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Differences in vertical and horizontal distribution of fish larvae and zooplankton, related to hydrography

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Running head: Vertical distribution of fish larvae in the North Sea.
Abstract

Planktonic fish larvae have little influence on their horizontal distribution, while they are able to control their vertical position in the water column. While prey and light are among the factors with an apparent influence on the vertical distribution, the effects of other factors are less clear. Notably, distributional differences between larvae of different fish species are poorly understood. Information on the horizontal distribution of larvae of 27 species and the vertical distribution of seven species of Gadidae, two Pleuronectidae and one Scopthalmidae, was compiled from one survey in the northern North Sea. Horizontally, fish larvae aggregated near frontal structures, correlating with high densities of zooplankton. Increasing length and decreasing numbers indicated an origin in the western North Sea, followed by an eastward drift. Vertically, the different species exhibited similarities but also notable differences in their vertical distribution. Most gadoid species aggregated in the upper (<40 m) or middle water column (>40 m) during the day with an increase in abundance at shallower depths during the night, while all flatfish were distributed at greater depths under all light conditions. Hence, larvae differed in their distributional patterns, but the relative depth distributions among the species in the larval community generally remained constant.

Keywords: Fish larvae, Gadidae, Flatfish, Vertical distribution, North Sea
Introduction

Compared to current speeds the swimming ability of fish larvae is of minor importance, limiting their capability to influence their location by horizontal swimming. However, larvae can migrate vertically in the water column and so influence their horizontal transport, as current speed and direction often changes with depth (Fortier & Leggett 1983; Sclafani et al. 1993). Vertical migration patterns of fish larvae can be broadly classified into three categories: i) type I migrations as upward movement at the beginning of night and downward movement at the beginning of day; ii) type II as the opposite (Neilson & Perry 1990) and iii) a pattern of aggregation during the day and dispersal throughout the night (Gray 1998; Leis 1991; Olivar & Sabatés 1997). Exogenous factors that influence the observed patterns are, for example, light, prey and predator distribution, as well as effects of temperature and salinity.

Individuals of given species and congeneres often exhibit similar distribution patterns, regardless of the prevailing environmental conditions and form distinct assemblages in different depth strata (Gray & Kingsford 2003; Olivar & Sabatés 1997; Röpke 1993; Southward & Barrett 1983). Size and consequently swimming ability, important for determining vertical distribution, changes throughout development and many species exhibit different vertical behaviours as the larvae develop (c. f. Table 1; Neilson & Perry 1990). Lough and Potter (1993) observed the initiation of vertical migration in cod (Gadus morhua Linnaeus, 1758) and haddock (Melanogrammus aeglefinus Linnaeus, 1758) at standard lengths (SL) of 6-8 mm, and a firmly established type I migration at lengths greater than 9 mm SL. Smaller larvae and particularly those in poor condition may be more strongly influenced by buoyancy (Sclafani et al. 1993). However, even in their earliest stages, larvae will migrate if unfavourable conditions make it necessary (Grønkjær & Wieland 1997). The influence of hydrography, in particular the position of the thermocline, is less clear. Some studies indicate a connection between larval distributions and the thermocline for certain taxa.
(Olivar & Sabatés 1997) and/or size classes (Lough et al. 1996; Lough & Potter 1993), while others show the same distributional patterns, both of single taxa and larval assemblages, irrespective of water column stratification (Gray 1998; Gray & Kingsford 2003). Gray and Kingsford (2003) attributed their failure to find a relationship between distributions and the thermocline, to a combination of the gradual and ephemeral character of thermoclines in their study region and the lag-phase between the occurrence of hydrographic cues and the reaction of the larvae.

The influence of prey and predator distributions was pointed out by Pearre (1973) who, based on his studies of an arrow worm *Sagitta elegans* (Verrill, 1873), introduced the hunger-satiation hypothesis. In this case vertical movements were related to the concurrent needs of feeding in the upper water column and hiding from visual predators at greater depths. The hypothesis was later applied to other planktonic organisms, including fish larvae (Pearre 2003). Visually hunting fish larvae can follow different strategies to satisfy these needs. They may rise in the water column at night, together with their zooplankton prey or may stay deeper and feed on vertically migrating prey (Lovetskaya 1953). Neilson and Perry (1990) suggested a feeding/avoidance window at dusk and dawn, when light conditions are sufficient for feeding but predators may still be at greater depths. The influence of light differs among species. Some species appear to select a specific isolume, which primarily governs their vertical distribution (Woodhead 1966). This has been suggested as the cause of aggregations during the day and diffuse distribution during the night when the primary cue is missing (Leis 1991). However, the effect of light is species specific as has been shown in concurrent laboratory studies (Catalán et al. 2011; Vollset et al., in press), for example some species are shown to be adapted to low illumination (e.g. Downing & Litvak 2001; Huse 1994; Yoon et al. 2010).
Statistical models of the vertical distribution of different taxa have high predictive power with several interacting factors (Hernandez et al. 2009) and even when only using a single factor (Huebert et al. 2010). Control by a single factor is, however, rare. While prey abundance was one controlling factor for mesopelagic larvae in the Arabian Sea (Röpke 1993) and for *Sardinella aurita* (Valenciennes, 1847) in the northwestern Mediterranean Sea (Sabatés et al. 2008), the fish species were also limited by physical factors. The mesopelagic species were limited by a warm mixed layer above, and *S. aurita* most likely by the cool (ca. 15°C) water below the pycnocline. The vertical distribution of larvae will influence horizontal transport, as different currents at different depths might lead to retention within or a displacement out of an area (Fortier & Leggett 1982; Fortier & Leggett 1983; Govoni & Pietrafesa 1994) and several studies have shown aggregations of fish larvae in or near fronts (Kiørboe et al. 1988; Munk et al. 2002; Sabatés 1990). Likewise, food availability, the relationship between illumination and prey abundance, is correlated with the distribution of Baltic cod larvae (Grønkjær & Wieland 1997).

Considering the apparent species differences in vertical distributions and migrations, a comparative approach might elucidate the factors that are of prime importance. Few studies have analysed the distributional patterns of a wide range of species in a comparative way (Frank et al. 1992; Gray 1996; Gray & Kingsford 2003). Such an opportunity was available in the northern North Sea in 2010. The area east of the Shetland Isles is particularly species rich (Economou 1987) with an assemblage primarily consisting of Gadidae, Lotidae, Pleuronectidae and Scophthalmidae. In regard to abundance, the dominant species were whiting, ling (*Molva molva*, Linnaeus, 1758), Norway redfish (*Sebastes viviparus*, Krøyer, 1845) and Norway pout. It is an important spawning ground for several fish species which spawn in spring and we were able to describe both the major horizontal distributional patterns from transects of stations, and the vertical patterns by vertical stratified sampling over an 18
hour period. In this contribution we focus on the distributional patterns of larval fish in relation to hydrography and in relation to the distribution of zooplankton 180 - 1000 µm. We hypothesize that relative to each other larvae of different species would retain their position in the water column.

Materials and Methods

Field sampling

Sampling was undertaken on the RV G.O. Sars (IMR, Bergen, Norway), between 25th April and 5th of May 2010, covering transects between 59.3 and 60.75°N (Figure 1). Five additional stations were sampled over the course of 18 hours in a 5 x 5 nautical miles (NM) sized area (designated 18h-station) east of the Shetland Islands.

Depth integrated samples were taken in double oblique hauls with a 76 cm diameter GULF VII high speed sampler (Nash et al. 1998), down to about 100 m depth. The sampler was equipped with a mechanical flow meter (General Oceanics, USA) in the mouth of the nose cone. A SCANMAR depth sensor was attached to the sampler and provided both depth and temperature measurements. For discrete depth sampling, a MOCNESS (Wiebe et al. 1985) with a 1 m² opening and 4 nets (180 µm mesh) was deployed to ca. 100 m and then hauled obliquely to the surface, sampling the water column in strata with nets opening at about 100, 75, 40 and 20 m. Flow meters and a CTD were attached to the MOCNESS and the filtered volume (m³) estimated for each stratum. Larvae were sorted on board and were preserved in borax buffered 4% formaldehyde. Zooplankton was split in two fractions before preservation, using a Motoda splitting device. One half was preserved for identification and enumeration whilst the other half was size fractioned into <1000 µm, 1000-2000 µm and >2000 µm.
samples. Each size fraction was dried at 60°C to constant weight in order to obtain dry weights, which were converted to milligrams dry weight per m$^3$ (mg DW m$^{-3}$) based on the volume of water filtered and to g DW m$^{-2}$ based on filtered volume and sampled depth.

**Laboratory procedures**

The preserved larvae were cleaned of formalin under running water for 10-15 minutes. All larvae were then identified to the lowest taxonomic level, using either Russell (1976), Schmidt (1906) or Munk and Nielsen (2005). Standard length (SL; tip of the snout to the end of the notochord) was measured to the nearest 0.1 mm with an ocular micrometer. To correct for shrinking, live SL was calculated using the equation from Bolz and Lough (1984), after correcting for formalin shrinkage (Theilacker 1980).

**Data treatment and analysis**

Density anomaly ($\sigma_t$) was calculated according to UN standards (Millero & Poisson 1981) from temperature and salinity measured by CTD casts during the transects. The vertical profiles of calculated densities were interpolated on a regular grid (0.5° x 5 m) with kriging in Surfer 8 (Golden Software 2002), while contour plots were constructed in Sigmaplot 12 (Systat Software 2011). The vertical profiles for the five hauls at the 18h-station are given as line graphs.

For each species in the depth integrated hauls, the catch was converted to nos. m$^{-2}$ by dividing by the filtered volume and multiplying by the maximum sampler depth. Catch of larvae in the depth discrete hauls was converted to nos. m$^{-3}$ by dividing by the filtered volume in a given
stratum and these values were used in calculation of the depth of the centre of abundance $(Z_{cm})$ from

$$Z_{cm} = \frac{\sum D_j \times WD_j \times A_j}{\sum WD_j \times A_j}$$  

(1)

Where $D_j$ is the midpoint of stratum $j$, $WD_j$ the width of the individual stratum and $A_j$ is the abundance of the larvae. The depth of mass for zooplankton <1000 µm was calculated using the same formula, but replacing abundance with dry weight in mg m$^{-3}$. The relative abundance of larvae in each stratum was plotted as a % of total abundance for day and night. $Z_{cm}$ was calculated and plotted for day, dusk, night and for single samples.

Only species for which the maximum abundance of larvae in a given stratum was above 2 per 100 m$^3$ were used (10 out of 27 species; 37%), as was the abundance of zooplankton <1000 µm. The station sampled at 06:20 UTC was excluded from calculations for day distributions and $Z_{cm}$, as it was the first sample after sunrise and considered to be biased by the night distribution. Abundances per stratum were compared visually between species and between day and night. Similarly, $Z_{cm}$ was compared among species for day (19:14 UTC, 08:22 UTC), dusk (21:52 UTC) and night (23:56 UTC) as well as the relationship of species to the hydrography in the transects.

The depth of the centre of abundance was tested for significant differences between species, using one-factorial ANOVA for all species together and for Gadidae and flatfish separately. Data were tested beforehand with a Shapiro-Wilks and Levene’s test and were found to fulfil the requirements for normality and homogeneity of variance. Post hoc Tukey’s HSD was applied to discern between which species significant differences occurred.
Results

Hydrography

Along both transects we observed a cool (<7°C), low saline (<34) surface layer over the Norwegian trench, extending to ca. 50 m depth (Figure 2), representing the Norwegian Coastal Current (NCC). Coldest temperatures occurred at ca. 30 m, while lowest salinities and densities were at about 10 m depth (Figures 2a, b). Correspondingly, $\sigma_t$ was increasing with depth and ranged from 25.5 kg m$^{-3}$ to 27 kg m$^{-3}$. Beneath the NCC water, the temperature increased down to 200-300 m, while at greater depths temperatures fell below 7°C and $\sigma_t$ rose to 27.6 in the deepest parts of the Norwegian trench. On the shallow plateau, between 1°W and 3°E, temperature changed markedly with depth, while salinity was almost homogenous throughout the water column, except for the eastern margins. In the southern transect a thermocline at about 50 m was separating water of >7°C and $\sigma_t$ of 27.5 kg m$^{-3}$ from cooler and denser water below. In the northern transect the warmer water reached down to a depth of 100 m and the thermocline was less strong. On the western margins of the southern transect water temperature increased rapidly between 0.5°W and 1°W, while salinity decreased from about 1.7°W westwards. Together this led to the formation of a frontal structure. In the North, temperature increased more gradually, while salinity did not change. Overall the highest temperatures were measured at >8°C on the western margins. Throughout the northern transect the surface water exhibited a $\sigma_t$ of <27.5 kg m$^{-3}$ while on the western margin these lower densities reached down to a hundred metres.

The hydrography at the 18h-station exhibited little variability in time or depth (Figure 3). Salinity was relatively high and stable, only changing from 35.32 to 35.33 in the sampled water column of 120 m. The temperature likewise varied little; it was about 8°C to 50 m and
then declined continuously to 7.6°C. Fluorescence peaked at 0.12 µg L⁻¹, but estimates varied during the period of investigation.

Horizontal distribution - zooplankton

At the stations closest to the Norwegian trench the total zooplankton concentration in both transects ranged between 3.7 g DW m⁻² and 5.0 g DW m⁻². Peak zooplankton concentrations were found at the stations near 1°E, 30.5 g DW m⁻² in the South and 38.7 g DW m⁻² in the North. However, at these stations the distribution between size fractions differed. While at the northern station, the zooplankton biomass was nearly equally distributed between the three different size fractions (Table 1), at the southern station the bulk of the zooplankton (20.1 g DW m⁻²) was in the 1000 – 2000 µm size fraction, while the zooplankton <1000 µm was at 7.1 g DW m⁻² and the >2000 µm size fraction was at 3.2 g DW m⁻². At the westernmost stations zooplankton concentrations were again lower, with 19.9 g DW m⁻² in the southern and 11.7 g DW m⁻² in the northern transect for all size fractions combined.

Horizontal distribution – fish larvae

During the survey, a total of 2030 fish larvae of 27 species in 9 families were identified (Table 2). Species richness and abundance of fish larvae increased from east to west. In the area of the Norwegian trench, abundances were mostly <30 m⁻² (Figures 2a, b). In this area there were no flatfish and there were only gadoid larvae close to the western slope of the trench. Over the shallow plateau abundances were mostly low ( <10 m⁻²), however long rough dab (Hippoglossoides platessoides Fabricius, 1780) and Norway pout (Trisopterus esmarkii Nilsson, 1855) occurred at abundances of ca. 200 m⁻² and 300 m⁻², respectively.
Both the stations with these high abundances were at the boundary of salinities between 35
and 35.2, where also sharp changes in $\sigma_t$ and high concentrations of zooplankton <1000 µm
(7.1 g DW m$^{-2}$ and 5.1 g DW m$^{-2}$) were observed. Along the northern transect larval
abundance and species diversity increased from the western slope of the Norwegian trench
westward to ca. 1°E, up to a maximum abundance of 500 m$^{-2}$ (Figure 2b), coinciding with
peak zooplankton densities. Along both transects the dominant species was Norway pout,
followed by whiting (*Merlangius merlangus* Linnaeus, 1758). Flatfish of the families
Pleuronectidae and Scophthalmidae were more abundant and species rich at the northern
transect than at the southern. Notably, Ammodytidae of 3 species were limited to the southern
transect with only lesser sandeel (*Ammodytes marinus* Raitt, 1934) at >10 m$^{-2}$. Ling (*Molva
molva* Linnaeus, 1758) was found in high abundance, (33.3 m$^{-2}$), at one station of the
northern transect, but did not occur elsewhere (Table 2a).

At the single location between the two transects whiting was almost twice as abundant as
Norway pout, while other gadoids were much less abundant (<20 m$^{-2}$) than either of these
(Table 2c). Blue ling (*Molva dipterygia* Pennant, 1784) and northern rockling (*Ciliata
septentrionalis* Collett, 1875) were found in abundances over 20 m$^{-2}$. Flatfish were similarly
species rich and abundant as in the northern transect. Long rough dab and brill
(*Scolthalmus rhombus* Linnaeus, 1758) were most abundant, with 25.2 m$^{-2}$ and 18.6 m$^{-2}$,
respectively. Clupeidae, Argentinidae and Gobiidae occurred sporadically along the transects
as well as at the 18h-station, in some hauls and in high numbers (Table 2).

**Vertical distribution – 18 hours station**

Changes in zooplankton distribution between day and night varied between the size fractions.
While the distribution of zooplankton <1000 µm varied only little (Figures 3b, c and 4) and
being most abundant in the two topmost strata (>30% each), coincided positively with the level of fluorescence. The larger size fractions exhibited stronger differences (Figures 3b, c), particularly the 1000 – 2000 µm fraction which was proportionally most abundant in the 0 – 20 m stratum during the day and almost homogenously distributed during the night. The trend towards a larger proportion in the deep strata during the night was common for all size fractions and was reflected in the depth of the mass of the small zooplankton which was relatively stable at around 40 m with noticeable but small deviations at night (Fig. 6) and when incorporating the station at 06:20 UTC (Fig. 7).

Seven gadoids and three flatfish species occurred in sufficient numbers to examine their vertical distribution. Cod was absent from the sample taken at dusk, otherwise all species occurred in all hauls. One group of gadoid larvae, consisting of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting and pollock (*Pollachius pollachius* Linnaeus, 1758), was distributed in the upper water column (0 – 40 m) during day and night. Cod (62%) and haddock (52%) were most abundant at 0 – 20 m during the day and at 20 – 40 m at night, with 100% and 69% respectively (Figures 4a, b). For whiting (Figure 4c) and pollock (Figure 4d) the change between these strata was reversed, as their abundance increased by 32 and 38 percent at 0 – 20 m during the night. While cod was never found below 40 m depth, the other species occurred in the deeper strata and ascended to shallower depths at night, \( Z_{cm} \) decreased accordingly (Figures 6a, 7a).

Saithe (*Pollachius virens* Linnaeus, 1758) and the two *Trisopterus* species (Figures 4e, g) were distributed in the strata below 40 m during the day. During the night saithe and poor cod (*Trisopterus minutus* Linnaeus, 1758) were most common in the upper water column, while 53% of Norway pout larvae remained at 75 – 100 m depth.
In daylight all three flatfish species, witch (*Glyptocephalus cynoglossus* Linnaeus, 1758), brill and long rough dab were most abundant at 40 – 75 m depth (Figure 5), varying between 45% for witch and 57% for brill. During the night, witch and long rough dab were most abundant in the upper water column, peaking with 47% at 0 – 20 m and 77% at 20 – 40 m, respectively. Brill remained most abundant at 40 – 75 m depth.

Except for brill, most larvae fell into a size range between 3 and 9 mm (Figs 8 - 10), with larger larvae occurring at low numbers. Brill was much more common at standard lengths of 2 - 3 mm than other species, while no brill larvae were longer than 5 mm. Even such small larvae exhibited substantial changes in their distribution across depth strata (Figure 10), indicating that they were capable of controlling their position in the water column. With increasing standard length, whiting exhibited a tendency to be proportionally more common in the 0 – 20 m stratum, which was particularly noticeable at night (Figure 8). Norway pout, the other gadoids found over a wide size range, did not exhibit such a trend and between 4 and 7 mm length exhibited a reversed trend of a larger proportion in the 20 – 40 m stratum at a small size, while the larger larvae were in the deepest stratum at night (Figure 9). Larvae above 9 mm appeared to aggregate in one or the other strata, depending on species and prevailing light conditions.

When testing the depth of the centre of mass for difference between species, results were only significant within a single family, *Gadidae* ($F_6=2.5; p=0.047$), but not for the group of flatfish ($F_2=0.2; p=0.82$) or in an analysis of all species together ($F_9=1.8; p=0.1$). The pattern in change of $Z_{cm}$ between different light conditions was similar for most species (Figures 6, 7). $Z_{cm}$ decreased at night, except for cod, Norway pout and brill. While cod was found at greater depth during the night, Norway pout and brill had already ascended between day and dusk.
Discussion

Our study provides evidence for type I vertical migrations in the species examined, except for cod (*Gadus morhua*). However, in regard to timing, the migration patterns were not identical, as Norway pout (*Trisopterus esmarkii*) and Brill (*Scophthalmus rhombus*) ascended earlier and pollock (*Pollachius pollachius*) continued to rise until the early morning. With the exception of the two *Trisopterus* species the centre of abundance of all species was within the 20 - 40 m stratum either at dusk or during the night. In contrast to previous studies (Gray 1996; Olivar & Sabatés 1997) we observed distinct assemblages in the upper and lower parts of the water column only during the day.

Our hydrographic observations are in accordance with findings described for the Feie-Shetland transect, reported by Hackett (1981). Hydrographic fronts were apparent at the western and eastern margins of the transects. Larval abundances and zooplankton concentrations were highest in the vicinity of these fronts which might imply that the frontal processes aggregate the zoo- and ichthyoplankton (Olson et al. 1994; Olson & Backus 1985).

Larval drift and dispersion from spawning grounds around the Shetland Isles is indicated by the general decline in larval abundance and diversity in parallel with an increase in larval mean lengths from these areas towards the East. Similar patterns have been suggested for Norway pout in other studies (Lambert et al. 2009; Nash et al. 2012).

In accordance with an east-west size gradient, the smallest average standard lengths were measured at the westerly positioned 18h-station. Cod and haddock (*Melanogrammus aeglefinus*) larvae were in the 6 – 8 mm size range in which Lough and Potter (1993) have observed the first appearance of vertical migrations. While our observations of cod larvae contain a high level of uncertainty, due to the low number of cod larvae in the samples, the distribution appears similar to earlier studies. The lack of cod larvae below 40 m is in
accordance with other observation of early cod larvae confined to the waters above the thermocline (Grønkjær et al. 1997; Grønkjær & Wieland 1997; Huwer et al. 2011; Lough & Potter 1993). Our observations of Type II distributions in cod larvae were described earlier for both the Atlantic and the Pacific cod (Gadus macrocephalus Tilesius, 1810) (Boehlert et al. 1985; Munk, in press). The depth distributions found for haddock, whiting, pollock, Norway pout, witch (Glyptocephalus cynoglossus) and long rough dab (Hippoglossoides platessoides) were similar to the findings of Economou (1987). The propensity for large whiting larvae to occur shallower at night may be explained by their greater ability to rise quickly. This is supported by the increasing proportion of smaller larvae in the 20 – 40 m stratum. Apparently all whiting larvae were rising through the water column but the larger larvae were rising more rapidly. In comparison, Norway pout showed a different trend and generally less distinct differences between day and night. Saithe exhibited less variation in $Z_{cm}$ in earlier studies (Munk, in press). Poor cod (Trisopterus minutus) was found shallower than in the present study (Olivar & Sabatés 1997). During the day Frank et al. (1992) found a shallower distribution of witch and long rough dab than in this study. However the bottom depth in their study was at 45 m, which may have restricted the depth distribution. The distribution of brill appears not to be described in the literature. In many ways it resembled the distribution of Norway pout, concerning the particularly deep $Z_{cm}$ and the timing of the ascent. However the extent of the vertical migration was greater, covering 43 m. Notably, brill larvae, which were on average smaller than those of other species, exhibited the largest difference in $Z_{cm}$ between day and night, suggesting that already at this small size brill larvae were capable of controlling their position in the water column. The overall tendency of large larvae to aggregate may reflect the developing patchiness in the distribution of older larvae (Hewitt 1981; Matsuura & Hewitt 1995). However, the low number of larvae above 9 mm SL resulted in a great deal of uncertainty concerning diel shifts in distribution.
Thermoclines have been described to lead either to larval aggregation (Lough & Potter 1993; Sabatés et al. 2008) or serve as a boundary for their migrations (Olivar & Sabatés 1997; Röpke 1993). Other studies found no apparent influence of thermoclines on larval vertical distribution and migration patterns (Conway et al. 1997; Gray & Kingsford 2003). The weak stratification resulting in a weak thermocline observed at the 18-hours station is similar to conditions in the studies of Gray and Kingsford (2003) and this might be the cause of the apparent weak influence of the thermocline in both studies.

The aggregation in the 20 - 40 m stratum during the night suggests a support for the hypothesis that a hungry population would ascend just far enough to find sufficient food (Pearre 2003). The zooplankton that could be quantitatively sampled with the available equipment was generally too large to be potential prey for all but the largest fish larvae. Even though the small-sized copepods and nauplii are under-sampled by the 180 µm mesh, we consider the distribution of the <1000 µm size fraction to reflect the distribution of smaller zooplankton. The smallest size fraction was concentrated in the upper water column which would be consistent with the aggregation of nauplii of most copepod species above the thermocline, which was observed in an earlier study (Krause & Trahms 1982).

Gadoid larvae in the observed size range primarily feed on *Calanus finmarchicus* (Gunnerus, 1770) eggs and copepod nauplii (Economou 1991) and require about 36% d⁻¹ of their own body mass (Jones 1973). For a larva of 6 mm standard length this would mean a requirement between 68 µg for saithe and 125 µg for cod (calculated following Economou 1987). Assuming a swimming speed and a reaction distance of one body length as well as proportions between *C. finmarchicus* eggs and nauplii and between nauplii stages as in Economou (1987) and Fransz et al. (1998) the corresponding number of food particles would be 3260 m⁻³ and 5973 m⁻³, respectively. In May such numbers are not unrealistic in the area (Economou 1987) and would be well within the 27.6% loss of biomass due to the mesh size
used (interpolated from table III in Gallienne & Robins 2001) However, zooplankton concentration in deeper strata should still have been sufficient to fulfil food requirements, which may explain why $Z_{cm}$ of Norway pout were not found any shallower than 51 m (equation from Economou 1987; based on: Jones 1973; Laurence 1985). The deepest $Z_{cm}$ observed after the apparent feeding period, could be due to larvae resting in deeper, cooler water to save energy and avoid visual predators (Brett 1971) or less buoyancy due to a full stomach (Sclafani et al. 1993).

In conclusion, whilst the general observation that most of the larvae occur at depths with high concentrations of zooplankton suggests a strong influence from the distribution of potential prey, the general vertical displacement of the mean depth indicates that other environmental factors might set a species-specific ‘background-depth’ of distribution. Therefore the physical water column structure might be the key factor determining the distribution of fish larvae, rather than the prey distributions. As suggested by Sclafani (1993), the neutral buoyancy of fish larvae is influenced by their condition. Further developed or better fed larvae, may be deeper in the water column, due to higher specific weight. As the species differ in the proportion of tissue types, the depth of neutral buoyancy may be different even when the larvae are in the same condition. We find that the comparative approach used in the present study has the potential for a new insight into the drivers behind vertical distribution patterns, and we suggest that further comparative community studies are undertaken.

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Table 1: Zooplankton densities (g DW m$^{-2}$), per size fraction for all sampled stations, based on GULF VII hauls. The highest abundances along transects were found at the stations at ca. 1°E. Proportions differed between transects. While the biomass in the southern transect was dominated by the 1000-2000 µm size fraction, proportions in the northern transect and at the 18h-station were more even between the two smaller size fractions. Large zooplankton (>2000 µm) was generally scarce with the exception of a few stations, where it contributed to a large proportion of the biomass.

<table>
<thead>
<tr>
<th>Transect</th>
<th>Station No.</th>
<th>Longitude</th>
<th>180-1000 µm</th>
<th>1000-2000 µm</th>
<th>&gt;2000 µm</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>60.75°N</td>
<td>423</td>
<td>0.47°W</td>
<td>7.0</td>
<td>4.6</td>
<td>0.1</td>
<td>11.7</td>
</tr>
<tr>
<td></td>
<td>429</td>
<td>0.91°E</td>
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<td>17.3</td>
<td>1.9</td>
<td>38.7</td>
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<tr>
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<td>433</td>
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<td>11.6</td>
<td>0.2</td>
<td>13.9</td>
</tr>
<tr>
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<td>3.7</td>
</tr>
<tr>
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<td>388</td>
<td>4.83°E</td>
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<td>1.3</td>
<td>0.6</td>
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<tr>
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<td>0.4</td>
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<tr>
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<td>406</td>
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<td>410</td>
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<td>0.1</td>
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<td>414</td>
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<td>10.1</td>
<td>4.7</td>
<td>19.9</td>
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<tr>
<td>18h-St.</td>
<td>418</td>
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<td>4.6</td>
<td>0.9</td>
<td>10.5</td>
</tr>
<tr>
<td></td>
<td>419</td>
<td>0.65°W</td>
<td>4.6</td>
<td>8.0</td>
<td>0.4</td>
<td>12.9</td>
</tr>
<tr>
<td></td>
<td>420</td>
<td>0.68°W</td>
<td>4.8</td>
<td>5.8</td>
<td>0.2</td>
<td>10.8</td>
</tr>
<tr>
<td></td>
<td>421</td>
<td>0.61°W</td>
<td>25.0</td>
<td>11.5</td>
<td>19.5</td>
<td>56.0</td>
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<tr>
<td></td>
<td>422</td>
<td>0.68°W</td>
<td>16.0</td>
<td>10.4</td>
<td>3.2</td>
<td>29.6</td>
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</table>
Table 2: Average abundances and standard lengths (±1 SD) for all species identified in the northern transect (a), the southern transect (b) and at the 18h-station (c). Numbers are based on depth integrated GULF VII, except for species which were only found in MOCNESS hauls. These species are denoted with asterisks.

<table>
<thead>
<tr>
<th>Transect</th>
<th>Family</th>
<th>Taxon</th>
<th>Species</th>
<th>Abundance (nos. m⁻²)</th>
<th>nos. caught</th>
<th>% measured</th>
<th>Std. Length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>60.75°N</td>
<td>Clupeidae</td>
<td><em>Clupea harengus</em></td>
<td>Clupea harengus</td>
<td>6.9 ± 5.8</td>
<td>30</td>
<td>93.3</td>
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<td>Gadidae</td>
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<td>Melanogrammus aeglefinus</td>
<td>2.7 ± 4.8</td>
<td>4</td>
<td>100.0</td>
<td>8.9 ± 3.1</td>
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<tr>
<td></td>
<td></td>
<td><em>Merlangius merlangus</em></td>
<td>Merlangius merlangus</td>
<td>22.4 ± 40.4</td>
<td>27</td>
<td>100.0</td>
<td>7.4 ± 1.4</td>
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<td></td>
<td><em>Pollachius pollachius</em></td>
<td>Pollachius pollachius</td>
<td>2.3 ± 2.4</td>
<td>7</td>
<td>100.0</td>
<td>8.5 ± 1.9</td>
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<tr>
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<td></td>
<td><em>Pollachius virens</em></td>
<td>Pollachius virens</td>
<td>8.5 ± 11.6</td>
<td>14</td>
<td>100.0</td>
<td>9.7 ± 2.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Trisopterus esmarkii</em></td>
<td>Trisopterus esmarkii</td>
<td>51.3 ± 71.9</td>
<td>100</td>
<td>100.0</td>
<td>9.2 ± 2.5</td>
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<tr>
<td></td>
<td></td>
<td><em>Trisopterus minutus</em></td>
<td>Trisopterus minutus</td>
<td>7.0 ± 14.7</td>
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<td>8.4 ± 1.0</td>
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<tr>
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<td>Unidentified</td>
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<td>62.5</td>
<td>6.6 ± 4.1</td>
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<td>Gobiidae</td>
<td><em>Gobiusculus flavescens</em></td>
<td>Gobiusculus flavescens</td>
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<td>100.0</td>
<td>6.9 ± 1.6</td>
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<tr>
<td></td>
<td>Lotidae</td>
<td><em>Ciliata septentrionalis</em></td>
<td>Ciliata septentrionalis</td>
<td>2.4 ± 4.9</td>
<td>3</td>
<td>100.0</td>
<td>5.4 ± 1.0</td>
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<td></td>
<td></td>
<td><em>Molva dipterygia</em></td>
<td>Molva dipterygia</td>
<td>1.1 ± 2.5</td>
<td>1</td>
<td>100.0</td>
<td>6.5 ± -</td>
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<td><em>Molva molva</em></td>
<td>Molva molva</td>
<td>6.7 ± 14.9</td>
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<td>5.2 ± 0.6</td>
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<td>Pleuronectidae</td>
<td><em>Glyptocephalus cynoglossus</em></td>
<td>Glyptocephalus cynoglossus</td>
<td>2.5 ± 4.8</td>
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<td>9.7 ± 1.0</td>
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<td>Hippoglossoides platessoides</td>
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<td>8.6 ± 1.8</td>
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<tr>
<td></td>
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<td>Limanda limanda</td>
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<td>8.0 ± 4.0</td>
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<tr>
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<td><em>Pleuronectes platessa</em></td>
<td>Pleuronectes platessa</td>
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<td>100.0</td>
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<td>Unidentified</td>
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<td>7.8 ± 1.1</td>
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<td>Lepidorhombus whiffiagonis</td>
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<td>100.0</td>
<td>10.6 ± -</td>
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<td>Phrynorhombus norvegicus</td>
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<td>9.2 ± 2.0</td>
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<tr>
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<td>Scophthalmus rhombus</td>
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<tr>
<td>Transect</td>
<td>Taxon</td>
<td>Species</td>
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<td>nos. caught</td>
<td>% measured</td>
<td>Std. Length (mm)</td>
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<td>18.8 ± 5.3</td>
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<td>17.5 ± 3.7</td>
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<tr>
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<td>100.0</td>
<td>10.0 ± -</td>
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<td>Gadidae</td>
<td><em>Gadus morhua</em></td>
<td>4.4 ± 7.7</td>
<td>11</td>
<td>90.9</td>
<td>8.3 ± 3.5</td>
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<td>9.7 ± 5.0</td>
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<td>5.9 ± 8.2</td>
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<td>100.0</td>
<td>9.6 ± 6.7</td>
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<td>100.0</td>
<td>10.4 ± 10.5</td>
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<td>6.3 ± 7.9</td>
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<td>11.2 ± 3.1</td>
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<td>3.8 ± 0.3</td>
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<td>Taxon</td>
<td>Species</td>
<td>Abundance (nos. m⁻²)</td>
<td>nos. caught</td>
<td>% measured</td>
<td>Std. Length (mm)</td>
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<td>100.0</td>
<td>11.9 ± 0</td>
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<tr>
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<td>0.8 ± 1.8</td>
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<td>100.0</td>
<td>40 ± -</td>
<td></td>
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<tr>
<td></td>
<td>Argentinidae</td>
<td><em>Argentina sphyraena</em></td>
<td>20.0 ± 29.2</td>
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<td>90.9</td>
<td>10.1 ± 2.4</td>
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<td><em>Clupea harengus</em></td>
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<td>1</td>
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<td>14.9 ± -</td>
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<td>Gadidae</td>
<td><em>Gadus morhua</em></td>
<td>1.3 ± 2.8</td>
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<td>100.0</td>
<td>5.8 ± -</td>
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<td><em>Melanogrammus aeglefinus</em></td>
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<td>6.3 ± 1.4</td>
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<td>100.0</td>
<td>7.1 ± 1.6</td>
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<td><em>Pollachius virens</em></td>
<td>15.3 ± 8.5</td>
<td>13</td>
<td>100.0</td>
<td>7.0 ± 2.4</td>
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<td>81.2 ± 77.6</td>
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<td>98.2</td>
<td>7.2 ± 1.6</td>
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<tr>
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<td><em>Trisopterus minutus</em></td>
<td>7.4 ± 7.6</td>
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<td>80.0</td>
<td>6.2 ± 1.4</td>
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<td>5.3 ± 1.0</td>
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<td>Gobiidae</td>
<td><em>Gobius niger</em></td>
<td>0.8 ± 1.8</td>
<td>1</td>
<td>100.0</td>
<td>5.5 ± -</td>
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<tr>
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<td></td>
<td><em>Gobiusculus flavescens</em></td>
<td>3.6 ± 8.0</td>
<td>1</td>
<td>100.0</td>
<td>6.8 ± -</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td><em>Unidentified</em></td>
<td>0.2 ± 0.4</td>
<td>1</td>
<td>100.0</td>
<td>2.7 ± -</td>
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<tr>
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<td>Lotidae</td>
<td><em>Ciliata septentrionalis</em></td>
<td>17.8 ± 22.0</td>
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<td>100.0</td>
<td>5.7 ± 0.9</td>
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</tr>
<tr>
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<td><em>Molva dipterygia</em></td>
<td>7.2 ± 16.0</td>
<td>2</td>
<td>100.0</td>
<td>7.9 ± 0.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Molva molva</em></td>
<td>2.5 ± 5.7</td>
<td>2</td>
<td>100.0</td>
<td>6.9 ± 0.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pleuronectidae</td>
<td><em>Glyptocephalus cynoglossus</em></td>
<td>6.2 ± 6.9</td>
<td>4</td>
<td>100.0</td>
<td>6.9 ± 1.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Hippoglossoides platessoides</em></td>
<td>20.2 ± 29.2</td>
<td>12</td>
<td>83.3</td>
<td>8.3 ± 3.3</td>
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<tr>
<td></td>
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<td><em>Limanda limanda</em></td>
<td>2.5 ± 5.6</td>
<td>5</td>
<td>80.0</td>
<td>6.8 ± 1.6</td>
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<tr>
<td></td>
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<td><em>Platichthys flesus</em></td>
<td>0.4 ± 0.9</td>
<td>5</td>
<td>100.0</td>
<td>3.5 ± 0.5</td>
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<tr>
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<td><em>Pleuronectes platessa</em></td>
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<td>1</td>
<td>100.0</td>
<td>10.4 ± -</td>
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<tr>
<td></td>
<td></td>
<td><em>Unidentified</em></td>
<td>1.3 ± 1.9</td>
<td>2</td>
<td>100.0</td>
<td>5.3 ± 0.5</td>
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<tr>
<td></td>
<td>Scophthalmidae</td>
<td><em>Scophthalmus rhombus</em></td>
<td>18.6 ± 20.2</td>
<td>12</td>
<td>100.0</td>
<td>4.5 ± 0.7</td>
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Figure captions:

**Figure 1:** CTD, GULF VII and MOCNESS stations sampled during the survey. The aggregation of samples in the black rectangle represents the 18 hours station, containing 5 hauls with each gear in a 5 x 5 NM square.

**Figure 2:** Profiles of $\sigma_t$, contoured for 0.1 kg m$^{-3}$ (thin grey lines) and 0.5 kg m$^{-3}$ (bold grey lines) and abundance of fish larvae along the transects at 59.3°N (panel a) and 60.75°N (panel b). Only the most common species are given, while gadoids other than Norway pout and whiting, and flatfish other than long rough dab and brill are combined. Miscellaneous species comprised Clupeidae, Argentinia, Ammodytidae, Lotidae and Gobidae which did not commonly occur.

**Figure 3:** Temperature, salinity and fluorescence at the 18h-station (panel a), averaged over all 5 hauls. The broken lines depict the boundaries between the sampled depth strata in depth discrete hauls. Most changes in hydrography and fluorescence occurred between 50 and 80 m, mainly in the stratum between 40 and 75 m. Error bars are only shown for every ten metres of depth. Panels b and c show the distribution of all size classes of zooplankton (<1000 µm, 1000-2000 µm and >2000 µm) during daylight and night conditions in % of total.

**Figure 4:** Vertical distribution of gadoid fish larvae and <1000 µm zooplankton by dry weight, during day and night as a % of total abundance or biomass. N represents the number
of larvae caught under the respective light conditions (in subscript). The y-axis depicts the boundaries between sampled strata.

**Figure 5:** Vertical distribution of flatfish larvae and <1000 µm zooplankton dry weight, during day and night in % of total abundance or biomass. N represents the number of larvae caught under the respective light conditions (in subscript). The y-axis depicts the boundaries between sampled strata.

**Figure 6:** Depth of the centre of abundance for gadoid (a) and flatfish larvae (b) in three different light environments. Due to the long days at this time of the year, there was only one station at dusk (21:52 UTC) and night (23:56 UTC), while three stations were in daylight (19:14 UTC, 06:20 UTC and 08:22 UTC). As it was shortly after sunrise the station at 06:20 UTC was not included into the calculation of Z_{cm}. The number of larvae caught under each light condition is given as N in the legend. The depth of mass for zooplankton (based on mg m^{-3}) is depicted in both panels.

**Figure 7:** Depth of the centre of abundance for gadoid (a) and flatfish larvae (b) for individual samples taken at the 18h-station. Daylight stations were at 19:14 UTC, 06:20 UTC and 08:22 UTC, the station at 21:52 UTC was during dusk and the station at 23:56 UTC in the night. The number of larvae caught at each station is given as N, with the time of sampling given in subscript. The depth of mass for zooplankton (based on mg m^{-3}) is depicted in both panels.
Figure 8: Rounded length distribution across strata and light conditions of cod, haddock and whiting as % of total abundance. The majority of larvae ranged from 3 to 6 mm standard length. Even for the larvae at the lower end of this range, changes in distribution across strata could change substantially between the different light conditions. Empty panels indicate zero findings for the respective species in this stratum, during the entire sampling period.

Figure 9: Rounded length distribution across strata and light conditions of saithe, pollock, Norway pout and poor cod in % of total abundance. The majority of saithe and pollock were in a relatively narrow size range from 4 to 8 mm SL. Smaller larvae tended to aggregate at the 20 – 40 m stratum with increasing darkness. Larger larvae were distributed throughout the water column, but this is again based on few individuals. Norway pout covered a large size range (2 – 11 mm) and, similar to saithe larvae (4 – 6 mm), tended to aggregate in the 20 - 40 m stratum with increasing darkness. During day and dusk conditions poor cod of all sizes were mostly found in the deeper strata. At night only a few large larvae in the 0 – 20 m stratum were found. Empty panels indicate zero findings for the respective species in this stratum, during the entire sampling period.

Figure 10: Rounded length distribution across strata and light conditions of witch, long rough dab and brill in % of total abundance. Witch and long rough dab ranged mostly between 3 and 9 mm in standard length but with a few larvae in the extreme upper range of the size distribution which were found in the two strata between 20 and 75 m. The medium sized larvae were relatively dispersed during day and dusk and for witch appeared to aggregate in the uppermost stratum during the night. Brill was unique, as the majority of
larvae were found at the low extreme of the size range and exhibited strong fluctuations across the depth range.
Figure 2:

(a) Longitude (deg.)

(b) Bottom Depth (m)
Figure 3:

(a) Salinity

(b) Zooplankton (% of total) - Day

(c) Zooplankton (% of total) - Night

- 1000 μm
- 1000-2000 μm
- >2000 μm
Figure 4:

Abundance (% of total)

Depth (m)

Cod
$N_{Day} = 7$ $N_{Night} = 2$

Haddock
$N_{Day} = 16$ $N_{Night} = 10$

Whiting
$N_{Day} = 236$ $N_{Night} = 100$

Pollock
$N_{Day} = 16$ $N_{Night} = 14$

Saithe
$N_{Day} = 34$ $N_{Night} = 4$

PO Pout
$N_{Day} = 102$ $N_{Night} = 26$

Day
Night
Zooplankton <1000 µm Day
Zooplankton <1000 µm Night
Figure 5:

**Figure a:**
- Witch
- $N_{\text{Day}} = 36$, $N_{\text{Night}} = 12$

**Figure b:**
- L.R. Dab
- $N_{\text{Day}} = 58$, $N_{\text{Night}} = 6$

**Legend:**
- Day
- Night
- Zooplankton <1000μm Day
- Zooplankton <1000μm Night
Figure 6:

(a) Light conditions

Day | Dusk | Night

Depth (m)

- Cod: N_{day}=7, N_{dusk}=2, N_{night}=10
- Haddock: N_{day}=16, N_{dusk}=18, N_{night}=10
- Whiting: N_{day}=236, N_{dusk}=70, N_{night}=100
- Pollock: N_{day}=16, N_{dusk}=6, N_{night}=14
- Saithe: N_{day}=34, N_{dusk}=16, N_{night}=4
- NO Pout: N_{day}=102, N_{dusk}=70, N_{night}=25
- Poor Cod: N_{day}=28, N_{dusk}=16, N_{night}=6
- Zooplankton: <1000 μm

(b) Day | Dusk | Night

Depth (m)

- Witch: N_{day}=36, N_{dusk}=4, N_{night}=12
- L. R. Dab: N_{day}=58, N_{dusk}=30, N_{night}=6
- Brill: N_{day}=26, N_{dusk}=4, N_{night}=10
- Zooplankton: <1000 μm
Figure 7:
Figure 8:

Abundance (% of total)

Standard Length (mm)

20 - 0 m

Cod

Day

Dusk

Night

Haddock

Whiting

40 - 20 m

75 - 40 m

100 - 75 m

Abundance (% of total)
Figure 9: 

Saithe

Pollock

NO Pout

Poor Cod

20–0 m (Abundance % of total)

40–20 m (Abundance % of total)

75–40 m (Abundance % of total)

100–75 m (Abundance % of total)

Standard Length (mm)
Figure 10: