Zooplankton diversity and the predatory impact by larval and small juvenile fish at the Fisher Banks in the North Sea

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Abstract. The biomass and diversity of the mesozooplankton and fish larvae community were investigated across a frontal zone in the central North Sea in the early summer, to investigate whether larval fish predation is a regulator of mesozooplankton production. Pronounced changes in the mesozooplankton community were observed across the front off the Jutlandic coast. The biomass and the diversity of copepods changed across the front as the population of Calanus finmarchicus became abundant in the deeper water. The crustaceans (Acartia spp. and Evadne spp.) and polychaete larvae dominated the mesozooplankton in the coastal water. The biomass of fish larvae was dominated by gadoid larvae. As in the copepods, a shift in fish diversity was observed in the frontal zone. On the coastal side of the front, whiting (Merlangius merlangus) dominated the biomass, while offshore from the front whiting were absent and cod (Gadus morhua) was the dominant larval fish species on the deeper stations. The present investigation demonstrates two different trophic pathways related to hydrography in the central North Sea. First, in the shallow coastal water, the abundant small neritic copepods are predominately predated by whiting, while in the offshore region the larger oceanic copepods are predated by cod larvae. However, the predation pressure by the fish larvae was in general low (<10%) relative to copepod production per day. Consequently, in the early summer, the copepod production potentially results in a build-up of copepod biomass on both sides of the front.

Introduction

The annual cycle of copepod biomass in temperate waters shows a characteristic unimodal pattern changing from a relatively low winter biomass to a peak in biomass in the late summer. This pattern reflects the integrated response of copepods to seasonality of the environmental factors, e.g. light intensity, water temperature and food availability. Temperature is a key factor for the growth and development rate of the copepod populations. In a recent review, Huntley and Lopez (1992) demonstrated that temperature alone explains 90% of the variation in observed growth rate, and they concluded that temperature, rather than food, is the limiting factor for copepod growth. In contrast, other studies have demonstrated that the egg production in marine copepod communities is strongly food limited during a large part of the year (Dagg, 1977; Checkley, 1980; Durbin et al., 1983; Kiørboe and Nielsen, 1994). This leads to a bimodal seasonal pattern of egg production where peaks in productivity primarily are associated with blooms of larger grazeable phytoplankton species (Kiørboe and Nielsen, 1994).

Few studies have considered the role of mortality in copepod population dynamics; however, significant invertebrate predation or adult cannibalism on copepod eggs, nauplii and smaller copepodite stages has been shown (Jeong, 1994; Peterson and Kimmerer, 1994; Liang and Uye, 1997). Another cause of copepod mortality is the predation by fish larvae, while copepods are the
dominating prey consumed during the early life of most fish species (Lebour, 1920). In limnic and estuarine ecosystems, fish larvae and planktivorous fish have been found to exert significant influence on the biomass and species/size composition of the zooplankton community (Brooks and Dodson, 1965; Fulton, 1984; Hansson et al., 1990). However, in open marine ecosystems, where the diversity is higher (Remane, 1934), and the food web is more complex, less information on the potential top-down effect of predation by planktivorous fish and fish larvae is available.

Copepod species and size composition show significant seasonal and geographical variation. The abundance of some species peaks in the spring, others peak in the autumn, while the abundance of others is more constant through time. Variation in the species/size composition of copepods influences their availability for fish larvae, with both size and species composition being important factors influencing larval prey preference (Munk, 1997). Spatial and temporal variation in copepod abundance would be expected to influence fish spawning behaviour and thereby the species/size composition of the given fish larvae community (match between larvae and prey; Cushing, 1972).

In the North Sea, the copepod communities show pronounced regional differences in biomass and species composition. These variations are often related to the bathymetry and hydrography of the area. In the coastal, relatively shallow areas, copepod communities are dominated by small neritic species (e.g. Acartia spp., Temora longiremis), while Calanus spp. and Pseudocalanus spp. are the dominant species in deeper areas influenced by influx of North Atlantic Water (Fransz et al., 1991; Hay et al., 1991; Nielsen and Sabatini, 1996).

In the month of September, Munk and Nielsen (1994) conducted a study close to the annual peak in copepod biomass. Owing to low phytoplankton biomass and production, the copepod production was relatively low. The results of this study indicated that the fish larval community would be able to graze down the daily copepod production at that time of the year. The present investigation was carried out in June during a period when the copepod egg production was high and the population was building up. Other trophic relationships would be expected during this period of increasing copepod biomass.

The present investigation was conducted in the southern North Sea across the shelf break off the Jutlandic coast (Figure 1). We hypothesize that different hydrographic regimes would lead to the development of different pelagic communities, evident at the higher trophic levels, e.g. copepods and fish. We examine the diversity of the larval fish and mesozooplankton communities across the area of a coastal front, and evaluate the grazing impact of larval and juvenile fish on the copepod community.

Method

Study site

The study was conducted during a cruise in the North Sea from 22 May to 3 June 1992 on the RV 'Dana' (Danish Food, Agriculture and Fisheries Ministry). Sampling was concentrated along two transects passing the Fisher Bank Area.
Predatory impact by larval fish

Fig. 1. Positions of stations along the two transects. Open circles indicate stations where only fish larvae were sampled; dark squares represent stations where larval abundance, copepod biomass and production were measured.

(Figure 1). The station-to-station distance was 10 km, and a total of 11 and 26 stations were sampled for zooplankton and fish larvae, respectively. The study considers a part of the findings during the cruise and further information on hydrography, nutrient dynamics, primary production and structure of the copepod community is published in Richardson et al. (1998) and Nielsen and Sabatini (1996).
Hydrography and phytoplankton

Depth profiles of salinity and temperature were recorded at 0.5 m intervals throughout the water column using a Neil Brown Mark III CTD system. The chlorophyll a fluorescence was recorded using a Q-instrument fluorometer (Hundahl and Holck, 1980) mounted on the CTD system. Samples for calibration of the salinity and fluorescence probe were taken at various depths covering the area. The chlorophyll a concentration of the samples was measured according to Strickland and Parsons (1972), and a linear regression was calculated between fluorescence and the measured chlorophyll a concentration.

Mesozooplankton composition, biomass and production

Mesozooplankton samples were collected by a submersible pump filtering 1.2 m³ min⁻¹ into a conical net of 30 µm mesh size. The pump was raised from the bottom to the surface at a speed of 10 m min⁻¹ during sampling. The samples were preserved in 2% buffered formalin. The zooplankton in subsamples (1/8 or 1/16 of the sample) were identified and counted. Four hundred copepods from the subsample were measured for length (within intervals of 20 µm) and classified as nauplii, copepodites, males and females. The copepod biomass was calculated using estimates of abundance and lengths and length–weight regressions for each species. The regressions were found in the literature: Acartia spp. (Berggreen et al., 1988), Centropages spp., Pseudocalanus and Temora longicornis (Klein Breteler et al., 1982), Paracalanus parvus (Cohen and Lough, 1981), Calanus spp. (Bottrell and Robins, 1984), Oithona spp. (Sabatini and Kiørboe, 1994). The biomasses of Metridia lucens and Microcalanus were calculated from the length–weight regressions for Calanus and Acartia, respectively. Dry weight was converted to carbon by a conversion factor of 45% (Kiørboe et al., 1985). The biomass of non-copepod zooplankters was calculated from abundance and length measurements of a subsample of 50 individuals from each taxon. Length–weight regressions were taken from the literature: Cladocera (Kankaala and Johansson, 1986), Polychaeta (Hansen, 1993), Bivalvia (Jespersen and Olsen, 1982) and Gastropoda (Hansen and Ockelmann, 1991).

Copepod egg production was estimated from incubation of females of the calanoid species. The production of the egg-carrying cyclopoid species was calculated from the temperature-dependent hatching rates and egg/female ratios, following the procedure described in Nielsen and Sabatini (1996). Total copepod production was then estimated from the specific egg production rate (SEP) and the depth-integrated biomass, assuming that SEP of the females corresponds to juvenile growth rates (Berggreen et al., 1988). The production of copepods from five selected stations is summarized in Table I; only P. parvus and Oithona similis were sufficiently abundant to allow egg production rate estimates on all stations. Calanus finmarchicus females were only abundant on the offshore side of the front; thus, the production on the remaining stations was estimated from the average Calanus egg production measured offshore. Acartia spp. were most abundant along transect C, while measurements of egg production of the other species were more scattered over the area investigated. For those species where no
<table>
<thead>
<tr>
<th>Zooplankton biomass (mg C m⁻²)</th>
<th>Trans C frontal</th>
<th>Trans B frontal</th>
<th>Zooplankton production (mg C m⁻² day⁻¹)</th>
<th>Trans C frontal</th>
<th>Trans B frontal</th>
<th>Cladocera</th>
<th>Zooplankton size classes</th>
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<td>Temora</td>
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<td>Oithona</td>
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fecundity measurements were made, the average egg production of the other small calanoid species was applied (i.e. excluding *Calanus* and *Oithona*). The production of the size classes of the copepod community presented in Table I was calculated as the biomass in the size class multiplied by the average of all species on the station. The production of the cladoceran *Evadne* spp. was estimated by assuming a specific production rate of 10% day\(^{-1}\).

**Distribution, growth and prey consumption of fish larvae**

Larval and juvenile fish were collected at night by oblique hauls sampling the water column to 5 m above the bottom. A large ring net was utilized following the handling procedures described in Munk (1988). This gear has an opening of 2 m diameter and a black net of mesh size 1.6 mm. It was hauled at a speed of 1.5 m s\(^{-1}\), with a calibrated flowmeter in the opening of the net determining the volume filtered. This gear has a good catchability of 1–3 cm larvae/juveniles at night (Munk, 1993).

After retrieval of the net, samples were immediately sorted for all fish. These were preserved in 96% ethanol, and later identified to species and measured for length within 0.5 mm intervals. Numbers per square metre were calculated based on numbers caught, volume filtered and water depth.

Length–weight relationships were estimated for the dominating species of fish larvae using the following procedure. Approximately 40 specimens of each species were measured for length and dried at 50° C for 24 h, and held in a desiccator until weighed on a microbalance. A length–weight relationship for both preserved and unpreserved larvae was established for cod and long rough dab, all other larvae were used in the preserved conditions only. The relationship weight = \(a \times \text{length}^b\) was used, and linear regressions were calculated using log-transformed data of length and weight. The estimates of weight loss due to preservation for long rough dab (20%) were used to convert weights of the flatfish species to weights before preservation, while the weight loss estimated for cod (18%) was used in the conversion of weights of all other species. Larval/juvenile abundance estimates were converted to biomass at each station using these length–weight relationships and the given length distribution of fish at each station. Dry weight estimates of larvae were finally converted to carbon weight using a factor of 45% (Kjørboe et al., 1987).

The relative amount of each copepod species eaten by a given larval fish species was estimated within a specified area. Size-representative subsamples of each species of fish larvae were taken from the area and all identifiable prey items in the guts were determined. It should be noted that potential prey without large hard structures, e.g. polychaete larvae, were probably underestimated/neglected in the analyses of the stomach contents due to rapid digestion. All measurable prey items were measured for length within 20 μm intervals. Based on the prey length measurements, the biomass of each prey species was estimated and this was related to the total prey biomass in the guts. The ingestion of copepods by the fish larvae was found assuming that 33% of the body weight was ingested per day. This estimate is based on an assumed mean specific growth rate of 0.1
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(P. Munk, unpublished results) and a gross growth efficiency of 0.3 (Houde, 1989). Finally, the total ingestion was estimated from larval biomass estimates and distributed into zooplankton species (or size) levels using the relative proportions of these in the gut.

Results

Hydrography and phytoplankton

Stable weather conditions with high solar insolation and low wind led to a strong stratification of the upper water column where a pronounced thermocline was observed at 10–15 m depth which separated 12°C surface water from 7°C bottom water. The water column was almost isothealine, as observed along the transects. However, at the inshore part of transect C, we observed a decrease in salinity; apparently, this was due to the Jutlandic Coastal Current which extended offshore due to easterly/southerly winds (Figure 2).

Surface values of chlorophyll $a$ were low (0.1–0.5 $\mu$g Chl $a$ l$^{-1}$), and we observed subsurface phytoplankton maxima on all stations. The peak in phytoplankton abundance was observed either as high values of chlorophyll associated with bottom fronts (transects B and C) or as a chlorophyll peak just below the pycnocline. The latter observation was associated with the spreading of water from the Jutlandic coastal water offshore, in the coastal part of transect C. Subsurface phytoplankton peaks also led to high integrated chlorophyll $a$ values observed on transect C (on the coastal side of the front) and on transect B (at 50 km offshore) (Figure 3).

Copepods

Ten species of copepods dominated the mesozooplankton biomass; they contributed 73–97% (88 ± 8%, mean ± SD) of the total mesozooplankton biomass, except on the inshore side of transect C which was influenced by coastal fresh water. In this region, copepods only contributed 49–54% (51 ± 2%, mean ± SD), while cladocerans and polychaetes increased in importance. The species $C$. finmarchicus, $P$. elongata, $O$. similis and $A$. spp. were most important, except on the Dogger Bank at the southern part of transect B, where $T$. longiremis contributed with 60% of the biomass. The copepod biomass along transect B varied between 500 and 4500 mg C m$^{-2}$. The peak biomass was associated with high concentrations of Calanus in the bottom water in central parts of this transect. This Calanus patch was also observed during a cruise 3 weeks earlier (Munk et al., 1995).

A quantitative and qualitative shift in the copepod community was observed along transect C. On the coastal, less saline side of the front, $A$. spp. dominated, constituting 83% of the integrated copepod biomass; offshore, $C$. finmarchicus and $P$. elongatus comprised 80% of the biomass (Figure 3). The change in the species composition of copepods led to a change in the copepod size distribution along the transects (Figure 4). On the coastal side of the front, most of the copepods were smaller than 1000 $\mu$m, but following the appearance
Fig. 2. Vertical distribution of density (lines: kg m$^{-3}$ (1000)) and phytoplankton biomass (shading; chlorophyll a ug l$^{-1}$; NB not linear scale) along the two transects; distances between stations are 10 km.
Predatory impact by larval fish

Fig. 3. Integrated biomass of zooplankton (mg C m$^{-2}$) and chlorophyll a (mg Chl a m$^{-2}$) along the two transects. The upper panel shows the biomass of *Calanus* spp., the middle the biomass of smaller copepod species and the lower the biomass of non-copepod zooplankton.

of *Calanus*, further offshore, a significant fraction of the copepod biomass was observed in the larger size classes. Associated with this shift in community structure, the average biomass doubled from ~500 to ~1000 mg C m$^{-2}$, primarily due to the high biomass of *C. finmarchicus*. 

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Mollusc larvae (Bivalvia) were the most important non-copepod mesozooplankton along both transects (Figure 3). A shift in the species composition and relative importance of non-copepods to the mesozooplankton biomass was associated with the change in water column characteristics along transect C. In the less saline coastal water, polychaete larvae and cladocerans (Evadne spp.) dominated the non-copepod fraction, with these groups constituting half of the mesozooplankton biomass (48 ± 2% of the biomass) (Figure 3).

**Copepod production**

The egg production of small calanoids was relatively high at the deeper stations north of the Dogger Bank. Along transect C, a pronounced increase in the egg production rate of the small calanoids was seen in association with the front (Nielsen and Sabatini, 1996). In contrast, the egg production rate of Oithona spp. was lower and more stable across the hydrographic discontinuities (Nielsen and Sabatini, 1996).

Despite the high egg production rate on the coastal part of transect C, the absolute production was highest on the deep stations north of the bank area and on the offshore part of transect C. That was due to the high biomasses of Calanus and Pseudocalanus found here (Figure 3, Table I). Non-copepod zooplankton contributed significantly to the production only on the coastal side of the front with the contribution of the cladoceran Evadne estimated to be 22% of the total zooplankton production (Table I) in this region.

**Species composition and abundance of larval and small juvenile fish**

Seven species of fish larvae were caught in significant numbers, i.e. these species constituted >99% of larval fish by numbers. The species include: cod (Gadus
Predatory impact by larval fish

morhua), whiting (Merlangius merlangus), Norway pout (Trisopterus esmarkii), sandeel (Ammodytes sp.), crystal goby (Crystallogobius sp.), long rough dab (Hippoglossoides platessoides) and dab (Limanda limanda). Figure 5 illustrates the abundance of fish larvae along the transect. The two flatfish species were the most numerous, we often observed flatfish densities (both species) of >1 m². Densities of the flatfish were low at the outermost stations along the transects; however, there was no apparent trend in the abundance of these species. Conversely, gadoid species showed marked changes in relative and absolute abundance along transects. On transect B, cod dominated (reaching a maximum in abundance at the 80 km distance), with few whiting and Norway pout caught. On transect C, whiting dominated in the shallow coastal region, 50 km offshore cod and Norway pout appeared in the samples, with the relative importance of whiting decreasing. Further offshore, maximal gadoid (cod) abundance was found in the area 80 km offshore, in the frontal zone. The two other species, sandeel and crystal goby, were caught sporadically (highest densities at transect B).

Fig. 5. Integrated abundance of fish larvae (number m⁻²) along the two transects. The upper panel shows the gadoid species and the lower shows the abundance of non-gadoid species. The group Hippog./Limanda includes small individuals that was not possible to identify to species.
The mean sizes of all fish species are given in Table II. Except for long rough
dab and dab, which showed a 40% increase in mean length from the innermost
to the outermost stations along transect B, no significant change in mean lengths
along the transect was apparent. Consequently, the change in biomass of larvae
along transects (Figure 6) followed the change in abundance (Figure 5). The
importance of the relatively small flatfish declined, while the larger sized species
increased in importance.

Prey consumption by fish larvae

Consumption of zooplankton by the total fish larvae community and the predation
pressure on dominating groups and size classes of copepods in five sections
are summarized in Table I and Figure 7. In general, the absolute food intake by
the larvae was highest on the deeper stations where the highest biomass of larval
fish occurred, i.e. the outer frontal station on transect C and the frontal station
on transect B. This last station is included in this comparison in order to get an
impression of the potential grazing where the highest biomass of fish larvae was
observed (Figure 6). On the illustrated stations, especially Calanus and Temora,
and Pseudo/Paracalanus contributed significantly to the larval fish diet. This
pattern is also evident when larval prey are divided into size classes; here, the
absolute grazing was most pronounced on the larger size classes which include
the previously mentioned species. In the coastal area where Calanus was rare,
Acartia and the cladoceran Evadne contributed significantly to the larval fish diet.
The decline in abundance of Calanus was also evident in the size distribution of
the prey, with the size classes 700-1120 μm as the most abundant in stomach
samples. In general, the grazing pressure (expressed as a percentage of the
copepod production grazed by the fish larvae community per day) was low (<10%
day-1). The highest accumulated predation pressure ('total' predation pressures
in Table I) was observed at the frontal stations along transect C, grazing pressure
being markedly lower on the coastal side of the front. It should be noted that in
some cases the predation was significantly higher than the daily production; on
the outer frontal station, especially, the grazing pressure on some species (Temora

| Table II. Mean length ± SD (mm) of the dominating fish larvae along the two transects. The group HippogLiLimanda includes small individuals that was not possible to identify to species |
|-----------------|---------|-----------------|---------|---------|
| Species         | Transect B |               | Transect C |               |
|                 | Mean     | SD   | Mean     | SD   |
| Gadus           | 25.2     | 2.5  | 28.0     | 3.5  |
| Trisopterus     | 14.5     | 8.5  | 16.6     | 4.4  |
| Merlangius      | 18.1     | 3.4  | 22.2     | 4.5  |
| Hipoglossoides  | 12.1     | 3.0  | 12.8     | 2.9  |
| Limanda         | 12.0     | 1.1  | 13.3     | 2.2  |
| HippogLiLimanda | 9.0      | 0.7  | 9.1      | 1.8  |
| Pleuronectes    | 13.3     | 0.7  |          |      |
| Ammodytes       | 38.8     | 7.1  | 32.1     | 11.9 |
| Crystallogobius | 26.6     | 2.9  | 25.5     | 3.2  |
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Fig. 6. Integrated biomass of fish larvae (mg C m$^{-2}$) along the two transects. The upper panel shows the gadoid species and the lower shows the biomass of non-gadoid species. The group *Hippoglossidae/Limanda* includes small individuals that was not possible to identify to species.

and *Acartia*) exceeds the daily production, due to the low production rate measured here. A high grazing pressure was also observed on *Temora* at the inner coastal station, primarily due to the low biomass. If the species composition of the copepod community is ignored and the grazing pressure is evaluated with respect to copepod size (right part of Table I), the predation pressure never exceeds the daily production (highest value 36% of the production per day).

**Discussion**

*Hydrography*

This investigation was conducted in the central part of the North Sea in the region between the shallow southern Bight and the deeper northern part which is influenced by water of Atlantic origin. The water depth in this area varies between 40 and 100 m, except on the shallow part of the Dogger Bank and along the Jutlandic west coast. During the summer, the salinity of the water in the central North Sea is relatively constant and the stratification of the water
column is primarily governed by temperature differences. The calm sunny weather during the present study caused the establishment of a very strong thermocline at 10 m depth (Figure 2). Along the Jutlandic coast, water from the less saline Jutland Coastal Current spreads over the more saline bottom water, intensifying the stratification in this region (Figure 2A). Along the eastern, southern, and western border of the central North Sea, a frontal zone is found where stratified water from the central part of the North Sea meets the mixed water in the bank area and the shallow coast (Holligan et al., 1989). The exact position and type of the fronts are primarily determined by bathymetry. Bo Pedersen (1994) defines two types of fronts in the Central North Sea: (i) surface fronts which develop in areas where tidal mixing dominates over wind stress, i.e. the western part of the central North Sea; (ii) bottom fronts which occur where wind mixing dominates, i.e. the shallow southern and eastern part of the central North Sea. The bottom fronts are identified as fronts where the strongest cross-frontal gradients are encountered in the bottom water (Bo Pedersen, 1994). The
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The present investigation is concentrated along transects across the coastal front (transect C) and the front at the edge of the Dogger Bank (transect B). Because of the calm weather, the front structure was very weak, even the shallow water over the Dogger Bank was stratified, but a bottom front 50 km offshore on transect B and on the northern slope of the Dogger Bank was identified (Figure 2). We observed enhanced phytoplankton biomass in association with the bottom fronts (Figure 3).

Plankton communities

The frontal zones are known to be sites of enhanced biological production. On the northern slope of Dogger Bank, Munk and Nielsen (1994) demonstrated that biomass and activities of all trophic levels from phytoplankton to fish larvae peaked in the frontal zone. The hydrography in frontal zones also plays a key role in the shaping of pelagic ecosystems as horizontal dispersion of plankton organisms is restricted across fronts (Cowen et al., 1993). In addition, the frontal zone in the study area is a site where different water masses and pelagic communities meet. Here, the north Atlantic fauna meets the neritic plankton community from the southern Bight (Fransz et al., 1991).

The horizontal distribution of mesozooplankton (Figure 3) and fish larvae (Figures 5 and 6) observed during this investigation shows the presence of two different communities, separated by the bottom front observed ~50 km offshore on transect C. On the coastal side of the front, the zooplankton community was dominated by small neritic copepod species (especially Acartia spp.), the cladoceran Evadne spp. and polychaete larvae. Here the most important fish larval species was whiting (M. merlangus), which dominated the biomass of fish larvae. Across the front, the copepod and fish larval communities changed. The copepod biomass increased as Calanus became abundant offshore of the front, and Evadne and the polychaetes disappeared. The non-copepod part of the mesozooplankton was totally changed to dominance by bivalve and gastropod larvae. The biomass of the fish larvae community increased in the frontal zone, and the species composition changed across the front, as was also the case for the copepod community. Outside the front, cod (G. morhua) dominated the gadoid larvae and the abundance of whiting decreased. Compared with the gadoids, the other fish species were more evenly distributed across the frontal zone.

The observed change in diversity and biomass of the mesozooplankton across the front is primarily caused by a combination of hydrography and the life strategy of the copepods, the small neritic species (Acartia spp., T. longicornis and Evadne spp.) on the shallow coastal side of the front have a life strategy including the production of resting eggs that overwinter on the bottom (Madhupratap et al., 1996). The establishment of a significant biomass of these species requires time to develop after the spring bloom and the biomass of the neritic species peaks in the late summer July–August (Fransz et al., 1991; Kiørboe and Nielsen, 1994). In the Atlantic-influenced water, Calanus dominates the biomass (Williams and Lindley, 1980). A large fraction of the Calanus population is brought to the North Sea as adults from the overwintering areas at the shelf off
the northern North Sea (Norwegian Sea) in the spring (Krause and Thrams, 1983; Backhaus et al., 1994). The residual circulation of the North Sea distributes them over the region, where they graze, grow and reproduce during the spring and summer months proper (Krause and Thrams, 1983). In May–June, the two communities meet in the frontal zone in the central North Sea. Analyses of data from three cruises in the central North Sea (Nielsen et al., 1993; Munk and Nielsen, 1994; and the present study) support the observed shift in the copepod community across the frontal zone. At water depths of <40 m, *Calanus* only contributes with 10% of the copepod biomass, while the biomass contribution increases to >40% outside the 40 m curve.

The observed separation of cod and whiting larvae indicates that spawning and the early drift of eggs and larvae of these species have taken place in different water masses. Limited information is available on the spawning grounds and dispersion pattern of the gadoid eggs and larvae in the North Sea. However, indications of a separation in spawning areas, with whiting spawning more coastal than cod, can be seen in the egg distribution patterns shown in Damas (1909), van der Land (1990) and van der Land et al. (1990). The cod larvae caught offshore of the front probably originate from a spawning stock off Dogger Bank (Graham et al., 1925). The observed distribution pattern with the highest abundance of cod in the frontal region along the coast corresponds to the pattern described by Graham et al. (1925) in June.

The observations on distribution patterns suggest the presence of two different food chains, responsible for the energy transfer from zooplankton to fish larvae on each side of the coastal front along the Jutland coast: (i) small neritic copepods → whiting in the coastal water; (ii) large oceanic copepods → cod in the deeper areas.

### Grazing impact in the two systems

Model considerations indicate that larval fish either are a significant source of mortality of marine zooplankton populations (Davis, 1984; Bollens, 1988) or that fish larvae in their early life are too dilute to affect their food (Cushing, 1983). Analysis of biomass data covering a 15 year period off the Northumberland coast led to the conclusion that predation was probably the most plausible explanation for the autumn decline in the copepod population (Roff et al., 1988). However, investigations based on simultaneous sampling and measurements of copepod and fish larvae biomass and production information are very limited.

Large seasonal and horizontal variation in grazing pressure on copepods must be expected, since fish larvae are patchily distributed. The present analysis of stomach contents of the fish larvae indicates the presence of two trophic pathways in the area investigated (Table I and Figure 7). In the coastal area, whiting was responsible for 73% of the predation on the zooplankton, compared with the frontal zone where cod, the primary larval predator, was responsible for 40% of the predation. The stomach contents of the fish larvae reflected the different zooplankton communities; *Eudone, ParalPseudo, Acartia* and *Temora* were the most important prey items on the shallow stations, while *Calanus* was the key
Predatory impact by larval fish

prey in the frontal zone followed by Temora, Para/Pseudo, Acartia. The maximal grazing pressure on the zooplankton by non-gadoid species during the investigation was seen at 30 km along transect B (4% of daily production). Here, larval biomass was dominated by Ammodytes, Hippoglosoides, Limanda and Crystallogobius; of these, Ammodytes was the predator of prime importance preying on Calanus and Temora. In general, grazing pressure was low: 1-4% and 7-9% of the daily production in the coastal and frontal zone, respectively. Thus, the predation by larvae and small juveniles (in the size range represented by our catch, of ~1-3 cm standard lengths) was insignificant for the development of the zooplankton population in the early summer in all of the hydrographic regions studied.

This study only considers larval fish predation on the zooplankton. The abundance of invertebrate predators that are known as important copepod grazers, e.g. chaetognaths, ctenophores and medusae (Roff et al., 1988), was, however, very low (T.G.Nielsen, unpublished results), and the impact of these organisms is assumed to be insignificant in the present case. Other potential predators are planktivorous fish (e.g. adult sandeel, herring) known to be abundant in the area (Daan et al., 1990). We do not have data available for an estimation of this predation; however, schools of planktivorous fish may potentially have a significant impact on the population dynamics of copepods, as demonstrated for other marine areas (Hassel, 1986; Hassel et al., 1991). In the Baltic, predation from adult herring and mysid shrimps is probably responsible for the autumn decline observed in the zooplankton biomass (Johansson, 1992).

The effect of larval predation on the annual zooplankton cycle

If fish larvae are the main predators on the mesozooplankton, the overall predation only amounts to <10% of the daily copepod production in the early summer (Table I). This low estimate of grazing impact is in accordance with the seasonal development of the North Sea copepod community, where the biomass of the copepod community show an approximately exponential growth in the early summer (Roff et al., 1988; Frantz et al., 1991). Investigations conducted in the same area in the late summer (August–September) (Munk and Nielsen, 1994), when the copepod population had started the autumn decline in biomass (Roff et al., 1988; Fransz et al., 1991), showed that larval predation was the same order of magnitude as the production of the copepod community (3–4% of the biomass per day). When predation by adult planktivorous fish and invertebrates was included, the decline in the copepod biomass could be explained by the total predation pressure.

The present investigation suggests that the frontal zones along the southern and western border of the central North Sea are biological ‘hot spots’. Within short distances, not only the productivity, but also the structure and diversity at the higher trophic levels in the pelagic food web change significantly. If the production within these important areas is to be fully understood, the changes in the trophic pathways (especially between copepod and larval fish) across the hydrodynamic discontinuities should be considered thoroughly.
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References


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168, 197–211.
the Northumberland coast: Productivity of small copepods and analysis of trophic interactions. J.
Board Can., 167, 1–310.
van der Land,M.A., Heessen,H.I.J. and Rijnsdorph (1990) The result of the 1989 egg surveys for cod
and plaice. ICES CM 1990/G:27.

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