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Seasonal abundance and development of krill in the Faroe-Shetland Channel

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Samples of krill were collected at three stations crossing the Faroe-Shetland Channel during the season from May 2001 until July 2002. Samples were collected down to a maximum depth of 900 m using a MIK-net. Of the ten krill species encountered in the area the large nordic krill *Meganyctiphanes norvegica* and the somewhat smaller *Thysanoessa longicaudata* dominated the population throughout the research period. Seasonal variability in temperature, salinity, chlorophyll *a*, and abundance of krill as well as data on krill egg and larvae is presented, and related to the environmental conditions in the area. In addition the seasonal and diel vertical variation in abundance was studied using moored ADCP's in the area. Length-frequency histograms of the two dominating species showed the 0-group to appear in the samples in June. Based on larvae and 0-group appearance and the ambient seawater temperature, the main time of spawning is estimated to be in late March/early April. In addition, the seasonal development in maturity of both males and females of the two dominating krill species is presented.

Introduction

Euphausiids (or krill) are an important group of zooplankton in the north Atlantic. They are a relatively small and uniform taxon of large pelagic shrimp-like filter-feeding crustaceans ranging in size from approximately 10-80 mm in total length. The two main species in the north Atlantic are *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* (Lindley, 1978). The reproduction of krill is coupled to the annual cycle of the phytoplankton spring bloom (Einarson, 1945; Gislason and Astthorsson, 1995; Dalpadado, 2006), and results have shown that krill egg production is synchronized with copepod feeding conditions (Hirche, 1996; Gislason, 2005).

Krill are of great ecological importance in the ocean. They stand for a large part of the secondary production in the sea, and in the Faroe-Shetland Channel it is the main food for several fish species on their feeding migration through the channel, especially for blue whiting where krill has been shown to make up about 50% (by weight) of the diet (Bjelland and Monstad, 1997). Krill is also an important prey item for mackerel in the Faroe-Shetland Channel, and on the shelf slopes it is also an important food for e.g. saithe. These are all commercially important fish species for the Faroese society. Krill is therefore an important link between phytoplankton as their prey and their fish predators.
In addition krill are also an important food source for cetaceans in the area e.g. blue-whales and fin-whales, as well as for several seabirds species e.g. Fulmar and Storm Petrel.

Despite this, krill is very poorly studied in the Faroe-Shetland Channel. This study aims to provide information on seasonal abundance, reproduction and development of the main krill species, *Meganychtiphanes norvegica* and *Thysanoessa longicaudata*, in the Faroe-Shetland Channel, and relate it to hydrography and phytoplankton spring bloom.

Materials and methods

Samples were collected at three stations (Faroe, Mid and Scot) on a section across the Faroe-Shetland Channel on 6 cruises with the research vessel Magnus Heinason during the period from May 2001 – July 2002 (Fig 1).

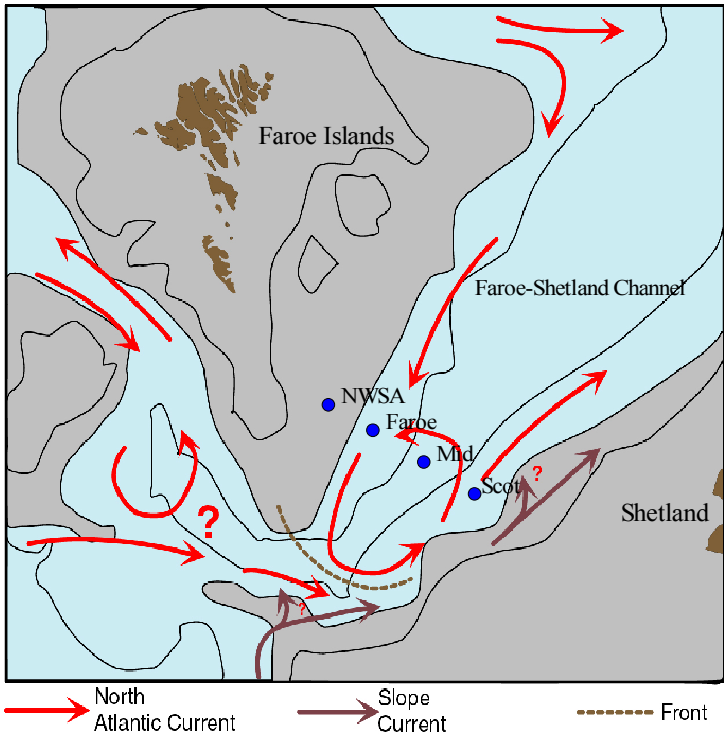


Figure 1 Position of biological sampling stations and ADCPs in the Faroe-Shetland Channel.

Temperature and salinity profiles were obtained at all stations using a Seabird Electronics 911plus CTD. A fluorometer was mounted on the CTD and the fluorescence was calibrated against selected samples analysed for chlorophyll *a*, according to the method from Baltic Marine Biologists (1979) and applying the equation of Jeffrey and Humprey (1975).

Krill samples were collected using a MIK-net with a mesh size of 1.5 mm on the main net and 0.5 mm on the last 2 m before the cod end. Samples were collected as oblique hauls from the surface down to 200, 300, 400, and 600m depths at stations Faroe and Scot, and 200, 300, 400, 600, and 900m depths at station Mid.

On the first four cruises one replicate was taken at each depth, but on the last two cruises triplicates were taken at each depth at each station.

All results of krill abundance are presented as average between all depths in numbers per $1000m^3$.

The MIK-net was shot and raised at a speed of approximately ⅔ m s^{-1} while towing at 2.5 knots. The depth of the net was recorded using a Scanmar acoustic depth recorder, mounted on the net opening, and the volume of water filtered was measured by a Hydro-Bios flowmeter with a back run stop. All samples were preserved in 10% buffered formaldehyde seawater solution.

At the laboratory the samples were split into sub-samples (when necessary) using a Motoda splitter. Krill were identified to species and separated into following groups according to Einarson (1945), Mauchline and Fisher (1969), Lindley (1978), Mauchline (1980), and Mauchline (1985): immature males; immature females; mature males (males with spermatophores in ejaculatory ducts); mature females (females with spermatophores attached to thelycum).

Krill larvae were species identified and separated into following groups: nauplii and metanauplii, calyptopis I-III, and furcilia I-VIII, according to Einarson (1945). Krill eggs were registered and the egg diameter was measured.

In addition the carapache length (the distance from base of eye-stalk to the mid-dorsal posterior edge of the carapache) and total length (distance from the base of the eye-stalk to the posterior end of the uropods, excluding their terminal setae) of each specimen was measured.

To describe the population structure and the different generations of the krill, we use the terminology of Einarson (1945). The 0-group covers the time period from hatching until 30 March the following year and the 1-group covers the period from 1 April that year until 30 March the next year, etc.

In addition data on seasonal krill and *Diatom* abundance from the Continuous Plankton Recorder (CPR) was obtained from SAHFOS for the period 1990-2001.

Acoustic backscatter

Acoustic Doppler Current Profilers (ADCP) were moored along standard hydrographic sections off Faroese waters (Fig 2). The ADCP data were compiled by the Faroese Fisheries Laboratory and processed by FRS Marine Laboratory Aberdeen.

Instead of absolute backscattering strength, which could be calculated using the methods described by Heywood (1996) or Deines (1999), we calculated relative acoustic backscattering strength (rSv) for each individual time series. This minimised the difficulties (Brierley *et al*, 1998) related to the calibration and monitoring of individual instruments and the need for a number of constants specific to each instrument, which we were unable to obtain from the manufacturer (Teledyne RD Instruments Inc.)

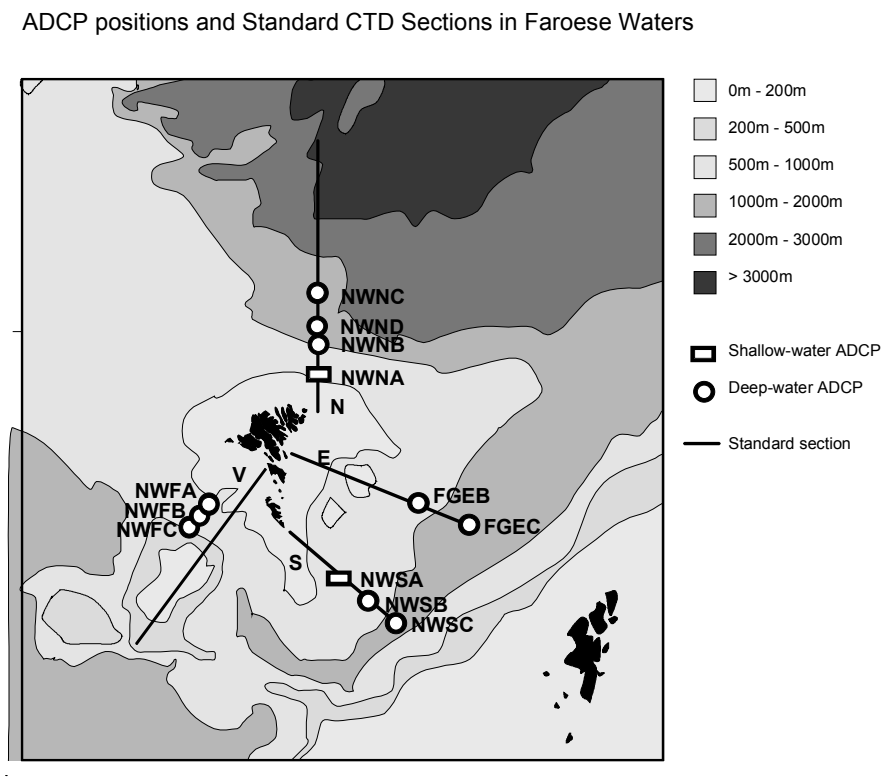


Figure 2 Location of deep-water and shallow-water ADCP moorings, along standard hydrographic (CTD) sections off Faroese waters.

Relative acoustic backscattering strength was calculated using the equation published by Batchelder *et al* (1995), using raw data (Automatic Gain Control; AGC) averaged over the 4 beams of each ADCP instrument.

$$rSv = Kc(E - Er) + Lc + 20\log R + 2\alpha R - \log(D * 10^{-3}) \quad (1)$$

In this equation, Kc is the conversion factor from counts to dB and is calculated as

$$Kc = 127.3 / (273.16 + Te) \quad (2)$$

as advised by RDI Instruments (1990), where Te is the temperature of the electronics. Because the instruments in this study were moored, Te was assumed to be the same as the transducer temperature, Tx, recorded at the transducer head.

Lc is the correction for circuit non-linearities (Heywood *el al*, 1991)

$$Lc = 1.15 * 10^{-16} * E^{7} \quad (3)$$

Where E is the AGC count for each bin.

Er is the noise value determined from the minimum value of AGC counts for each deployment. R is the range of the bin (m)

$$R(i) = |\text{center depth bin}(i) - \text{instrument depth}| \quad (4)$$

α (see below) is the absorption coefficient of the sound in the water (dB m^{-1}) and D is the size of the bin or bin length (m).

Computation of the absorption coefficient α

Some temperature and salinity profiles data were available for the study area (approximately 4 - 5 profiles per year from 1994 to 2001). For each site, we modelled the closest data set using LOESS smoothing in order to fill the missing periods in the time series (see section below).

For each CTD deployment, temperature (T; ^{o}C) and salinity (S) data were used to compute the sound velocity (V; m s^{-1}) at each depth (D; m). See section below for more details on hydrographic data.

$$V = 1412 + 3.21T + 1.19S + 0.0167D \quad (5)$$

The absorption coefficient α (dB km^{-1}) was calculated for each depth according to Francois and Garrison (1982)

$$\alpha = A_1P_1f_1f^2/(f^2 + f_1^2) + A_2P_2f_2f^2/(f^2 + f_2^2) + A_3P_3f^2 \quad (6)$$

f = frequency of the adcp (kHz)
A_1 (dB km^{-1} kHz^{-1}) = $(8.86/V) * 10^{(0.78pH - 5)}$
$P_1 = 1$
F_1 (kHz) = $2.8(S/35)^{0.5} * 10^{(4 - 1425 / (273 + T))}$
A_2 (dB km^{-1} kHz^{-1}) = $21.44 * S/V * (1 + 0.025T)$
$P_2 = 1 - 1.67 * 10^{-4} * D + 6.2 * 10^{-9} * D^2$
F_2 (kHz) = $(8.17 * 10^{(8 - 1990 / (273 + T))}) / (1 + 0.0018(S - 35))$
A_3 (dB km^{-1} kHz^{-1})
$= 4.937 * 10^{-4} - 2.59 * 10^{-5}T + 9.11 * 10^{-7}T^2 - 1.50 * 10^{-8}T^3$ (for $T \leq 20\ ^{o}C$) or
$= 3.964 * 10^{-4} - 1.146 * 10^{-5}T + 1.45 * 10^{-7}T^2 - 6.5 * 10^{-8}T^3$ (for $T > 20\ ^{o}C$)
$P_3 = 1 - 3.83 * 10^{-5}D + 4.9 * 10^{-10}D^2$

To calculate relative backscattering strength, all α values between the instrument depth and the given bin depth were averaged and this average was then used in formula (1).

Hydrographic (temperature and salinity) data

For each site, the closest data set was modelled using LOESS smoothing in order to fill the missing periods in the time series. Raw temperature data, where available, were plotted against smoothed data and the "span" of the LOESS smoother modified until the smoothed data presented the best fit to the raw data.

In the absence of data from the NWN transect after Nov. 1999, all the NWN data available for every month and every station were averaged, so the smoothed data from 12/1999 to 06/2001 are derived from averaged data and those data were used to process NWN9907 and NWN0007 backscattering data.

There were no Faroe Bank Channel CTD data for the NWFB station, so the sparse data available from NWF (July and September 1998) were compared with the corresponding data from NWS and NWN. The thermocline was much deeper in NWF, but the surface and bottom temperatures were similar at both NWS and NWN transects. NWNB temperature and salinity data were selected to process NWFB. Indeed, NWNB was the location where the thermocline was the deepest. This choice has been reinforced by the suggestion (Hansen and Østerhus, 2000) that the water masses from the Faroe - Shetland Channel were significantly different from the water masses in the Faroe Bank Channel.

A sensitivity analysis was carried out to investigate how sensitive relative acoustic backscattering strength was to temperature and salinity variability (not presented here). The results showed relatively litte sensitivity to temperature. Very close to the instrument (range = 50 m), the relative backscattering strength is no more than 1 dB for a temperature range of 15 °C (0 to 15 °C). For range of 700 m, close to the maximum range of the instrument, the relative backscattering strength variability is ~ 13 dB for a 15 °C temperature range. The effect of salinity variations was even smaller. For a 50 m range, the effect was almost unnoticeable (less than 0.5 dB at the salinity extremes). At a range of 700 m, the difference in relative backscattering strength was ca. 3.7 dB, which was the maximum observed effect.

Results

Hydrography and chlorophyll

The temperature profiles from the three stations show the presence of a occasionally strong termocline during the summer months (Fig. 3), while during winter the temperature was constant down to a depth of over 400 m.

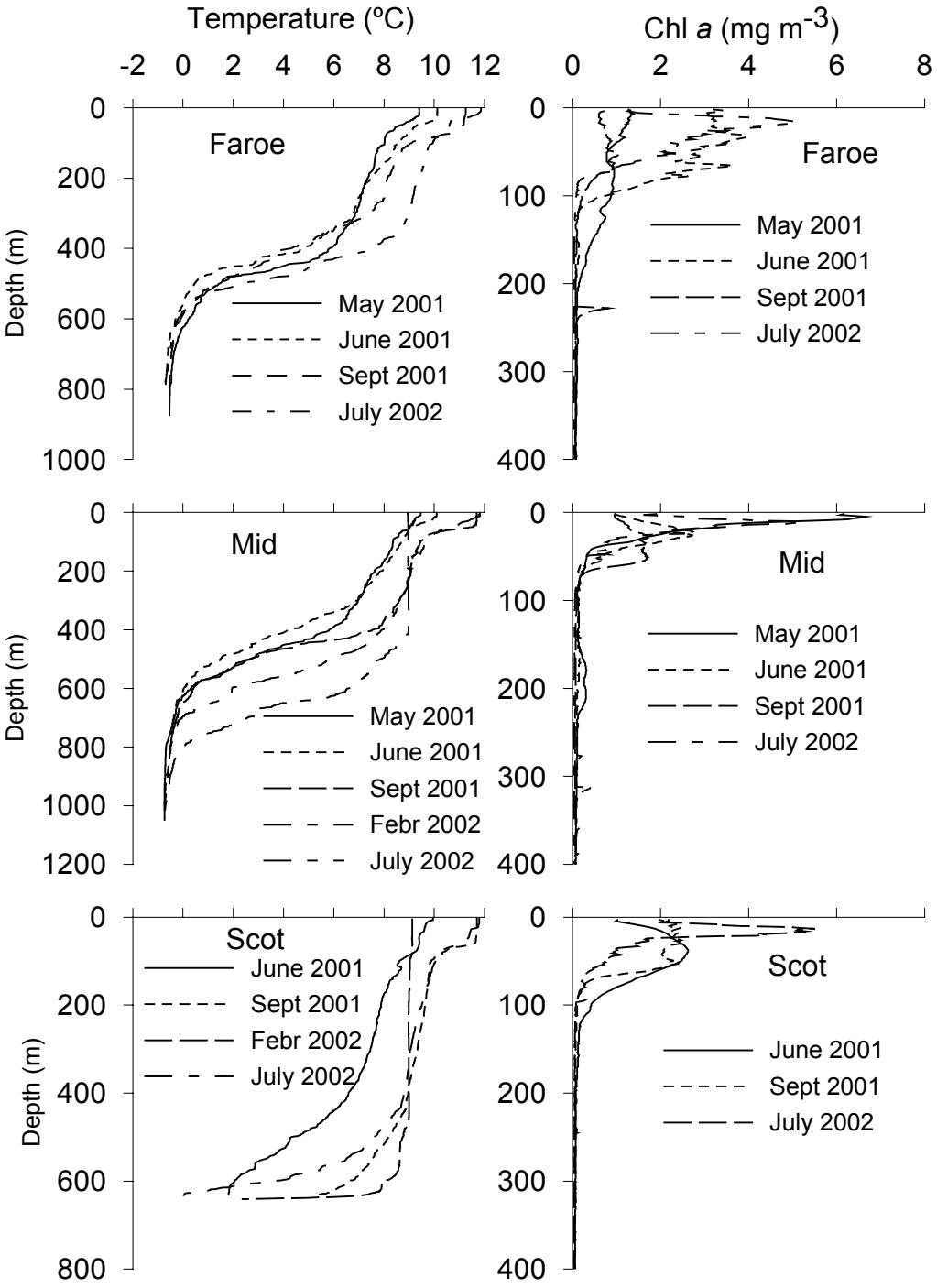


Figure 3. Temperature and chlorophyll profiles from the three stations in the Faroe-Shetland Channel.

The chlorophyll concentration in May was relatively low at station Faroe, but at station Mid the spring bloom had started and the concentrations in the surface layer reached >6 mg m^{-3}. Unfortunately data on both temperature and chlorophyll from station Scot are missing. In September the chlorophyll concentrations were still relatively high at all three stations.

Krill abundance

Of the twelve species listed in Euphausiids of the World Ocean (ETI) for the area including the Faroe-Shetland Channel, ten were found during this research (Table 1).

	Faroe	Mid	Scot
Meganyctiphanes norvegica	x	x	x
Thysanoessa longicaudata	x	x	x
Stylocheiron longicorne	x	x	x
Nematocelis megalops	x	x	x
Nyctiphanes couchii	x	x	x
Euphausia krohnii	x	x	x
Thysanoessa inermis	x	x	x
Stylocheiron elongatum		x	x
Nematobrachion boopis	x	x	x
Thysanopoda acutifrons		x	x
Unidentified krill	x	x	x

Table 1. Krill species encountered at the three stations during the research period.

However, two of them, *Meganychtiphanes norvegica* and *Thysanoessa longicaudata*, dominated the species composition by more than 90% of the krill community most of the time. Occasionally other species as a group, constituted a relative large fraction. This was, however, only observed at times when krill abundances were low mainly due to reduced numbers of *M. norvegica* and *T. longicaudata*.

During the first three cruises, krill abundance was generally relatively low at all three stations with only small differences amongst the stations (Fig 4).

However, in November 2001 the abundance was high at station Faroe with 191 and 130 indv per 1000 m^{-3} of *M. norvegica* and *T. longicaudata*, respectively. At the other two stations the abundance was low.

In February the abundance was low at all three stations, but in July 2002 large variations appeared again between the stations, this time with high abundances at station Scot, with 187 and 107 indv per 1000 m^{-3} of *M. norvegica* and *T. longicaudata*, respectively.

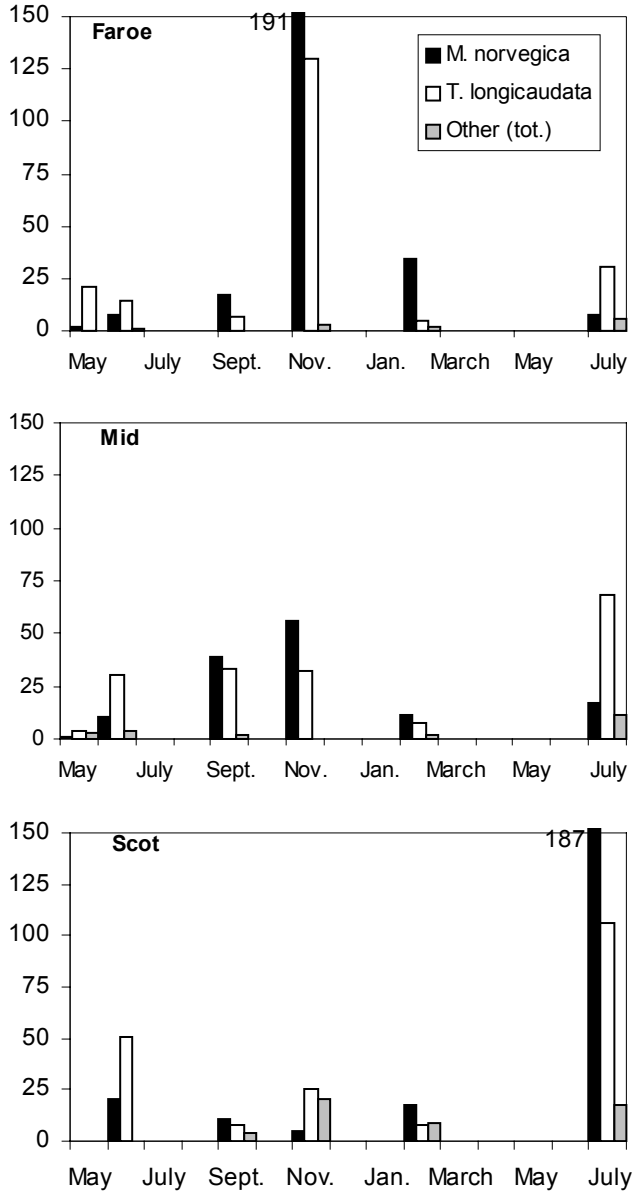


Figure 4. Abundance (numbers per 1000 m^{-3}) of *Meganychtiphanes norvegica*, *Thysanoessa longicaudata* and other krill species at the three stations during the research period.

Meganyctiphanes norvegica

The length-frequency histograms of *M. norvegica* in May 2001 showed one length mode, with relatively large overwintered 1-group and a possible 2-group animals (Fig 5).

In June 2001 two length modes were apparent at all three stations with the 0-group as a distinct peak in the lower range of the length scale (< 3 mm carapache length in Fig. 5).

By September and November 2001 the 0-group had advanced up the length scale, but small individuals were still present in the samples. However, in late February 2002 there was no clear size distinction between the generations.

In July 2002 the new 0-group was apparent at all stations, while last years 0-group (now the 1-group) is seen as a peak at the upper end of the length scale (Fig 5).

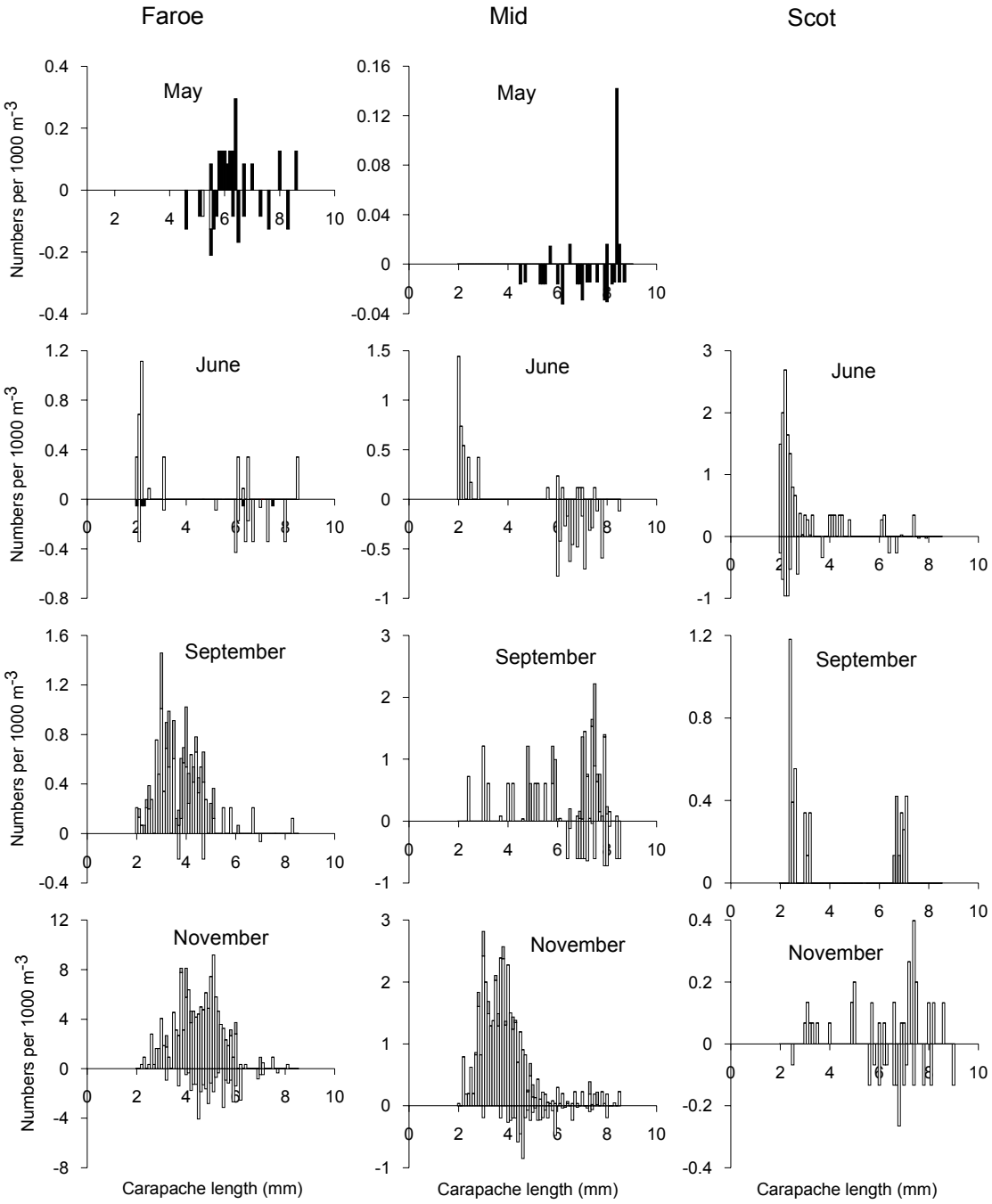
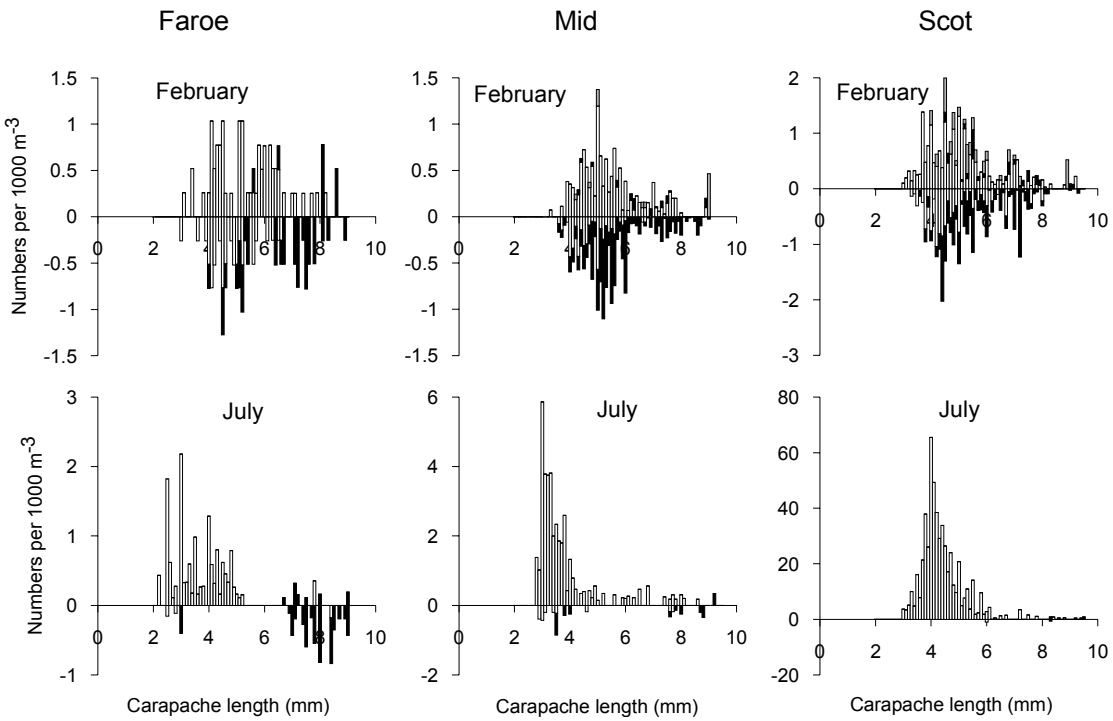


Figure 5. Length-frequency histograms of *Meganychtiphanes norvegica* at the three stations during the research period. Females above x-abscissas and males below. Black bars are mature individuals, white are immature and grey are unidentified.



(Figure 5. continued) Length-frequency histograms of *Meganychtiphanes norvegica* at the three stations during the research period. Females above x-abscissas and males below. Black bars are mature individuals, white are immature and grey are unidentified.

One striking feature about the *M. norvegica* population during winter is the total dominance of females in the samples. In September and November 2001 only a few males were observed at all three stations. However, in February 2002 males were observed again in about the same numbers as females.

Thysanoessa longicaudata

In early May 2001 the *T. longicaudata* population consisted of individuals with a carapache length ranging from 2.0 - 3.5 mm (Fig 6). These are relatively large krill (corresponding to a total length of approximately 12 - 15 mm) and represent the adult overwintered 1-group of the population. There was a distinct size difference between males and females, with females being significantly larger

In June 2001 the 0-group had appeared at station Scot, while at station Faroe and Mid, only the 1-group was observed.

In September and November 2001, and February 2002 the population was dominated by one length mode corresponding to the 0-group, but in July 2002 the new 0-group was observed at all three stations in addition to the 1-group.

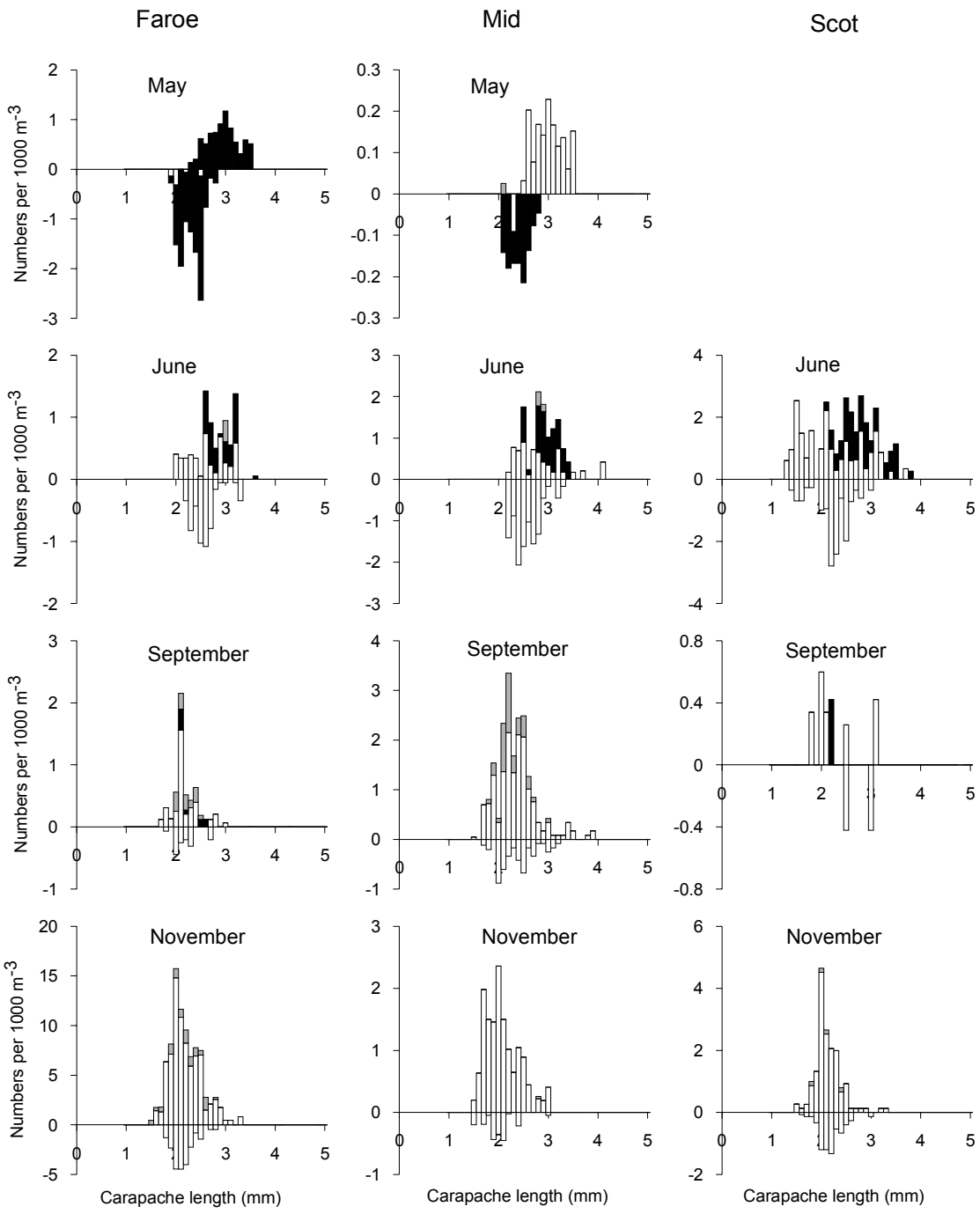
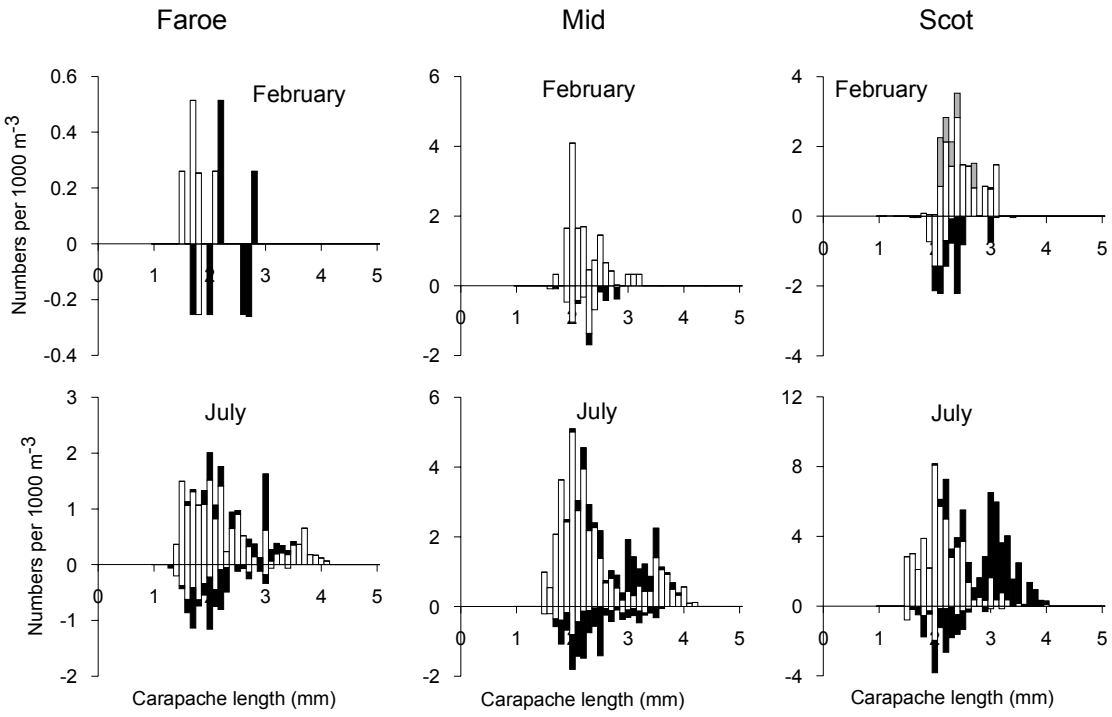


Figure 6. Length-frequency histograms of *Thysanoessa longicaudata* at the three stations during the research period. Females above x-abscissas and males below. Black bars are mature individuals, white are immature and grey are unidentified.



(Figure 6. continued) Length-frequency histograms of *Thysanoessa longicaudata* at the three stations during the research period. Females above x-abscissas and males below. Black bars are mature individuals, white are immature and grey are unidentified.

There was no marked difference in species composition between the three stations. The two species *M. norvegica* and *T. longicaudata* dominated at all three stations throughout the research period. The two species also seemed to be abundant at the same time at the same location e.g. in November 2001 at station Faroe and in July 2002 at station Scot. However, the group "other krill" including species with a more southern distribution showed a tendency to be more abundant at station Scot, and might indicate an influence of different water masses at this station compared to the other two stations.

Acoustic backscatter

Seasonal patterns of abundance:
In order to study the seasonal signal of relative acoustic backscattering strength, indicative of the relative seasonal changes in the abundance of macrozooplankton, the average relative acoustic backscattering strength per ensemble was plotted against Julian day, for individual instrument deployments. For illustration purposes only time series is shown (See Fig 7).

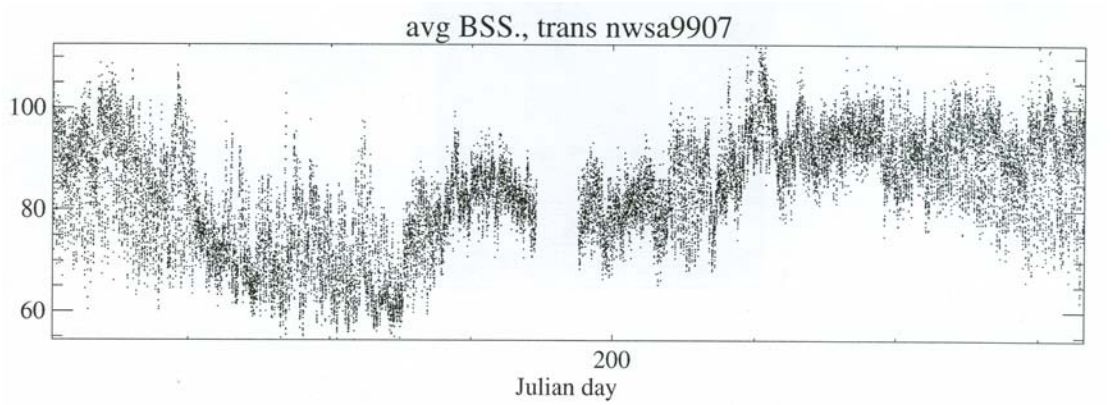


Figure 7. Average relative acoustic backscattering strength plotted against Julian day for the shallow-water ADCP NWSA (see Fig. 1).

Two consistent patterns were observed in the majority of the data sets. In general, macrozooplankton abundance was lower in spring (mid April to end of May or June) and relatively higher the rest of the year. Also, greater variability was observed in the first half of the year, possibly as a consequence of physical processes (mixing), an interpretation supported by the greater variability in the weighted average depth of center of density of relative acoustic backscattering strength (see below). These patterns were present in transect FG, NWN (although the degree of variability in winter varied somewhat between stations), NWS (again, the degree of variability in winter varied between stations) and NWF, although here the differences between months were smaller and the peak in relative acoustic backscattering strength appeared to occur later in the year (autumn – early winter). The seasonal patterns in observed average relative acoustic backscattering strength were fairly consistent among different years.

Short term variability:
There was a considerable degree of variability in acoustic backscattering, especially in the shallowest depth of the sound scattering layer. In order to study such variability in more detail, time series of the weighted average depth of the center of density of relative acoustic backscattering strength data per ensemble were calculated. The series showed persistent high frequency variability in this index, consistent with diel vertical migration behaviour. To test for the presence of this pattern in each series, Partial Autocorrelation Functions (PACF) were plotted for each of the time series. Table 2 shows that most series showed significant PACF at lags of approximately 24 h.

Transect	Station	No. of series	No. with diel periodicity
FGE	B	2	2
	C	2	2
NWF	A	1	0
	B	8	1
	C	1	0
NWN	A	6	5
	B	6	3
	C	5	4
	D	1	1
	E	1	1
	F	1	1
	G	1	1
NWS	A	4	3
	B	6	6
	C	7	5

Table 2. Number of series with significant PACF at lag ca. 24 h, out of the total number of deployments at a particular station. See Materials and methods section for the location of the individual transects and stations.

All transects, perhaps with the exception of the western transect (NWF) showed clear diel periodicity in the series of the average depth of relative acoustic backscattering strength. For illustration, a typical partial autocorrelation function (PACF) plot (series NWSA9907) is shown in Figure 8. Note that 24 h corresponds with a lag of 72 (at 20 min sampling interval).

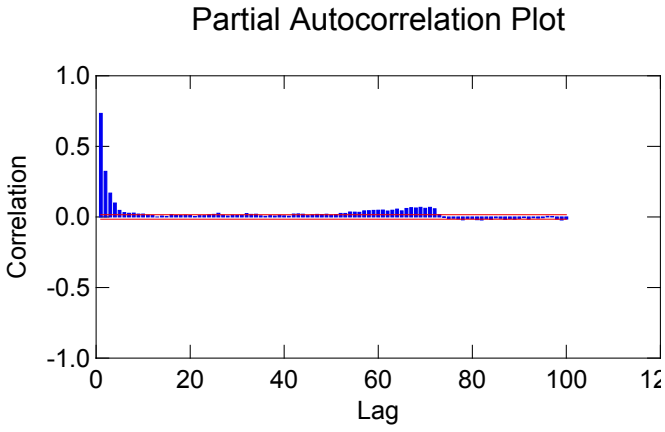


Figure 8 Partial Autocorrelation Function plot for a time series of the weighted average depth of the center of density of relative acoustic backscattering strength data per ensemble, for ADCP deployment NWSA9907 (see text for information on transect and station location).

Maturity and spawning

The majority of the population of both *M. norvegica* and *T. longicaudata* was mature in early May 2001. All females in both species had ripened gonads and carried spermatophores, indicating that they were ready to spawn. In addition the carapache of most females was swollen indicating that they contained mature oocytes. Approximately 90% of the males of both species contained spermatophores in the ejaculatory ducts indicating that they had reached maturity (Fig 5 and 6).
No mature *M. norvegica* were observed during the rest of the 2001 season.
For the smaller species *T. longicaudata* the proportion of mature females decreased steadily through the summer, and in September less than 5% of the females were mature. However, no mature males of *T. longicaudata* were encountered during this period.

Already in February 2002 a relatively large fraction of both the *M. norvegica* and *T. longicaudata* males contained spermatophores in their ejaculatory ducts, but only a small fraction of the females had spermatophores attached to their thelycum.
In July 2002 mature males and females of both species were observed, although males dominated the mature fraction of the population for both species.

The maturation patterns were similar at all three stations for both species during the research period.

The maturity results of the two dominating krill species *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* in the Faroe-Shetland Channel show that spawning most likely starts already in late February, but that the main spawning period seems to be during April – May.

Although our sampling equipment does not retain krill eggs quantitatively, the eggs were registered and used as an indication of spawning activity. Krill eggs were especially encountered during late spring and early summer (Table 3).

	Faroe		Mid		Scot	
	Small eggs	Large eggs	Small eggs	Large eggs	Small eggs	Large eggs
May 2001	2-4	2-4	5-5	5-5	-	-
June 2001	0	0	0	0	0	0
September 2001	0	0	0	0	0	0
November 2001	0	0	0	0	0	0
February 2002	0	0	0	1-15	1-15	2-12
July 2002	4-12	3-12	10-15	9-15	3-12	3-12

Table 3 Number of samples including krill eggs during the research period, e.g. 2-4 = two out of four samples contained krill eggs. Small eggs were between 0.4 - 0.6 mm and large eggs between 0.6 - 0.75 mm in diameter.

No attempt was made to assign the eggs to species, but all eggs were separated into two size fractions, 0.4 – 0.6 mm and 0.6 – 0.75 mm. The larger size fraction corresponding to the size of *M. norvegica* eggs, while the smaller size fraction most likely are eggs of *T. longcaudata*.

Krill larvae from the two dominating species *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* were by far most abundant at all three stations. Larvae from other krill species were very rare and are not included in the results.
The abundance of krill larvae, including all developmental stages, is shown in (Table 4).

	Faroe		Mid		Scot	
	M. norv.	*T. long.*	*M. norv.*	*T. long.*	*M. norv.*	*T. long.*
May 2001	0.6	2.1	0.2	0.2	-	-
June 2001	12.5	6.0	0.9	1.2	22.9	135
September 2001	1.2	-	-	-	-	-
November 2001	-	-	-	-	-	-
February 2002	-	-	-	-	-	-
July 2002	1.4	4.1	1.0	4.3	1.3	5.6

Table 4. Abundance of *M.* norvegica and *T. longicaudata* larvae at the three stations in the Fareo-Shetland Channel. Numbers are per 1000 m^3.

Krill larvae were only observed during the productive season, in May and June in 2001, and July 2002.
The low numbers of larvae observed in May 2001 were mainly calyptopis and furcilia I and II. These early larval stages are obviously not sampled quantitatively with a mesh size of 1.5 mm. However, their occurrence might indicate relatively high abundances in the water column.

The abundance of larva of both krill species was by far highest in June 2001. Larvae of *T. longicaudata* dominated the samples, especially at station Scot, but the abundance of *M. norvegica* larvae was also relatively high. The krill larvae in June 2001 were dominated by mid/late furcilia stages in both species, but earlier larval stages were also observed.
The krill larvae observed in July 2002 were mainly late furcilia stages, but some earlier larval stages, especially of *T. longicaudata*, were also frequently observed.

Continuous Plankton Recorder (CPR)

CPR data from the Faroe-Shetland Channel during the period 1990-2001 show a marked seasonality in krill abundance (Fig. 9). During winter from December until March krill abundance is generally low, while peak abundances seem to be during early summer and late autumn.

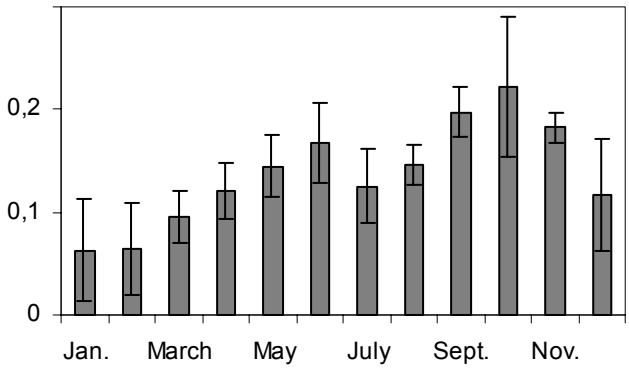


Figure 9. Seasonal abundance of krill in the Faroe-Shetland Channel during the period 1990-2001 obtained from CPR. Vertical lines indicate standard error of the mean.

The CPR data on the seasonal abundance of *Diatoms* in the Faroe Shetland Channel show an increase during March and April, indicating the initiation of the annual phytoplankton spring bloom (Fig. 10). The abundance peaks in May but is relatively high throughout the summer months before decreasing again in September.

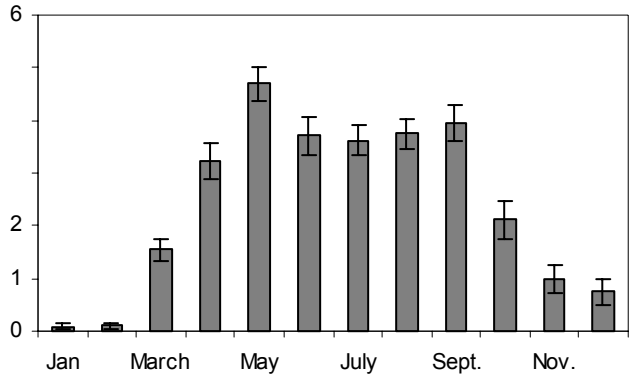


Figure 10. Abundance of *Diatoms* in the Faroe-Shetland Channel based on CPR data from the period 1900-2001. Vertical lines indicate standard error of the mean.

Discussion

The large Nordic krill *Meganyctiphanes norvegica* and the somewhat smaller species *Thysanoessa longicaudata* were by far the most abundant krill species observed during the research period. This is in accordance with findings by other scientists, except for the lack of *Thysanoessa inermis* in our samples (Dalpadado and Skjoldal, 1991; 1996; Dalpadado et al., 1998; Dalpadado, 2006). The most likely reason for this is that *T. inermis* being a neritic species, is usually most numerous in shelf areas, and often associated with relatively cold waters e.g. the Barents Sea (Dalpadado and Skjoldal, 1996; Dalpadado et al., 1998). However, *T. inermis* is also frequently found in oceanic environments like the central Norwegian Sea (Dalpadado et al., 1998)
M. norvegica and *T. longicaudata*, on the other hand, are oceanic species, and according to CPR data these two species are the dominating krill species in the north Atlantic and the Nordic Seas both in numbers and biomass (Lindley, 1978). Our results from the Faroe-Shetland Channel are in agreement with these results showing *M. norvegica* and *T. longicaudata* as the most abundant species, with the former dominating.

Abundance

There were large seasonal variations in krill abundance as well as variations between the three stations during our research period.

The overall abundances of *M. norvegica* and *T. longicaudata* in our study are in accordance with findings elsewhere. Astthorsson and Gislason, (1997), found annual peak abundances of 73 and 62 indv. per $1000m^3$ in the sub-artic waters north of Iceland for *M. norvegica* and *T. longicaudata* respectively, compared to 84 and 68 indv. per $1000m^3$ in our research. The abundance of *M. norvegica* in the Faroe-Shetland Channel were also very similar to those observed by Dalpadado (2006) on the Norwegian shelf, Dalpadado and Skjoldal (1991) in the Barents Sea, and by Buckholz and Boysen-Ennen (1988) in the Kattegat.

Seasonal peaks in krill abundances in the Faroe-Shetland Channel were in November 2001 and July 2002 for the two dominant species *M. norvegica* and *T. longicaudata* as well as for other krill species as a group. This pattern is difficult and complicated to interpret. To some extent it is in accordance with the results from CPR-data in the area, showing peaks in abundance in early summer and late autumn (Fig. 9). Einarson (1945), however, found krill to be most abundant in Faroese waters during late summer, slightly later than we find in our results

However, the low abundances in May and June 2001 in our results are not reflected in the CPR-data from the channel showing high abundance during these months.
A possible explanation for this discrepancy may be that the krill sampled by the continuous plankton recorder might be biased to a certain degree towards smaller individuals and especially krill larvae due to the relatively small entrance aperture on the CPR device. Krill larvae, on the other hand, are not sampled quantitatively in our research due to the relatively large mesh size of the MIK-net. Thus, the increase in abundance from March until June we see in the CPR-data in Fig 9 might to a certain

degree reflect the reproductive activity of the krill, while our results reflect adult abundances.

The large variations in abundance between the stations are difficult to interpret. To some extent these variations could reflect krill behaviour and sampling. Several authors have pointed out that changes and variations in abundance are likely to reflect difficulties in quantitative sampling because of net avoidance as well as patchiness (Hollingshead and Corey, 1974; Falk-Petersen and Hopkins, 1981; Dalpadado and Skjoldal, 1991).

Net avoidance especially concerns large krill, and especially the largest size fraction of *M. norvegica*, which thus probably are under represented in our results.
However, this only affects the large size fraction. The factor that most likely has the greatest influence on variable abundances among the stations is spatial patchiness. Krill are known to form swarms leading to spatial patchiness, and this behaviour makes quantitative sampling very difficult.

Reproduction

Meganyctiphanes norvegica
Several authors have previously pointed out the close relationship between krill spawning and the onset of the phytoplankton spring bloom (Einarson, 1945; Falk-Petersen and Hopkins, 1981; Astthorsson, 1990; Dalpadado and Skjoldal, 1991; 1996; Gislason and Astthorsson, 1995; Dalpadado, 2006).
According to Heath et al. (2000) the phytoplankton spring bloom in the Faroe-Shetland Channel starts in mid April and peaks in mid May, and according to CPR-data from the area the abundance of *Diatoms* increases in March and peaks in May (Fig. 10) supporting the findings by Heath et al. 2000.

Based on this we would therefore expect krill spawning to be intense in May. As indicated in Table 3 and 4, *M. norvegica* eggs and larvae were found in the samples in May at station Faroe and Scot. The presence of eggs in the samples indicates that spawning was taking place at this time, and that some eggs had hatched and developed into krill larvae. Also the data on maturity of the *M. norvegica* population show that almost 100% of the population was mature in May.

The *M. norvegica* larvae found in the May-samples in our research were calyptopis and early furcilia stages. Krill larvae grow in size at each molt from one larval stage to another, and the duration of the intermoult period is inversely proportional to the ambient seawater temperature. Research made by Sameoto (1976) showed that at an ambient seawater temperature of 10ºC, the intermoult period of *Meganyctiphanes norvegica* varies between 4 and 11 days (on average 7.5 days). If we adjust this to the ambient seawater temperature in the Faroe-Shetland Channel in mid May of about 8.5ºC, using a Q_{10} of 1.9-2 typical for simple poikliotheremic animals, it is possible to calculate the time of spawning to be around early April or late March. In addition, due to the absence of later larval stages in the May samples, this is most likely the start of successful spawning by *M. norvegica*. This is in accordance with Einarson (1945), who suggested that spawning by *M. norvegica* in Faroese waters starts in April or possibly in late March.

The 0-group appeared in the length/frequency histograms in June, and by using the same intermoult period as above, the time of spawning can be calculated to be in April. The 0-group in June therefore probably represents the early larval population observed in May, and thus supports the estimated start of successful spawning of *M. norvegica* in the Faroe-Shetland Channel mentioned above.

No *M. norvegica* eggs were found in the samples from June 2001 and the rest of the year. However, some *M. norvegica* larvae were observed in September 2001, indicating that spawning was still occurring during summer. This is also supported by the relatively large fraction of mature individuals in July 2002. These results are in accordance with other results showing the reproductive season of *M. norvegica* to be during spring and summer (Mauchline, 1980), although the main spawning period probably is during April and May (Einarson, 1945; Gislason and Astthorsson, 1995).
The mature individuals observed in July 2002 mostly belong to the 1 and 2-group with only some sporadic individuals from the 0-group. This is also in agreement with results from Icelandic waters (Einarson, 1945) and the Clyde Sea (Mauchline, 1960) and the Passamaquoddy Bay (Hollingshead and Corey, 1974) showing that *M. norvegica* becomes mature at an age of about one year.

Thysanoessa longicaudata
In May 2001 the *T.* longicaudata population consisted of large overwintering animals belonging to the 1-group. There was no sign of an appearance of the 0-group. Just as for *M. norvegica*, we would expect *T. longicaudata* to be spawning at this time considering the relatively high chl *a* concentration.

Eggs and early larval stages of *T. longicaudata* were frequently observed in the samples from May 2001, indicating that spawning had started sometime in April.

As for *M. norvegica* the *T. longicaudata* larva found in the May samples were only calyptopis stages and early furcilia stages. We have not been able to find any data on the duration of the intermoult period for *T. longicaudata* larva, but using the same data as for *M. norvegica* it is possible to estimate the start of successful spawning to be around early/mid April or late March.

There was a striking size difference between *T. longicaudata* males and females in May with the females being significantly larger. This is most likely due to the reproductive status of the *T. longicaudata* females. During the last stages of female maturation just before spawning, the female thorax and the first two abdominal segments swell, as the ovary grows larger, and are still swollen some time after spawning (Everson, 2000). Considering that the length measurements made during our study were made of the thorax, the observed size difference most likely indicates that the *T. longicaudata* females were mature and spawning.
This is also supported in Figure 6 showing that almost 100% of the *T. longicaudata* females were mature in May.
This size difference between the genders was however, not observed in *M. norvegica*.

In June the size difference between males and females of *T. longicaudata* had disappeared. This, together with the lack of krill eggs in the samples, might indicate that females of *T. longicaudata* were not spawning intensively at this time.

In contrast to *M. norvegica* the 0-group of *T. longicaudata* appeared in June only at station Scot, and *T. longicaudata* larvae were also much more numerous at this station compared to the other two stations.
Several possible explanations could be for these deviations, e.g. earlier initiation of successful spawning, higher growth rates, or possible advection from warmer water masses to the south.

The earlier appearance of the 0-group at station Scot could be due to favourable conditions for successful spawning appearing at an earlier time during spring at this station e.g. an earlier start of the spring bloom. Time of spawning has been shown to be closely linked to the phytoplankton spring-bloom (see above). However, this is only on a speculative level due to lack of data during spring and early summer.

However, research by Falk-Petersen et al. (1999) has shown that *T. longicaudata* depends primarily on lipid reserves for spring reproduction. Indeed we also found some *T. longicaudata* eggs in the samples already in late February 2002 at station Scot most likely several weeks prior to the initiation of the annual spring bloom in the area. However, we are not able to tell whether this pre-bloom spawning was successful due to lack of sample during spring and early summer 2002.

The lack of krill larvae in the samples from September 2001, indicates that the reproductive season had ended in about June 2001. However, in July 2002 krill eggs were found in several of the samples at all three stations indicating that the length of the reproductive season most likely varies interannually.

Some sporadic krill eggs were found in the samples from February 2002, indicating that pre-bloom spawning activity probably starts already in late winter. However, considering that in 2001 the 0-group appeared in June, successful spawning does not seem to occur before later in spring in late March/early April.

Males of both the dominant species matured earlier than the females since already in late February about 50% of both the *M. norvegica* and the *T. longicaudata* males were mature. This is in agreement with results from Zelikman (1958), Mauchline (1968) and Dalpadado and Skjoldal (1991) who found that *T. longicaudata* males mature at least one month earlier than the females.

Some scientists have shown *T. longicaudata* to produce two generations during the productive season in some regions of the North Atlantic (Glover, 1952; Lindley, 1978) and in New Zealand (Jillett, 1971). We are, however, not able to tell from our data the number of generation of *T. longicaudata* populations in the Faroe-Shetland Channel. However, we observed mature *T. longicaudata* 0-group females in September 2001, and in July 2002 a relatively large fraction of especially 0-group males were mature, giving a slight indication of a second generation spawned during mid/late summer. This is, however, not reflected in abundance of krill larvae in September 2001, and without samples during the summer months leaves this at speculative level only.

Acoustic backscatter

Seasonal patterns of abundance:
The acoustic backscattering data analysed in the present paper is most likely to be krill, given the frequency of the instruments (150 kHz and 75 kHz), although it is impossible to be absolutely certain about the presence of other zooplankters in the absence of direct in-situ validation. The seasonal patterns of relative acoustic backscattering strength suggest in general lower abundance of animals in spring and higher abundance later in the year.

Diel vertical migration:
The high-frequency variability in the depth of the centre of distribution of weighted average backscattering strength shows a clear diel pattern in most time series. This is entirely consistent with the widely acknowledge view that many zooplankters in general, and krill in particular, perform extensive diel vertical migrations in the water column (Zaret and Suffern, 1976; Bollens and Frost, 1989; Ritz, 2000). To be able to detect such a signal in the context of other important sources of variability (e.g. as a result of physical mixing of the water column) is indicative of the strength and consistency of such behavioural patterns.

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