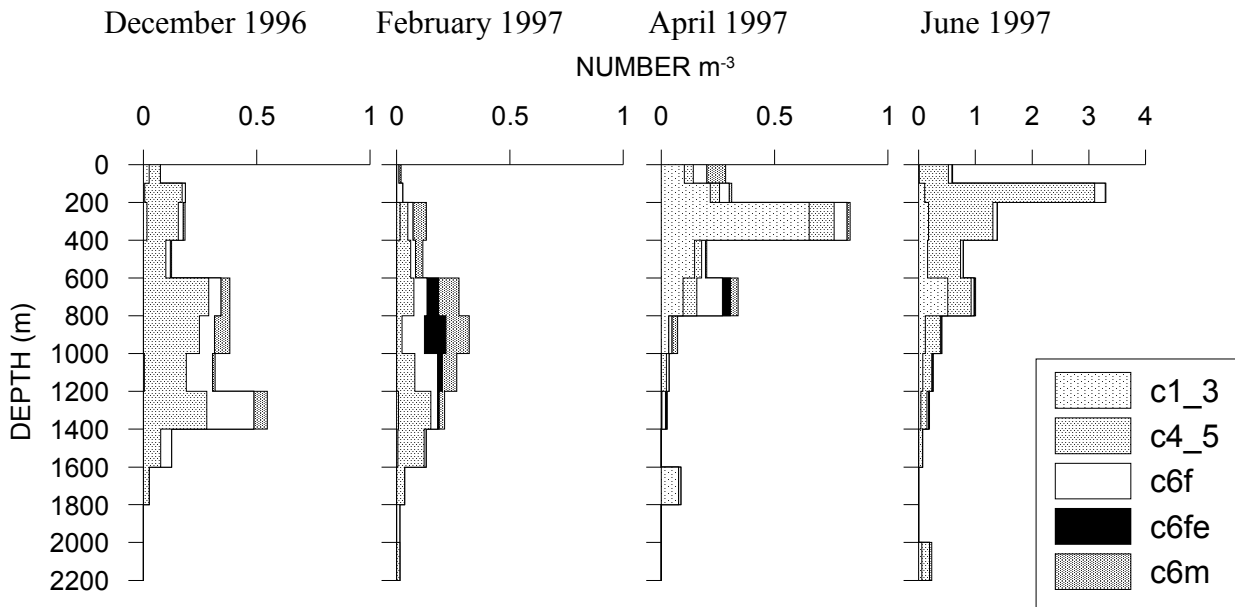


Figure 6. *Pareuchaeta norvegica*. Vertical distribution in the Iceland Basin from December 1996 to June 1997. Note the change in abundance scales between April and June. The values are means from three stations.

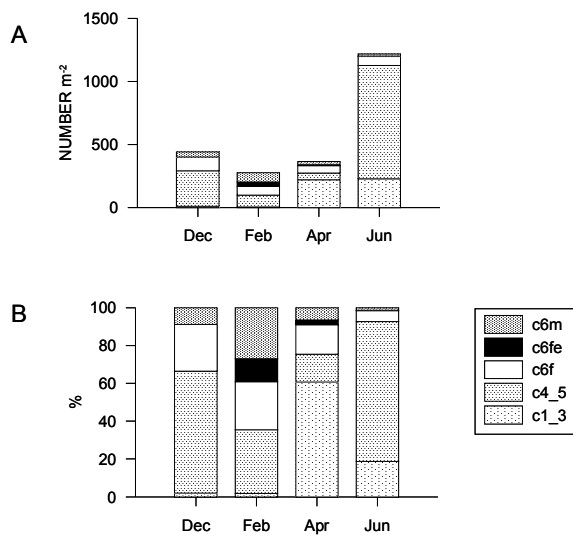


Figure 7. *Pareuchaeta norvegica*. Total depth integrated (0-2200 m) number (A) and relative number (B) of copepodite stages in the Iceland Basin from December 1996 to June 1997. The values are means from three stations.

of males in the population indicates breeding activity (Mauchline 1994), and this ratio was highest in February (~30%, Fig. 7B). The frequency of ovigerous females was also highest in February (~10%, Fig. 7B), and a few males and females with spermatophores were also observed in the samples during this time. Taken together, this suggests that the main reproductive activity occurred around February. Young developmental stages from this reproduction appeared mainly in April (Fig. 7B), when the population became dominated by juvenile stages C1-3 (~60%). In June the percentage of stages C4-5 was highest (~80%), suggesting that the offspring from the winter spawning were being recruited to the older stages (Fig. 7B).

On the basis of the description above it is concluded that February is the main breeding season of *P. norvegica* in the Iceland Basin. The vertical distribution by stages (Fig. 6), suggests that the species reproduces mainly at depth (~600-1200 m), and the nauplii and/or the youngest copepodite stages swim or drift up to the surface layer after the eggs hatch. Figure 6 further suggests that the growth to the more advanced copepodite stages (C4-5) mainly takes place at relatively shallow depth (100-400 m), between April and June.

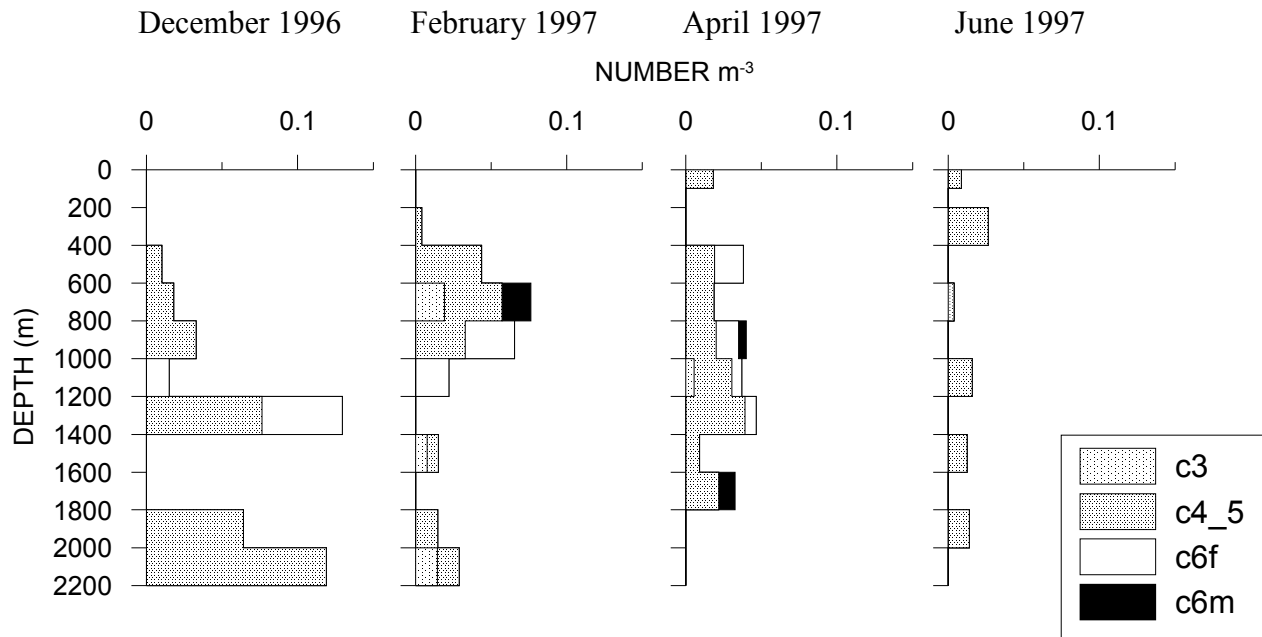


Figure 8. *Calanus hyperboreus*. Vertical distribution in the Iceland Basin from December 1996 to June 1997. The values are means from three stations.

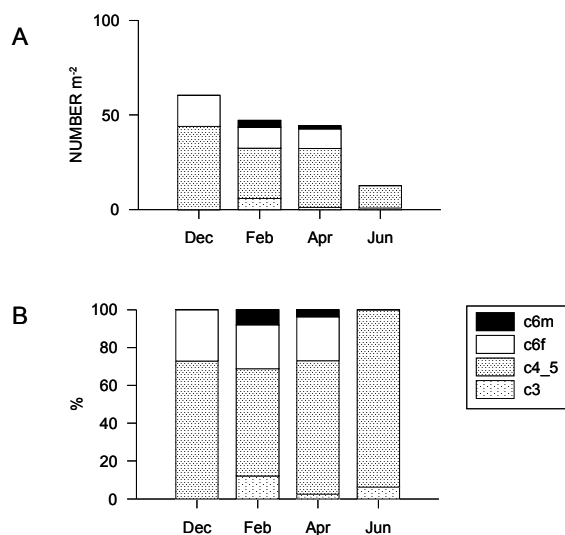


Figure 9. *Calanus hyperboreus*. Total depth integrated (0-2200 m) number (A) and relative number (B) of copepodite stages at sampling station in the Iceland Basin from December 1996 to June 1997. The values are means from three stations.

Calanus hyperboreus

Calanus hyperboreus was the third most abundant copepod in biomass (~3%). However, numerically it was very rare (Table 1). From December to April, almost the whole population stayed below 400 m depth, and by June, virtually the whole population had disappeared (Fig. 9A).

Depth integrated abundance decreased from ~60 individuals m⁻² in December to ~10 individuals m⁻² in June (Fig. 9A). From this and the fact that the youngest copepodite stages (C1 and C2) were never found it is concluded that *C. hyperboreus* do not reproduce in the Iceland Basin. Similarly, Gislason (2003) concluded that *C. hyperboreus* was an expatriate in the nearby Irminger Sea.

Oithona spp.

Two species belonging to the genus *Oithona* spp., namely *O. similis* and *O. spinirostris*, were found in the samples. *O. similis* was more numerous, while *O. spinirostris* was also regularly found. As they were usually counted as belonging to one group, they are treated together in the present analysis.

Numerically, *Oithona* spp. was the most abundant taxon encountered during the present study, contributing ~49% of the copepod numbers in the Iceland Basin. However, due to its small size, it only contributed ~2% of the biomass (Table 1).

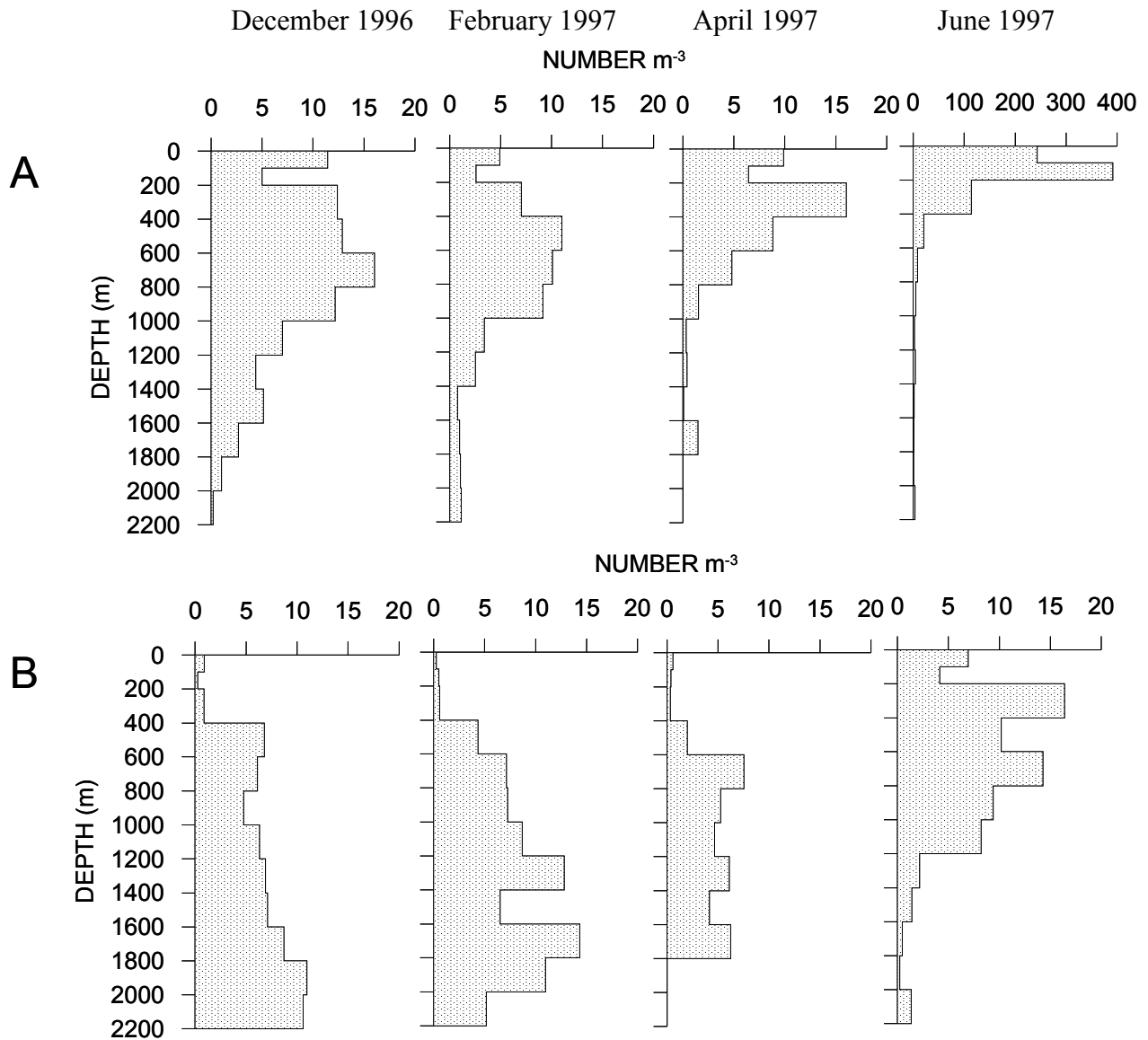


Figure 10. Vertical distribution of *Oithona* spp. (A), and *Oncaea* spp. (B) in the Iceland Basin from December 1996 to June 1997. Note the change in abundance scales between April and June in (A). The values are means from three stations.

The seasonal depth distribution is shown in Fig. 10A. From December to February the population was mainly found from the surface and down to 1400–1600 m depth, with a tendency for the highest values to occur between ~200 and ~1000 m depth (Fig. 10A). In April the population had shifted to somewhat shallower depths, with highest numbers being caught in the 200–400 m depth layer. In June the population was mainly found between 0 and 200 m depth.

During winter and spring (December–April), the depth integrated numbers fluctuated between ~8000 and ~15,000 individuals m⁻² (Fig. 4B). After April the numbers increased markedly to a maximum in June (~100,000 individuals m⁻²).

As the developmental stages of *Oithona* spp. were not separated it is difficult to evaluate to what extent the increase after April reflects reproduction of the animals. However, since the seasonal pattern is very clear, with low values during the winter and one main increase from April to June, it is considered most likely that the main breeding activity occurred sometime between April and June. As judged by the vertical distribution (Fig. 10A) the spawning probably took place in the upper layers.

Metridia lucens

Metridia lucens accounted for ~1% of the copepod biomass, and less than ~1% of the numbers (Table 1).

In December, the animals were rather evenly distributed from the surface and to the bottom (Fig. 11). In spring and summer (February to June) the animals showed a bimodal depth distribution with one maximum

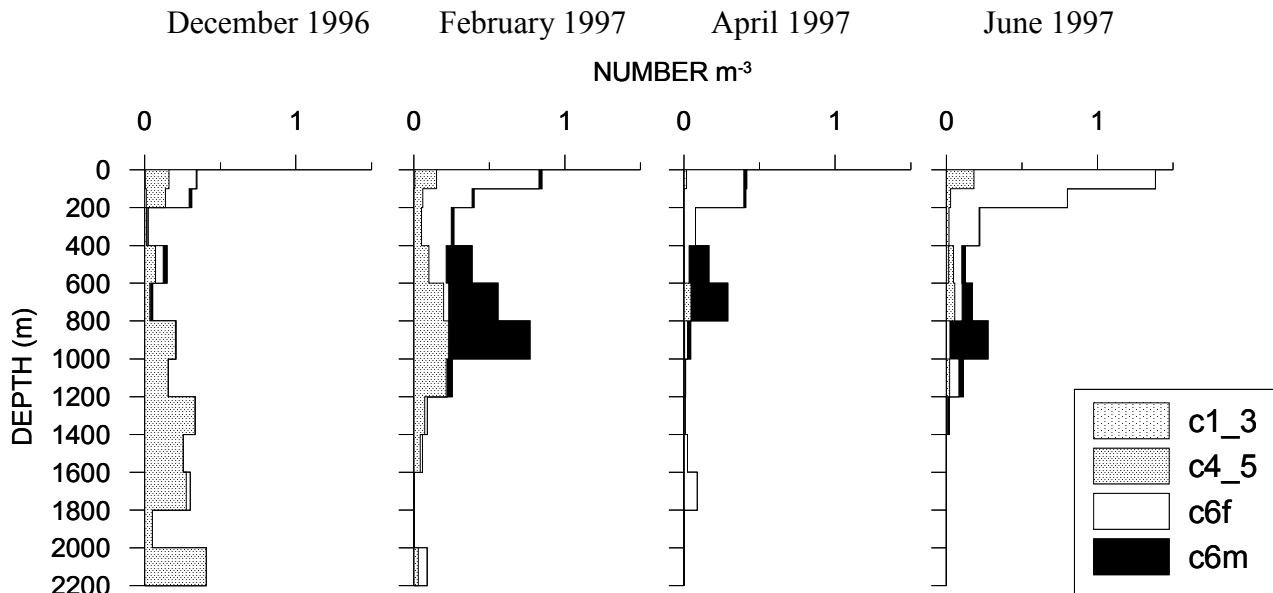


Figure 11. *Metridia lucens*. Vertical distribution in the Iceland Basin from December 1996 to June 1997. The values are means from three stations.

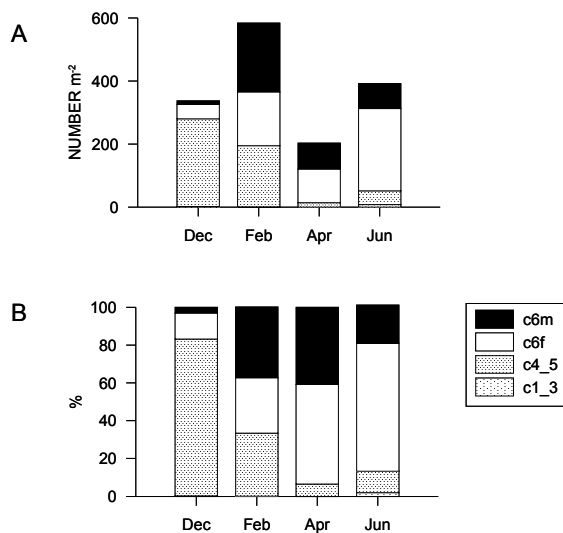


Figure 12. *Metridia lucens*. Total depth integrated (0-2200 m) number (A) and relative number (B) of copepodite stages in the Iceland Basin from December 1996 to June 1997. The values are means from three stations.

near in the surface (0-200 m) and another deeper (600-1000 m). It is interesting to observe that during this time the adult females were mainly located near the surface, whereas the adult males stayed deeper.

Depth integrated numbers fluctuated somewhat irregularly through the year, between ~200 and ~600 individuals m^{-2} (Fig. 12A).

The seasonal stage frequency suggests that animals of stages C4 and C5 were developing to adults in February and April (Fig. 12B). From the high incidence of adults of both sexes in April and June (>90%, Fig. 12B) it is likely that reproduction took place mainly during spring and summer. In June a small increase of the youngest copepodites (C1-3) was observed, which supports this. It should be noted in this context that the abundance of the youngest copepodite stages is likely to be grossly underestimated because their small size allows them to slip through the coarse mesh nets used on our surveys.

Pleuromamma robusta

Pleuromamma robusta ranked 6th in copepod biomass (~1%) while it was very rare numerically (Table 1).

The vertical distribution was rather similar during winter and spring (December-April), with highest numbers being observed in relatively shallow waters, above ~200-400 m depth (Fig. 13). In June, however, the bulk of the stock stayed somewhat deeper (~100-800 m).

Depth integrated abundance fluctuated rather irregularly through the year, between ~50 and ~150

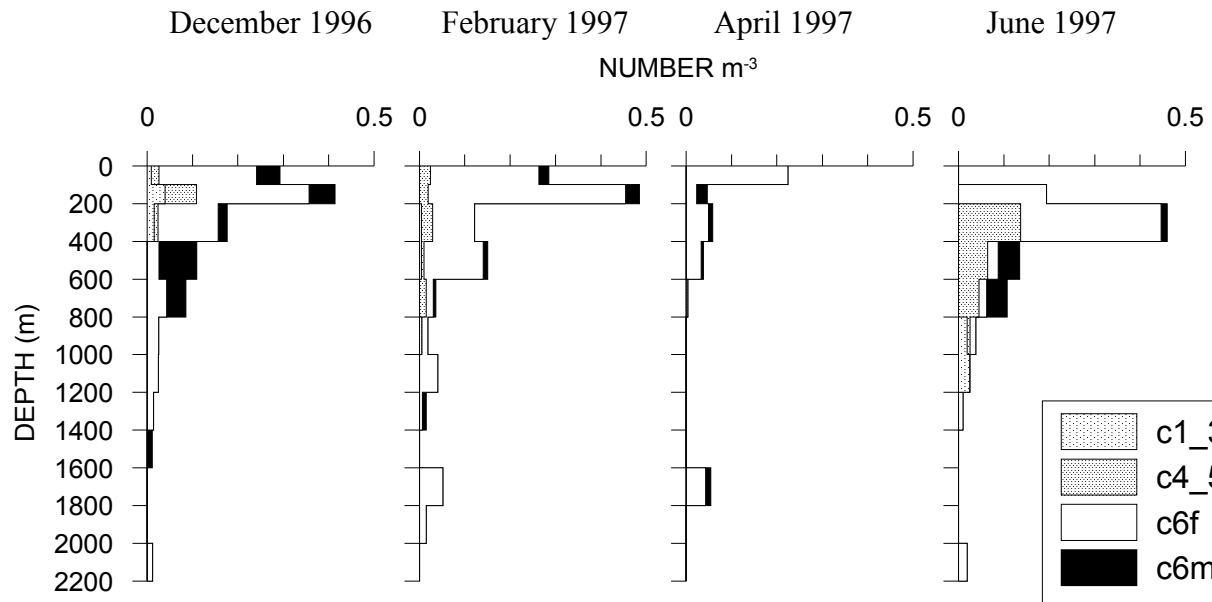


Figure 13. *Pleuromamma robusta*. Vertical distribution in the Iceland Basin from December 1996 to June 1997. The values are means from three stations.

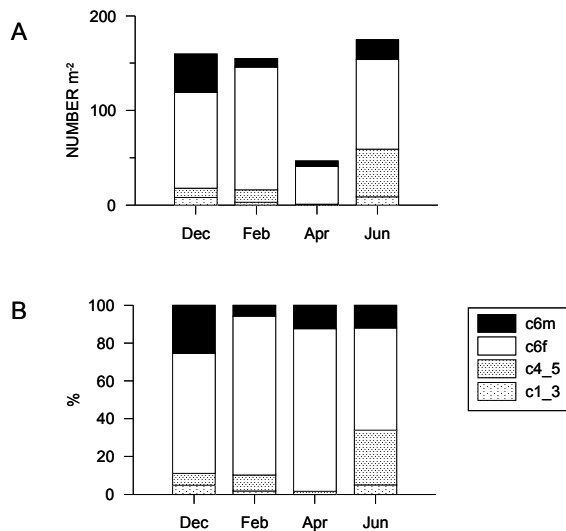


Figure 14. *Pleuromamma robusta*. Total depth integrated (0-2200 m) number (A) and relative number (B) of copepodite stages in the Iceland Basin from December 1996 to June 1997. The values are means from three stations.

individuals m^{-2} , with the lowest values being recorded in April (Fig. 14A).

As with *M. lucens*, the youngest developmental stages were very rare (Fig. 14). However, in contrast to *M. lucens*, they were found year round. This, and the fact that adults of both sexes were very abundant during all seasons (>60-90%), indicates that *P. robusta* were reproducing during all seasons. As with *M. lucens*, the juveniles of *P. robusta* were probably undersampled because of the rather large meshes used in the present study.

Oncaea spp.

The genus *Oncaea* spp. was represented by two species: *O. borealis* and *O. conifera*, of which the former species was more numerous. For the same reasons as with *Oithona* spp. they are treated together in the present analysis.

Oncaea spp. accounted for ~14% of copepod numbers in the Iceland Basin (Table 1). In terms of biomass animals belonging to this genus were less important (~1%).

The numbers of *Oncaea* spp integrated over the depth range of the samples fluctuated rather irregularly from ~6,000 to ~10,000 individuals m^{-2} during winter and spring (December-April) with only an insignificant increase in June (~13,000 individuals m^{-2} , Fig. 4B).

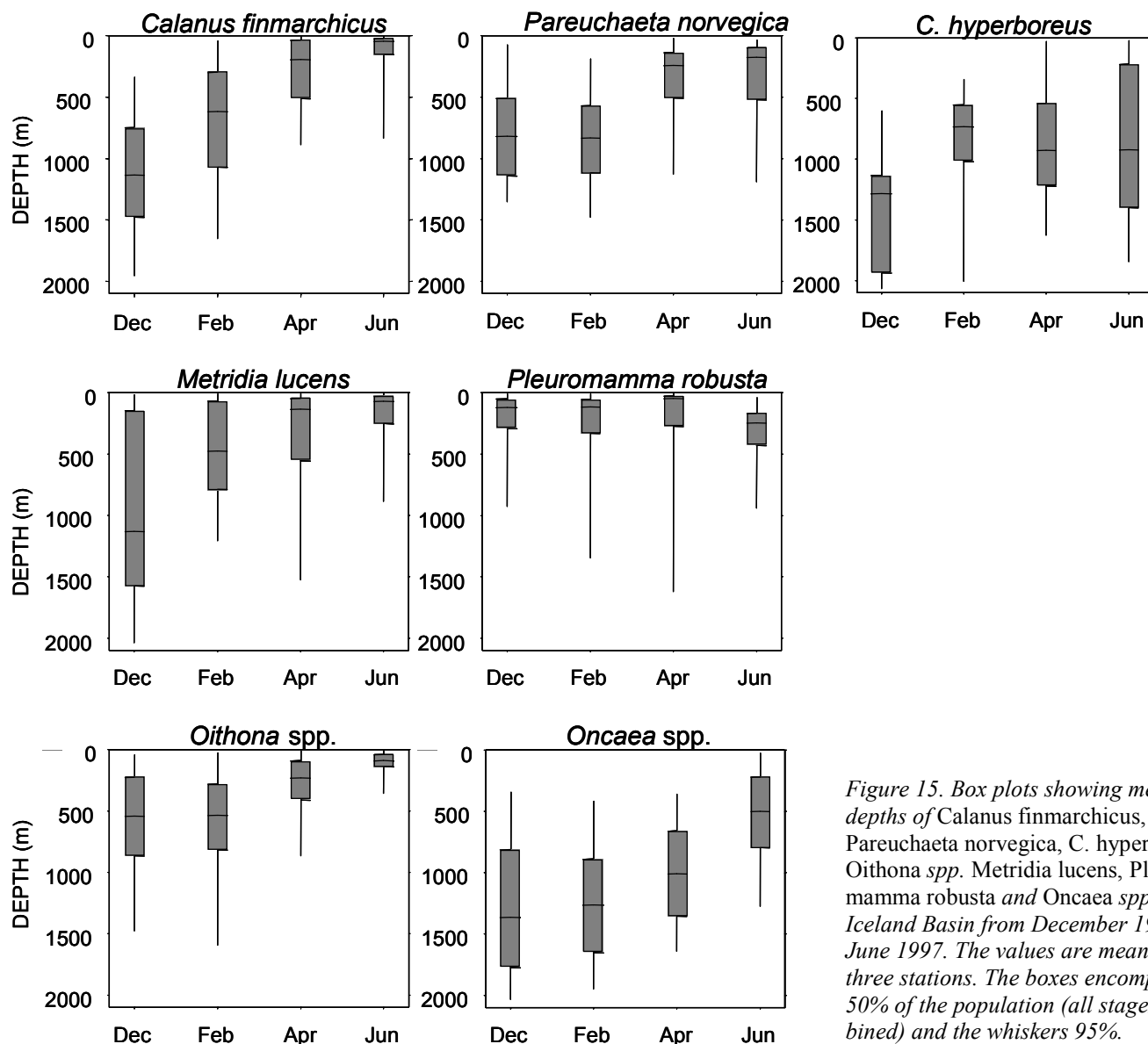


Figure 15. Box plots showing median depths of *Calanus finmarchicus*, *Pareuchaeta norvegica*, *C. hyperboreus*, *Oithona* spp., *Metridia lucens*, *Pleuromamma robusta* and *Oncaea* spp. in the Iceland Basin from December 1996 to June 1997. The values are means from three stations. The boxes encompass 50% of the population (all stages combined) and the whiskers 95%.

During winter and spring (December–April), the animals were mainly caught below 400 m depth (Fig. 10B). In June the animals were mainly found between ~200 and ~1200 m depth.

As with *Oithona* spp., the stages of *Oncaea* spp. were not separated, and therefore it is difficult to evaluate when reproduction took place. However, the fact that the abundance was rather stable during the study period, with no clear seasonal trend, suggests that breeding activity was not confined to a particular season of the year.

Discussion

In spite of the broad spacing between sampling dates, it may be deduced from Fig. 2 that the phytoplankton spring bloom started in April, following increased stratification of the surface layer due to warming of surface waters, and that the growth continued at least until June. This is in line with long term monitoring results, showing that in offshore waters south of Iceland the spring bloom generally starts in April (Gudmundsson 1998), and results from the Icelandic spring survey in 1997 showing a vigorous phytoplankton growth in the oceanic area south of Iceland in mid May 1997 (Anonymous 1999).

In the present material copepods were by far the most dominant group, accounting for 90% or more of the plankton, which is in accordance with earlier zooplankton investigations from the oceanic north Atlantic (Einarsson 1960; Bainbridge and Corlett 1968, Williams 1988, Gislason 2003). The most numerous copepods of the present study were also reported among the most abundant ones in earlier investigations in the Iceland Basin (Williams (1988). In the Labrador Sea (Sameoto 1984), the Iceland Sea

(Gislason and Astthorsson 1998) and the Norwegian Sea (Østvedt 1955) copepods are also the dominating group.

The dominant copepods exhibited clear differences in seasonal abundance, vertical distribution and age structure, reflecting differences between the life histories of these species. Except for *P. robusta* that showed almost no seasonal variability in depth distribution, the copepods stayed relatively deep during winter and some rose almost to the surface during spring (*C. finmarchicus*, *P. norvegica*, *M. lucens*, *Oithona* spp.), while others did not (*Oncaea* spp., *C. hyperboreus*) (Fig. 15).

In the Iceland Basin *C. finmarchicus* overwinters in deep waters and rises to the surface mainly during March and April to spawn (Fig. 15 this study, Gislason and Astthorsson 2000). This is in accordance with the general behavior of the species in other regions, with arrested development and diapause at depth during the winter and termination of diapause and spring ascent in late winter and spring (see Hirche 1996 for review). Its closely related species, *C. hyperboreus*, did not reproduce in the Iceland Basin, where it is most likely an expatriate, being advected to the area from the Norwegian Sea with deep currents overflowing the Iceland Scotland Ridge (Fig. 1).

Pareruchaeta norvegica also stayed at depth during winter, rising to the upper layers during spring (Fig. 6). However, in contrast to *C. finmarchicus*, the spawning of *P. norvegica* was uncoupled to the spring bloom. Liberation of the nauplii took place in the deeper layers, probably mainly in February and March, and the early copepodites drifted or migrated to the upper layers in March and April to utilize the biological production there. This accords with previous studies from the Iceland Basin (Williams 1988, Gislason and Astthorsson 1992), the nearby Irminger Sea (Gislason 2003), and the Rockall Through (Mauchline (1994). The different spawning times and spawning habitats of *C. finmarchicus* and *P. norvegica* may contribute to minimizing interactions between them. However, as pointed out by Gislason *et al.* (2007), *P. norvegica* is a tactile predator with *Calanus* being an important part of the diet (Auel 1999), and therefore it is likely that these copepods are involved in a predator-prey relationship, especially during spring and summer when their vertical distributions generally overlap (Fig. 15).

While *Oithona* spp. had a generally shallower depth distribution than both *C. finmarchicus* and *P. norvegica*, the ontogenetic migration pattern was similar, the animals staying deep during winter and rising to the upper waters in spring (Figs 10A and 15). This is the same pattern as observed recently for these species in the nearby Irminger Sea (Gislason 2003). As judged by the seasonal vertical distribution (Fig. 10A) and abundance (Fig. 4B), the main growth of *Oithona* spp. probably took place in the upper layer in May and June. From the Greenland Sea, Richter (1994) reported *Oithona* spp. as mesopelagic species (0-500 m) with the main breeding period in early summer in the surface layer (0-100 m). In the Irminger Sea, Castellani *et al.* (2005) did not find significant seasonal differences in individual egg production rates of *O. similis*. However, with the much higher stocks (Fig. 4B), the population production is likely to be higher during spring.

In December, the depth distribution of *M. lucens* was most expanded of the copepods studied here, and a considerable fraction stayed near the surface at all sampling times (Fig. 11). This, together with an omnivorous feeding mode (Haq 1967), indicates that the animals were active year round. This appears to be in accordance with the general behavior of the genus (Gronvik and Hopkins 1984, Båmstedt *et al.* 1985, Batchelder 1985). Information of the seasonal depth distribution of *M. lucens* in oceanic environments is limited, but the data of Williams (1988) from farther south in the Iceland Basin show that the animals are mainly found between 300 and 500 m depth during winter with the animals migrating up to shallower layers in spring and summer, which is similar as found here. The vertical distribution was bimodal from late winter and until summer (Fig. 11), and as shown by Pearre (1979) this may indicate diel vertical migration behavior, which accordingly should be greater in spring and summer than during winter, when there was no bimodality in the depth distribution data. This accords with the findings of Hays *et al.* (1995), who found for a large area of the North Atlantic, that *M. lucens* was a stronger diel vertical migrator during summer than winter, thus avoiding the illuminated upper layers and reducing the risk of getting detected by visual predators. The seasonal stage frequency diagram indicates that during winter and spring the C4s and C5s developed to adults of both sexes (Fig. 12). The high incidence of adults during late winter and spring and the observed increase in the youngest copepodite stages in June (Fig. 12), indicate that reproduction was mainly taking place during spring and summer. Farther south, off the US northeast continental shelf, *M. lucens* produces several generations per year (Kane 2003).

In contrast to the other species studied here, the bulk of *Pleuromamma robusta* occupied the surface layers during winter and spring (~0-400 m), while showing a somewhat deeper depth distribution in summer (~100-800 m) (Fig. 13). This contrasts with what Williams (1988) found at weather station India farther south, namely that the population tended to stay deep (below ~400 m) until August-September when part of the stock ascended to the upper layers. The reasons for this discrepancy are unclear, however, from the data presented by Williams (1988) it seems as there is considerable between-year variability in the seasonal ontogenetic migration behavior of the species. The limited seasonal variation in numerical abundance, the high incidence of adults of both sexes, and the fact that the youngest developmental stages (C1-3) were present year round, indicate that the animals were reproducing at all seasons (Fig. 14).

Most *Oncaea* spp. stayed below 400 m depth during the whole study period, and only a limited part of the population rose to shallower waters during the summer (Fig. 10B). The biology of *Oncaea* spp. is poorly understood, but like *Oithona* spp. it is probably mainly omnivorous (Paffenhöfer 1993, Kattner *et al.* 2003). As with *Oithona* spp., very little is known about its life cycle. In the Greenland Sea *Oncaea* spp. maintains high stocks in deep waters year-round and the breeding season is more extended than that of *Oithona* spp. (Richter 1994). The present data from the Iceland Basin, with limited seasonal variations in total integrated abundance (Figs 4B), suggest that for *Oncaea* spp., the breeding activity is not confined to a particular season of the year. This is similar as observed recently in the Irminger Sea (Gislason 2003).

Deep scattering layers, mainly located from 400-500 m to 700-800 m depth, are a characteristic feature of the Iceland Basin (Gislason *et al.* 2007). Various mesopelagic fish species are abundant in these layers, and a significant part of their diet consists of copepods (Gjøsæter 1981, Magnusson 1996; Bagøien *et al.* 2001). Several of the copepods considered here (*C. finmarchicus*, *P. norvegica*, *Metridia lucens* and *Oncaea* spp.) were centered below the reported depth of the deep scattering layers, at least during the early winter months (Fig. 15), thus suggesting that the visual predators were in fact shaping the vertical distribution of the copepods during winter. However, whether this is operating through habitat preference of the copepods, i.e. that they are selecting the deeper habitats so as to reduce encounters with the visually hunting predators, or depth-specific mortality during winter, cannot be decided on the basis of the present data. As discussed by Gislason (2003), the shallower depth distribution of *Oithona* spp. during winter may be related to its much smaller size and to its transparency, making it less susceptible to visual predation. On the other hand, *Oncaea* spp. with its strong pigmentation is likely to be better detected by visually hunting predators than the similarly sized *Oithona* spp., and this may explain its deeper depth distribution.

In conclusion, the most abundant copepods in the Iceland Basin differ in migratory behavior, life cycles and trophic positions, which may provide a mechanism by which they share the resources of the pelagic environment. In addition, visual predators may also shape the life history of the copepods.

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