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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.

22 **Abstract**

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

38

39 **Keywords:** Fish larvae, Gadidae, Flatfish, Vertical distribution, North Sea

40

41 **Introduction**

42 Compared to current speeds the swimming ability of fish larvae is of minor importance,
43 limiting their capability to influence their location by horizontal swimming. However, larvae
44 can migrate vertically in the water column and so influence their horizontal transport, as
45 current speed and direction often changes with depth (Fortier & Leggett 1983; Sclafani et al.
46 1993). Vertical migration patterns of fish larvae can be broadly classified into three
47 categories: i) type I migrations as upward movement at the beginning of night and downward
48 movement at the beginning of day; ii) type II as the opposite (Neilson & Perry 1990) and iii)
49 a pattern of aggregation during the day and dispersal throughout the night (Gray 1998; Leis
50 1991; Olivar & Sabatés 1997). Exogenous factors that influence the observed patterns are, for
51 example, light, prey and predator distribution, as well as effects of temperature and salinity.

52 Individuals of given species and congeners often exhibit similar distribution patterns,
53 regardless of the prevailing environmental conditions and form distinct assemblages in
54 different depth strata (Gray & Kingsford 2003; Olivar & Sabatés 1997; Röpke 1993;
55 Southward & Barrett 1983). Size and consequently swimming ability, important for
56 determining vertical distribution, changes throughout development and many species exhibit
57 different vertical behaviours as the larvae develop (c. f. Table 1; Neilson & Perry 1990).

58 Lough and Potter (1993) observed the initiation of vertical migration in cod (*Gadus morhua*
59 Linnaeus, 1758) and haddock (*Melanogrammus aeglefinus* Linnaeus, 1758) at standard
60 lengths (SL) of 6-8 mm, and a firmly established type I migration at lengths greater than 9
61 mm SL. Smaller larvae and particularly those in poor condition may be more strongly
62 influenced by buoyancy (Sclafani et al. 1993). However, even in their earliest stages, larvae
63 will migrate if unfavourable conditions make it necessary (Grønkjær & Wieland 1997). The
64 influence of hydrography, in particular the position of the thermocline, is less clear. Some
65 studies indicate a connection between larval distributions and the thermocline for certain taxa

66 (Olivar & Sabatés 1997) and/or size classes (Lough et al. 1996; Lough & Potter 1993), while
67 others show the same distributional patterns, both of single taxa and larval assemblages,
68 irrespective of water column stratification (Gray 1998; Gray & Kingsford 2003). Gray and
69 Kingsford (2003) attributed their failure to find a relationship between distributions and the
70 thermocline, to a combination of the gradual and ephemeral character of thermoclines in their
71 study region and the lag-phase between the occurrence of hydrographic cues and the reaction
72 of the larvae.

73

74 The influence of prey and predator distributions was pointed out by Pearre (1973) who, based
75 on his studies of an arrow worm *Sagitta elegans* (Verrill, 1873), introduced the hunger-
76 satiation hypothesis. In this case vertical movements were related to the concurrent needs of
77 feeding in the upper water column and hiding from visual predators at greater depths. The
78 hypothesis was later applied to other planktonic organisms, including fish larvae (Pearre
79 2003). Visually hunting fish larvae can follow different strategies to satisfy these needs. They
80 may rise in the water column at night, together with their zooplankton prey or may stay
81 deeper and feed on vertically migrating prey (Lovetskaya 1953). Neilson and Perry (1990)
82 suggested a feeding/avoidance window at dusk and dawn, when light conditions are sufficient
83 for feeding but predators may still be at greater depths. The influence of light differs among
84 species. Some species appear to select a specific isolume, which primarily governs their
85 vertical distribution (Woodhead 1966). This has been suggested as the cause of aggregations
86 during the day and diffuse distribution during the night when the primary cue is missing (Leis
87 1991). However, the effect of light is species specific as has been shown in concurrent
88 laboratory studies (Catalán et al. 2011; Vollset et al. , in press), for example some species are
89 shown to be adapted to low illumination (e.g. Downing & Litvak 2001; Huse 1994; Yoon et
90 al. 2010).

91 Statistical models of the vertical distribution of different taxa have high predictive power
92 with several interacting factors (Hernandez et al. 2009) and even when only using a single
93 factor (Huebert et al. 2010). Control by a single factor is, however, rare. While prey
94 abundance was one controlling factor for mesopelagic larvae in the Arabian Sea (Röpke
95 1993) and for *Sardinella aurita* (Valenciennes, 1847) in the northwestern Mediterranean Sea
96 (Sabatés et al. 2008), the fish species were also limited by physical factors. The mesopelagic
97 species were limited by a warm mixed layer above, and *S. aurita* most likely by the cool (ca.
98 15°C) water below the pycnocline. The vertical distribution of larvae will influence
99 horizontal transport, as different currents at different depths might lead to retention within or
100 a displacement out of an area (Fortier & Leggett 1982; Fortier & Leggett 1983; Govoni &
101 Pietrafesa 1994) and several studies have shown aggregations of fish larvae in or near fronts
102 (Kjørboe et al. 1988; Munk et al. 2002; Sabatés 1990). Likewise, food availability, the
103 relationship between illumination and prey abundance, is correlated with the distribution of
104 Baltic cod larvae (Grønkjær & Wieland 1997).

105 Considering the apparent species differences in vertical distributions and migrations, a
106 comparative approach might elucidate the factors that are of prime importance. Few studies
107 have analysed the distributional patterns of a wide range of species in a comparative way
108 (Frank et al. 1992; Gray 1996; Gray & Kingsford 2003). Such an opportunity was available
109 in the northern North Sea in 2010. The area east of the Shetland Isles is particularly species
110 rich (Economou 1987) with an assemblage primarily consisting of Gadidae, Lotidae,
111 Pleuronectidae and Scophthalmidae. In regard to abundance, the dominant species were
112 whiting, ling (*Molva molva*, Linnaeus, 1758), Norway redfish (*Sebastes viviparus*, Krøyer,
113 1845) and Norway pout. It is an important spawning ground for several fish species which
114 spawn in spring and we were able to describe both the major horizontal distributional patterns
115 from transects of stations, and the vertical patterns by vertical stratified sampling over an 18

116 hour period. In this contribution we focus on the distributional patterns of larval fish in
117 relation to hydrography and in relation to the distribution of zooplankton 180 - 1000 μm . We
118 hypothesize that relative to each other larvae of different species would retain their position
119 in the water column.

120

121 **Materials and Methods**

122 *Field sampling*

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

127 Depth integrated samples were taken in double oblique hauls with a 76 cm diameter GULF
128 VII high speed sampler (Nash et al. 1998), down to about 100 m depth. The sampler was
129 equipped with a mechanical flow meter (General Oceanics, USA) in the mouth of the nose
130 cone. A SCANMAR depth sensor was attached to the sampler and provided both depth and
131 temperature measurements. For discrete depth sampling, a MOCNESS (Wiebe et al. 1985)
132 with a 1 m² opening and 4 nets (180 μm mesh) was deployed to ca. 100 m and then hauled
133 obliquely to the surface, sampling the water column in strata with nets opening at about 100,
134 75, 40 and 20 m. Flow meters and a CTD were attached to the MOCNESS and the filtered
135 volume (m³) estimated for each stratum. Larvae were sorted on board and were preserved in
136 borax buffered 4% formaldehyde. Zooplankton was split in two fractions before preservation,
137 using a Motoda splitting device. One half was preserved for identification and enumeration
138 whilst the other half was size fractioned into <1000 μm , 1000-2000 μm and >2000 μm

139 samples. Each size fraction was dried at 60°C to constant weight in order to obtain dry
140 weights, which were converted to milligrams dry weight per m³ (mg DW m⁻³) based on the
141 volume of water filtered and to g DW m⁻² based on filtered volume and sampled depth.

142

143 *Laboratory procedures*

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

150

151 *Data treatment and analysis*

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

158 For each species in the depth integrated hauls, the catch was converted to nos. m⁻² by dividing
159 by the filtered volume and multiplying by the maximum sampler depth. Catch of larvae in the
160 depth discrete hauls was converted to nos. m⁻³ by dividing by the filtered volume in a given

161 stratum and these values were used in calculation of the depth of the centre of abundance
162 (Z_{cm}) from

163

$$Z_{cm} = \frac{\sum D_j \times WD_j \times A_j}{\sum WD_j \times A_j} \quad (1)$$

164

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

170 Only species for which the maximum abundance of larvae in a given stratum was above 2 per
171 100 m^3 were used (10 out of 27 species; 37%), as was the abundance of zooplankton <1000
172 μm . The station sampled at 06:20 UTC was excluded from calculations for day distributions
173 and Z_{cm} , as it was the first sample after sunrise and considered to be biased by the night
174 distribution. Abundances per stratum were compared visually between species and between
175 day and night. Similarly, Z_{cm} was compared among species for day (19:14 UTC, 08:22 UTC),
176 dusk (21:52 UTC) and night (23:56 UTC) as well as the relationship of species to the
177 hydrography in the transects.

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

183 **Results**

184 *Hydrography*

185 Along both transects we observed a cool ($<7^{\circ}\text{C}$), low saline (<34) surface layer over the
186 Norwegian trench, extending to ca. 50 m depth (Figure 2), representing the Norwegian
187 Coastal Current (NCC). Coldest temperatures occurred at ca. 30 m, while lowest salinities
188 and densities were at about 10 m depth (Figures 2a, b). Correspondingly, σ_t was increasing
189 with depth and ranged from 25.5 kg m^{-3} to 27 kg m^{-3} . Beneath the NCC water, the
190 temperature increased down to 200-300 m, while at greater depths temperatures fell below
191 7°C and σ_t rose to 27.6 in the deepest parts of the Norwegian trench. On the shallow plateau,
192 between 1°W and 3°E , temperature changed markedly with depth, while salinity was almost
193 homogenous throughout the water column, except for the eastern margins. In the southern
194 transect a thermocline at about 50 m was separating water of $>7^{\circ}\text{C}$ and σ_t of 27.5 kg m^{-3} from
195 cooler and denser water below. In the northern transect the warmer water reached down to a
196 depth of 100 m and the thermocline was less strong. On the western margins of the southern
197 transect water temperature increased rapidly between 0.5°W and 1°W , while salinity
198 decreased from about 1.7°W westwards. Together this led to the formation of a frontal
199 structure. In the North, temperature increased more gradually, while salinity did not change.
200 Overall the highest temperatures were measured at $>8^{\circ}\text{C}$ on the western margins. Throughout
201 the northern transect the surface water exhibited a σ_t of $<27.5 \text{ kg m}^{-3}$ while on the western
202 margin these lower densities reached down to a hundred metres.

203 The hydrography at the 18h-station exhibited little variability in time or depth (Figure 3).
204 Salinity was relatively high and stable, only changing from 35.32 to 35.33 in the sampled
205 water column of 120 m. The temperature likewise varied little; it was about 8°C to 50 m and

206 then declined continuously to 7.6°C. Fluorescence peaked at 0.12 $\mu\text{g L}^{-1}$, but estimates varied
207 during the period of investigation.

208

209 *Horizontal distribution - zooplankton*

210 At the stations closest to the Norwegian trench the total zooplankton concentration in both
211 transects ranged between 3.7 g DW m^{-2} and 5.0 g DW m^{-2} . Peak zooplankton concentrations
212 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
213 North. However, at these stations the distribution between size fractions differed. While at the
214 northern station, the zooplankton biomass was nearly equally distributed between the three
215 different size fractions (Table 1), at the southern station the bulk of the zooplankton (20.1 g
216 DW m^{-2}) was in the 1000 – 2000 μm size fraction, while the zooplankton <1000 μm was at
217 7.1 g DW m^{-2} and the >2000 μm size fraction was at 3.2 g DW m^{-2} . At the westernmost
218 stations zooplankton concentrations were again lower, with 19.9 g DW m^{-2} in the southern
219 and 11.7 g DW m^{-2} in the northern transect for all size fractions combined.

220

221 *Horizontal distribution – fish larvae*

222 During the survey, a total of 2030 fish larvae of 27 species in 9 families were identified
223 (Table 2). Species richness and abundance of fish larvae increased from east to west. In the
224 area of the Norwegian trench, abundances were mostly <30 m^{-2} (Figures 2a, b). In this area
225 there were no flatfish and there were only gadoid larvae close to the western slope of the
226 trench. Over the shallow plateau abundances were mostly low (<10 m^{-2}), however long
227 rough dab (*Hippoglossoides platessoides* Fabricius, 1780) and Norway pout (*Trisopterus*
228 *esmarkii* Nilsson, 1855) occurred at abundances of ca. 200 m^{-2} and 300 m^{-2} , respectively.

229 Both the stations with these high abundances were at the boundary of salinities between 35
230 and 35.2, where also sharp changes in σ_t and high concentrations of zooplankton $<1000 \mu\text{m}$
231 (7.1 g DW m^{-2} and 5.1 g DW m^{-2}) were observed. Along the northern transect larval
232 abundance and species diversity increased from the western slope of the Norwegian trench
233 westward to ca. 1°E , up to a maximum abundance of 500 m^{-2} (Figure 2b), coinciding with
234 peak zooplankton densities. Along both transects the dominant species was Norway pout,
235 followed by whiting (*Merlangius merlangus* Linnaeus, 1758). Flatfish of the families
236 *Pleuronectidae* and *Scophthalmidae* were more abundant and species rich at the northern
237 transect than at the southern. Notably, *Ammodytidae* of 3 species were limited to the southern
238 transect with only lesser sandeel (*Ammodytes marinus* Raitt, 1934) at $>10 \text{ m}^{-2}$. Ling (*Molva*
239 *molva* Linnaeus, 1758) was found in high abundance, (33.3 m^{-2}), at one station of the
240 northern transect, but did not occur elsewhere (Table 2a).

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

249

250 *Vertical distribution – 18 hours station*

251 Changes in zooplankton distribution between day and night varied between the size fractions.
252 While the distribution of zooplankton $<1000 \mu\text{m}$ varied only little (Figures 3b, c and 4) and

253 being most abundant in the two topmost strata (>30% each), coincided positively with the
254 level of fluorescence. The larger size fractions exhibited stronger differences (Figures 3b, c),
255 particularly the 1000 – 2000 μm fraction which was proportionally most abundant in the 0 –
256 20 m stratum during the day and almost homogeneously distributed during the night. The trend
257 towards a larger proportion in the deep strata during the night was common for all size
258 fractions and was reflected in the depth of the mass of the small zooplankton which was
259 relatively stable at around 40 m with noticeable but small deviations at night (Fig. 6) and
260 when incorporating the station at 06:20 UTC (Fig. 7).

261 Seven gadoids and three flatfish species occurred in sufficient numbers to examine their
262 vertical distribution. Cod was absent from the sample taken at dusk, otherwise all species
263 occurred in all hauls. One group of gadoid larvae, consisting of cod (*Gadus morhua*),
264 haddock (*Melanogrammus aeglefinus*), whiting and pollock (*Pollachius pollachius* Linnaeus,
265 1758), was distributed in the upper water column (0 – 40 m) during day and night. Cod (62%)
266 and haddock (52%) were most abundant at 0 – 20 m during the day and at 20 – 40 m at night,
267 with 100% and 69% respectively (Figures 4a, b). For whiting (Figure 4c) and pollock (Figure
268 4d) the change between these strata was reversed, as their abundance increased by 32 and 38
269 percent at 0 – 20 m during the night. While cod was never found below 40 m depth, the other
270 species occurred in the deeper strata and ascended to shallower depths at night, Z_{cm} decreased
271 accordingly (Figures 6a, 7a).

272 Saithe (*Pollachius virens* Linnaeus, 1758) and the two *Trisopterus* species (Figures 4e, g)
273 were distributed in the strata below 40 m during the day. During the night saithe and poor cod
274 (*Trisopterus minutus* Linnaeus, 1758) were most common in the upper water column, while
275 53% of Norway pout larvae remained at 75 – 100 m depth.

276 In daylight all three flatfish species, witch (*Glyptocephalus cynoglossus* Linnaeus, 1758),
277 brill and long rough dab were most abundant at 40 – 75 m depth (Figure 5), varying between
278 45% for witch and 57% for brill. During the night, witch and long rough dab were most
279 abundant in the upper water column, peaking with 47% at 0 – 20 m and 77% at 20 – 40 m,
280 respectively. Brill remained most abundant at 40 – 75 m depth.

281 Except for brill, most larvae fell into a size range between 3 and 9 mm (Figs 8 - 10), with
282 larger larvae occurring at low numbers. Brill was much more common at standard lengths of
283 2 - 3 mm than other species, while no brill larvae were longer than 5 mm. Even such small
284 larvae exhibited substantial changes in their distribution across depth strata (Figure 10),
285 indicating that they were capable of controlling their position in the water column. With
286 increasing standard length, whiting exhibited a tendency to be proportionally more common
287 in the 0 – 20 m stratum, which was particularly noticeable at night (Figure 8). Norway pout,
288 the other gadoids found over a wide size range, did not exhibit such a trend and between 4
289 and 7 mm length exhibited a reversed trend of a larger proportion in the 20 – 40 m stratum at
290 a small size, while the larger larvae were in the deepest stratum at night (Figure 9). Larvae
291 above 9 mm appeared to aggregate in one or the other strata, depending on species and
292 prevailing light conditions.

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

299

300 **Discussion**

301 Our study provides evidence for type I vertical migrations in the species examined, except for
302 cod (*Gadus morhua*). However, in regard to timing, the migration patterns were not identical,
303 as Norway pout (*Trisopterus esmarkii*) and Brill (*Scophthalmus rhombus*) ascended earlier
304 and pollock (*Pollachius pollachius*) continued to rise until the early morning. With the
305 exception of the two *Trisopterus* species the centre of abundance of all species was within the
306 20 - 40 m stratum either at dusk or during the night. In contrast to previous studies (Gray
307 1996; Olivar & Sabatés 1997) we observed distinct assemblages in the upper and lower parts
308 of the water column only during the day.

309 Our hydrographic observations are in accordance with findings described for the Feie-
310 Shetland transect, reported by Hackett (1981). Hydrographic fronts were apparent at the
311 western and eastern margins of the transects. Larval abundances and zooplankton
312 concentrations were highest in the vicinity of these fronts which might imply that the frontal
313 processes aggregate the zoo- and ichthyoplankton (Olson et al. 1994; Olson & Backus 1985).
314 Larval drift and dispersion from spawning grounds around the Shetland Isles is indicated by
315 the general decline in larval abundance and diversity in parallel with an increase in larval
316 mean lengths from these areas towards the East. Similar patterns have been suggested for
317 Norway pout in other studies (Lambert et al. 2009; Nash et al. 2012).

318 In accordance with an east-west size gradient, the smallest average standard lengths were
319 measured at the westerly positioned 18h-station. Cod and haddock (*Melanogrammus*
320 *aeglefinus*) larvae were in the 6 – 8 mm size range in which Lough and Potter (1993) have
321 observed the first appearance of vertical migrations. While our observations of cod larvae
322 contain a high level of uncertainty, due to the low number of cod larvae in the samples, the
323 distribution appears similar to earlier studies. The lack of cod larvae below 40 m is in

324 accordance with other observation of early cod larvae confined to the waters above the
325 thermocline (Grønkjær et al. 1997; Grønkjær & Wieland 1997; Huwer et al. 2011; Lough &
326 Potter 1993). Our observations of Type II distributions in cod larvae were described earlier
327 for both the Atlantic and the Pacific cod (*Gadus macrocephalus* Tilesius, 1810) (Boehlert et
328 al. 1985; Munk , in press). The depth distributions found for haddock, whiting, pollock,
329 Norway pout, witch (*Glyptocephalus cynoglossus*) and long rough dab (*Hippoglossoides*
330 *platessoides*) were similar to the findings of Economou (1987). The propensity for large
331 whiting larvae to occur shallower at night may be explained by their greater ability to rise
332 quickly. This is supported by the increasing proportion of smaller larvae in the 20 – 40 m
333 stratum. Apparently all whiting larvae were rising through the water column but the larger
334 larvae were rising more rapidly. In comparison, Norway pout showed a different trend and
335 generally less distinct differences between day and night. Saithe exhibited less variation in
336 Z_{cm} in earlier studies (Munk , in press). Poor cod (*Trisopterus minutus*) was found shallower
337 than in the present study (Olivar & Sabatés 1997). During the day Frank et al. (1992) found a
338 shallower distribution of witch and long rough dab than in this study. However the bottom
339 depth in their study was at 45 m, which may have restricted the depth distribution. The
340 distribution of brill appears not to be described in the literature. In many ways it resembled
341 the distribution of Norway pout, concerning the particularly deep Z_{cm} and the timing of the
342 ascent. However the extent of the vertical migration was greater, covering 43 m. Notably,
343 brill larvae, which were on average smaller than those of other species, exhibited the largest
344 difference in Z_{cm} between day and night, suggesting that already at this small size brill larvae
345 were capable of controlling their position in the water column. The overall tendency of large
346 larvae to aggregate may reflect the developing patchiness in the distribution of older larvae
347 (Hewitt 1981; Matsuura & Hewitt 1995). However, the low number of larvae above 9 mm SL
348 resulted in a great deal of uncertainty concerning diel shifts in distribution.

349 Thermoclines have been described to lead either to larval aggregation (Lough & Potter 1993;
350 Sabatés et al. 2008) or serve as a boundary for their migrations (Olivar & Sabatés 1997;
351 Röpke 1993). Other studies found no apparent influence of thermoclines on larval vertical
352 distribution and migration patterns (Conway et al. 1997; Gray & Kingsford 2003). The weak
353 stratification resulting in a weak thermocline observed at the 18-hours station is similar to
354 conditions in the studies of Gray and Kingsford (2003) and this might be the cause of the
355 apparent weak influence of the thermocline in both studies.

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

365 Gadoid larvae in the observed size range primarily feed on *Calanus finmarchicus* (Gunnerus,
366 1770) eggs and copepod nauplii (Economou 1991) and require about $36\% \text{ d}^{-1}$ of their own
367 body mass (Jones 1973). For a larva of 6 mm standard length this would mean a requirement
368 between 68 μg for saithe and 125 μg for cod (calculated following Economou 1987).

369 Assuming a swimming speed and a reaction distance of one body length as well as
370 proportions between *C. finmarchicus* eggs and nauplii and between nauplii stages as in
371 Economou (1987) and Fransz et al. (1998) the corresponding number of food particles would
372 be 3260 m^{-3} and 5973 m^{-3} , respectively. In May such numbers are not unrealistic in the area
373 (Economou 1987) and would be well within the 27.6% loss of biomass due to the mesh size

374 used (interpolated from table III in Gallienne & Robins 2001) However, zooplankton
375 concentration in deeper strata should still have been sufficient to fulfil food requirements,
376 which may explain why Z_{cm} of Norway pout were not found any shallower than 51 m
377 (equation from Economou 1987; based on: Jones 1973; Laurence 1985). The deepest Z_{cm}
378 observed after the apparent feeding period, could be due to larvae resting in deeper, cooler
379 water to save energy and avoid visual predators (Brett 1971) or less buoyancy due to a full
380 stomach (Sclafani et al. 1993).

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

393

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404

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562

563

564 **Table 1:** Zooplankton densities (g DW m⁻²), per size fraction for all sampled stations, based on GULF VII hauls. The highest abundances along
565 transects were found at the stations at ca. 1°E. Proportions differed between transects. While the biomass in the southern transect was dominated
566 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
567 fractions. Large zooplankton (>2000 µm) was generally scarce with the exception of a few stations, where it contributed to a large proportion of
568 the biomass.

Transect	Station No.	Longitude	Density per size fraction (g DW m ⁻²)			Total
			180-1000 µm	1000-2000 µm	>2000 µm	
60.75°N	423	0.47°W	7.0	4.6	0.1	11.7
	429	0.91°E	19.5	17.3	1.9	38.7
	433	2.60°E	2.1	11.6	0.2	13.9
	437	3.28°E	0.9	2.7	0.2	3.7
	444	4.45°E	1.7	2.0	0.0	3.7
59.3°N	388	4.83°E	3.1	1.3	0.6	5.0
	402	2.52°E	0.7	2.8	0.4	3.9
	406	1.32°E	7.2	20.1	3.2	30.5
	410	0.00°E	0.7	5.8	0.1	6.6
	414	1.32°W	5.1	10.1	4.7	19.9
18h-St.	418	0.61°W	5.0	4.6	0.9	10.5
	419	0.65°W	4.6	8.0	0.4	12.9
	420	0.68°W	4.8	5.8	0.2	10.8
	421	0.61°W	25.0	11.5	19.5	56.0
	422	0.68°W	16.0	10.4	3.2	29.6

569

570 **Table 2:** Average abundances and standard lengths (± 1 SD) for all species identified in the northern transect (a), the southern transect (b) and at
 571 the 18h-station (c). Numbers are based on depth integrated GULF VII, except for species which were only found in MOCNESS hauls. These
 572 species are denoted with asterisks.

a

Transect	Taxon Family	Species	Abundance (nos. m ⁻²)	nos. caught	% measured	Std. Length (mm)
60.75°N	Clupeidae	<i>Clupea harengus</i>	6.9 ± 5.8	30	93.3	17.8 ± 2.7
		Gadidae	<i>Melanogrammus aeglefinus</i>	2.7 ± 4.8	4	100.0
	<i>Merlangius merlangus</i>		22.4 ± 40.4	27	100.0	7.4 ± 1.4
	<i>Pollachius pollachius</i>		2.3 ± 2.4	7	100.0	8.5 ± 1.9
	<i>Pollachius virens</i>		8.5 ± 11.6	14	100.0	9.7 ± 2.9
	<i>Trisopterus esmarkii</i>		51.3 ± 71.9	100	100.0	9.2 ± 2.5
	<i>Trisopterus minutus</i>		7.0 ± 14.7	8	100.0	8.4 ± 1.0
	Unidentified		3.0 ± 4.3	8	62.5	6.6 ± 4.1
	Gobiidae		<i>Gobiusculus flavescens</i>	3.3 ± 7.4	3	100.0
	Lotidae	<i>Ciliata septentrionalis</i>	2.4 ± 4.9	3	100.0	5.4 ± 1.0
		<i>Molva dipterygia</i>	1.1 ± 2.5	1	100.0	6.5 ± -
		<i>Molva molva</i>	6.7 ± 14.9	6	100.0	5.2 ± 0.6
	Pleuronectidae	<i>Glyptocephalus cynoglossus</i>	2.5 ± 4.8	3	100.0	9.7 ± 1.0
		<i>Hippoglossoides platessoides</i>	6.0 ± 9.7	10	100.0	8.6 ± 1.8
		<i>Limanda limanda</i>	4.7 ± 6.9	6	100.0	8.0 ± 4.0
		<i>Pleuronectes platessa</i>	2.2 ± 5.0	2	100.0	6.3 ± 0.4
		Unidentified	0.7 ± 1.1	3	66.7	7.8 ± 1.1
	Scophthalmidae	<i>Lepidorhombus whiffiagonis</i>	1.1 ± 2.5	1	100.0	10.6 ± -
		<i>Phrynorhombus norvegicus</i>	0.4 ± 0.6	2	100.0	9.2 ± 2.0
		<i>Scophthalmus rhombus</i>	3.6 ± 7.3	4	100.0	4.9 ± 1.5

b

Transect	Taxon Family	Species	Abundance (nos. m ⁻²)	nos. caught	% measured	Std. Length (mm)
59.3°N	Ammodytidae	<i>Ammodytes marinus</i>	3.1 ± 6.9	7	100.0	16.2 ± -
		<i>Hyperoplus lanceolatus</i>	1.8 ± 2.8	10	100.0	18.8 ± 5.3
		<i>Unidentified</i>	0.5 ± 1.0	2	100.0	17.5 ± 3.7
	Argentinidae	<i>Argentina sphyraena</i>	0.4 ± 1.0	1	100.0	10.0 ± -
	Clupeidae	<i>Clupea harengus</i>	5.8 ± 12.6	117	94.9	17.1 ± 26.3
	Gadidae	<i>Gadus morhua</i>	4.4 ± 7.7	11	90.9	8.3 ± 3.5
		<i>Melanogrammus aeglefinus</i>	7.6 ± 9.8	22	100.0	9.7 ± 5.0
		<i>Merlangius merlangus</i>	5.2 ± 8.7	12	100.0	5.9 ± 8.2
		<i>Pollachius pollachius</i>	3.1 ± 4.8	8	100.0	9.6 ± 6.7
		<i>Pollachius virens</i>	2.6 ± 4.8	6	100.0	10.4 ± 10.5
		<i>Trisopterus esmarkii</i>	60.9 ± 79.9	159	96.2	8.8 ± 5.0
		<i>Trisopterus minutus</i>	4.4 ± 7.7	10	100.0	6.3 ± 7.9
		<i>Unidentified</i>	2.2 ± 3.8	5	20.0	9.2 ± -
	Lotidae	<i>Ciliata mustela</i>	0.9 ± 2.0	2	100.0	5.1 ± 0.2
	Pleuronectidae	<i>Hippoglossoides platessoides</i>	4.6 ± 5.6	14	100.0	11.2 ± 3.1
		<i>Limanda limanda</i>	2.6 ± 4.8	6	83.3	7.8 ± 1.7
	Scophthalmidae	<i>Scophthalmus rhombus</i>	0.9 ± 2.0	2	100.0	3.8 ± 0.3

c

Transect	Family	Taxon Species	Abundance (nos. m ⁻²)		nos. caught	% measured	Std. Length (mm)	
18h-St.	Ammodytidae	<i>Hyperoplus immaculatus</i> *	0.2	± 0.4	1	100.0	11.9	± 0
		<i>Hyperoplus lanceolatus</i>	0.8	± 1.8	1	100.0	40	± -
	Argentinidae	<i>Argentina sphyraena</i>	20.0	± 29.2	11	90.9	10.1	± 2.4
	Clupeidae	<i>Clupea harengus</i>	0.5	± 1.1	1	100.0	14.9	± -
	Gadidae	<i>Gadus morhua</i>	1.3	± 2.8	1	100.0	5.8	± -
		<i>Melanogrammus aeglefinus</i>	3.6	± 2.4	4	100.0	6.3	± 1.4
		<i>Merlangius merlangus</i>	152.3	± 138.5	113	99.1	6.3	± 1.3
		<i>Pollachius pollachius</i>	9.4	± 15.0	5	100.0	7.1	± 1.6
		<i>Pollachius virens</i>	15.3	± 8.5	13	100.0	7.0	± 2.4
		<i>Trisopterus esmarkii</i>	81.2	± 77.6	57	98.2	7.2	± 1.6
		<i>Trisopterus minutus</i>	7.4	± 7.6	5	80.0	6.2	± 1.4
		<i>Unidentified</i>	14.4	± 11.7	13	76.9	5.3	± 1.0
	Gobiidae	<i>Gobius niger</i>	0.8	± 1.8	1	100.0	5.5	± -
		<i>Gobiusculus flavescens</i>	3.6	± 8.0	1	100.0	6.8	± -
		<i>Unidentified</i> *	0.2	± 0.4	1	100.0	2.7	± -
	Lotidae	<i>Ciliata septentrionalis</i>	17.8	± 22.0	14	100.0	5.7	± 0.9
		<i>Molva dipterygia</i>	7.2	± 16.0	2	100.0	7.9	± 0.2
		<i>Molva molva</i>	2.5	± 5.7	2	100.0	6.9	± 0.8
	Pleuronectidae	<i>Glyptocephalus cynoglossus</i>	6.2	± 6.9	4	100.0	6.9	± 1.3
		<i>Hippoglossoides platessoides</i>	20.2	± 29.2	12	83.3	8.3	± 3.3
		<i>Limanda limanda</i>	2.5	± 5.6	5	80.0	6.8	± 1.6
		<i>Platichthys flesus</i> *	0.4	± 0.9	5	100.0	3.5	± 0.5
		<i>Pleuronectes platessa</i>	0.8	± 1.8	1	100.0	10.4	± -
		<i>Unidentified</i>	1.3	± 1.9	2	100.0	5.3	± 0.5
	Scophthalmidae	<i>Scophthalmus rhombus</i>	18.6	± 20.2	12	100.0	4.5	± 0.7

577 **Figure captions:**

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

581

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

588

589 **Figure 3:** Temperature, salinity and fluorescence at the 18h-station (panel a), averaged over
590 all 5 hauls. The broken lines depict the boundaries between the sampled depth strata in depth
591 discrete hauls. Most changes in hydrography and fluorescence occurred between 50 and 80
592 m, mainly in the stratum between 40 and 75 m. Error bars are only shown for every ten
593 metres of depth. Panels b and c show the distribution of all size classes of zooplankton
594 ($<1000 \mu\text{m}$, $1000\text{-}2000 \mu\text{m}$ and $>2000 \mu\text{m}$) during daylight and night conditions in % of
595 total.

596

597 **Figure 4:** Vertical distribution of gadoid fish larvae and $<1000 \mu\text{m}$ zooplankton by dry
598 weight, during day and night as a % of total abundance or biomass. N represents the number

599 of larvae caught under the respective light conditions (in subscript). The y-axis depicts the
600 boundaries between sampled strata.

601

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

606

607 **Figure 6:** Depth of the centre of abundance for gadoid (a) and flatfish larvae (b) in three
608 different light environments. Due to the long days at this time of the year, there was only one
609 station at dusk (21:52 UTC) and night (23:56 UTC), while three stations were in daylight
610 (19:14 UTC, 06:20 UTC and 08:22 UTC). As it was shortly after sunrise the station at 06:20
611 UTC was not included into the calculation of Z_{cm} . The number of larvae caught under each
612 light condition is given as N in the legend. The depth of mass for zooplankton (based on mg
613 m^{-3}) is depicted in both panels.

614

615 **Figure 7:** Depth of the centre of abundance for gadoid (a) and flatfish larvae (b) for
616 individual samples taken at the 18h-station. Daylight stations were at 19:14 UTC, 06:20 UTC
617 and 08:22 UTC, the station at 21:52 UTC was during dusk and the station at 23:56 UTC in
618 the night. The number of larvae caught at each station is given as N, with the time of
619 sampling given in subscript. The depth of mass for zooplankton (based on mg m^{-3}) is depicted
620 in both panels.

621

622 **Figure 8:** Rounded length distribution across strata and light conditions of cod, haddock and
623 whiting as % of total abundance. The majority of larvae ranged from 3 to 6 mm standard
624 length. Even for the larvae at the lower end of this range, changes in distribution across strata
625 could change substantially between the different light conditions. Empty panels indicate zero
626 findings for the respective species in this stratum, during the entire sampling period.

627

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

638

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

645 larvae were found at the low extreme of the size range and exhibited strong fluctuations
646 across the depth range.

647

Figure 1:

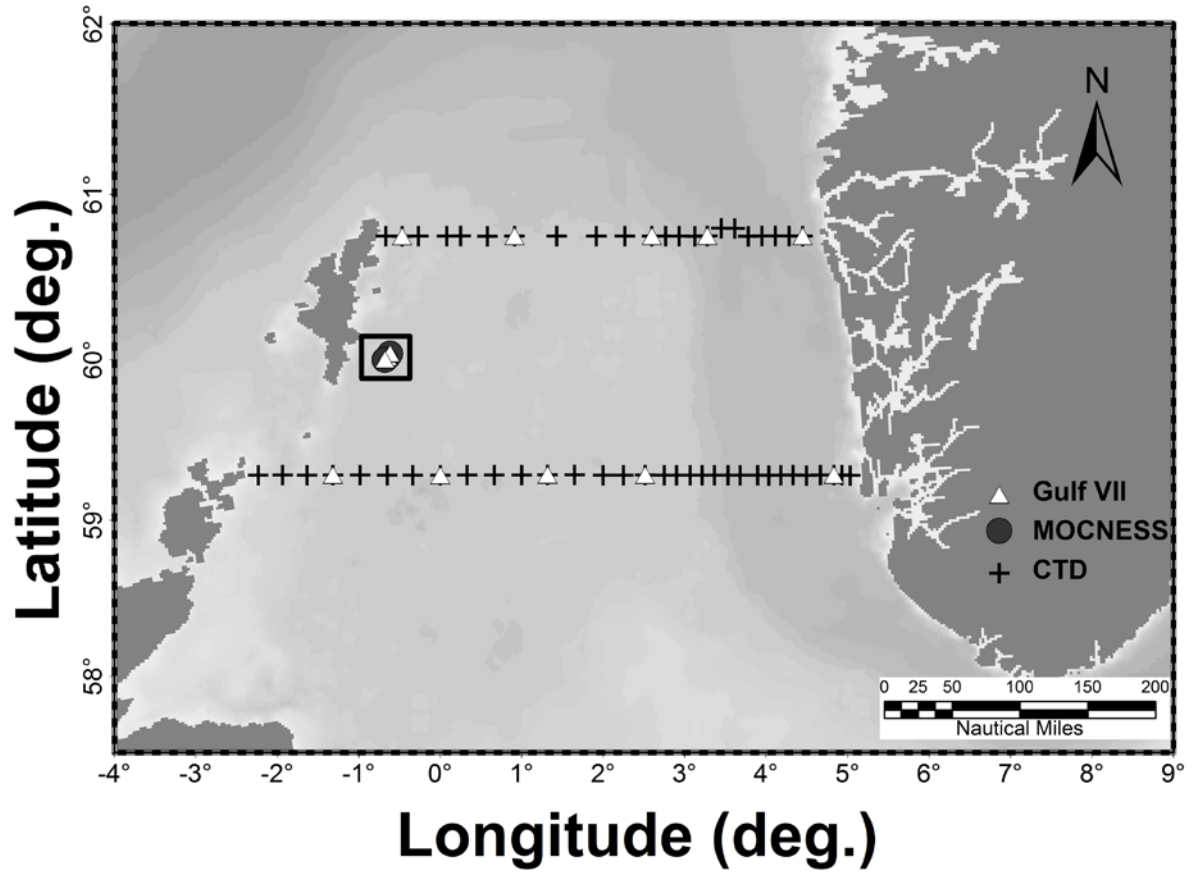


Figure 2:

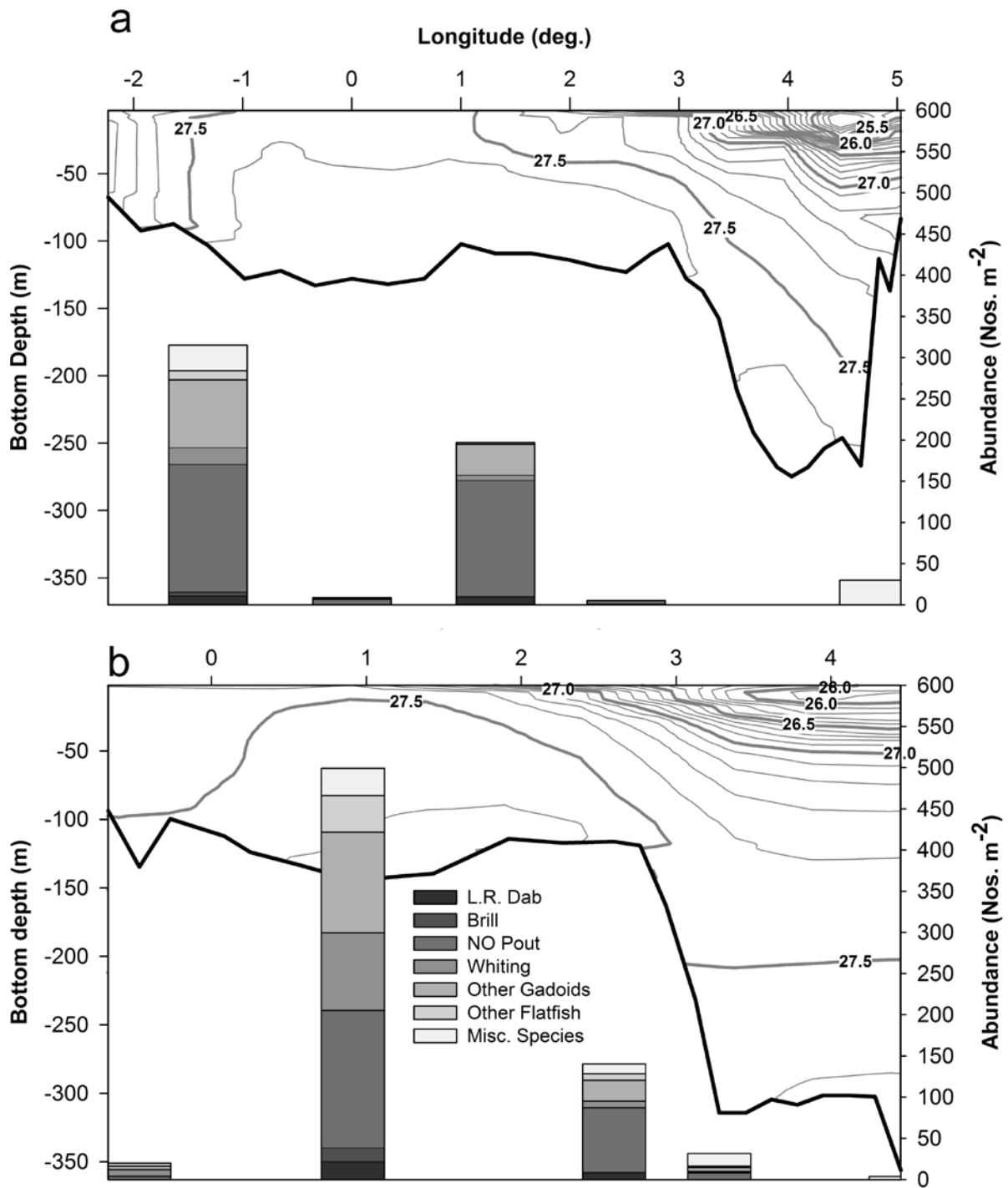


Figure 3:

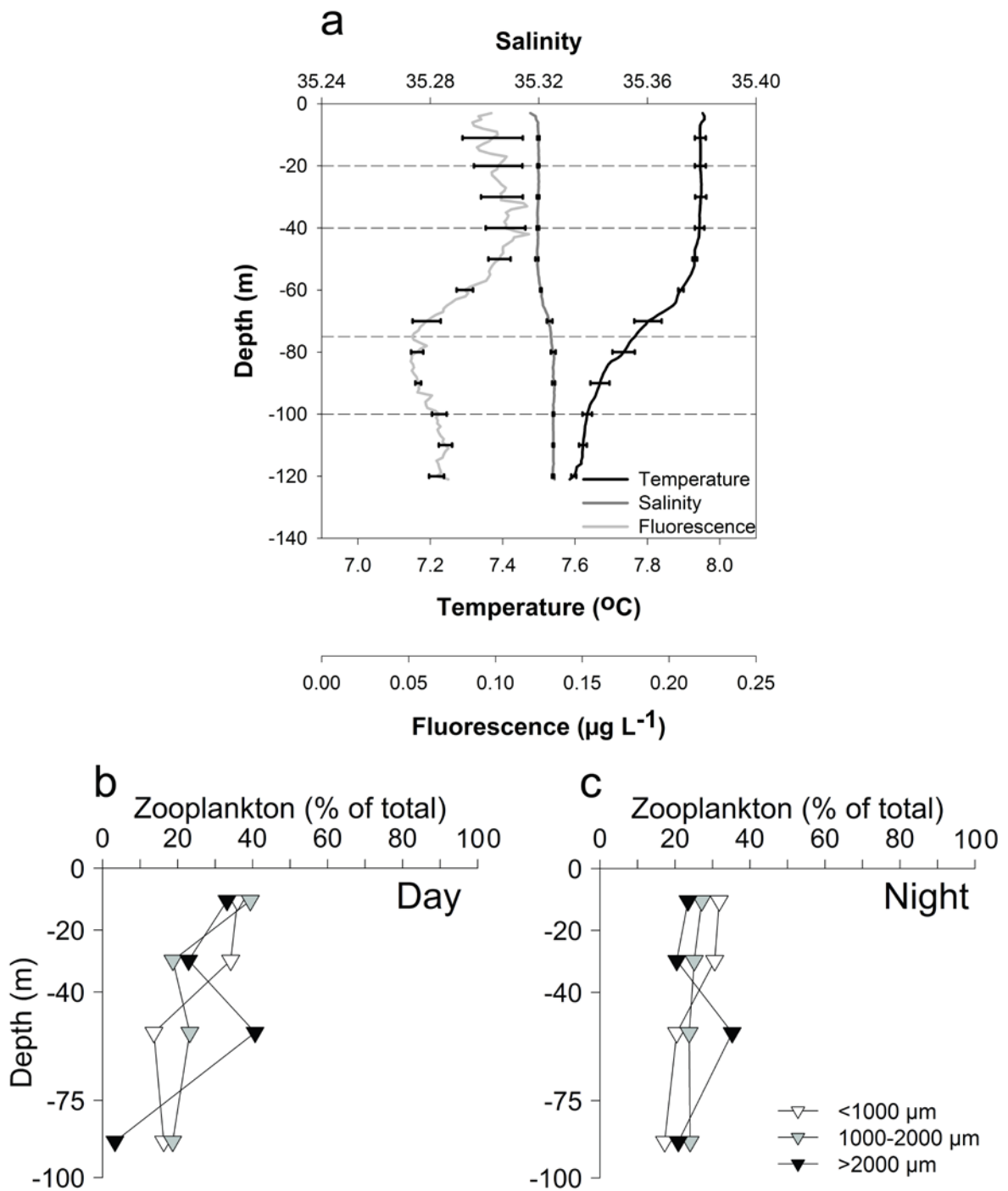


Figure 4:

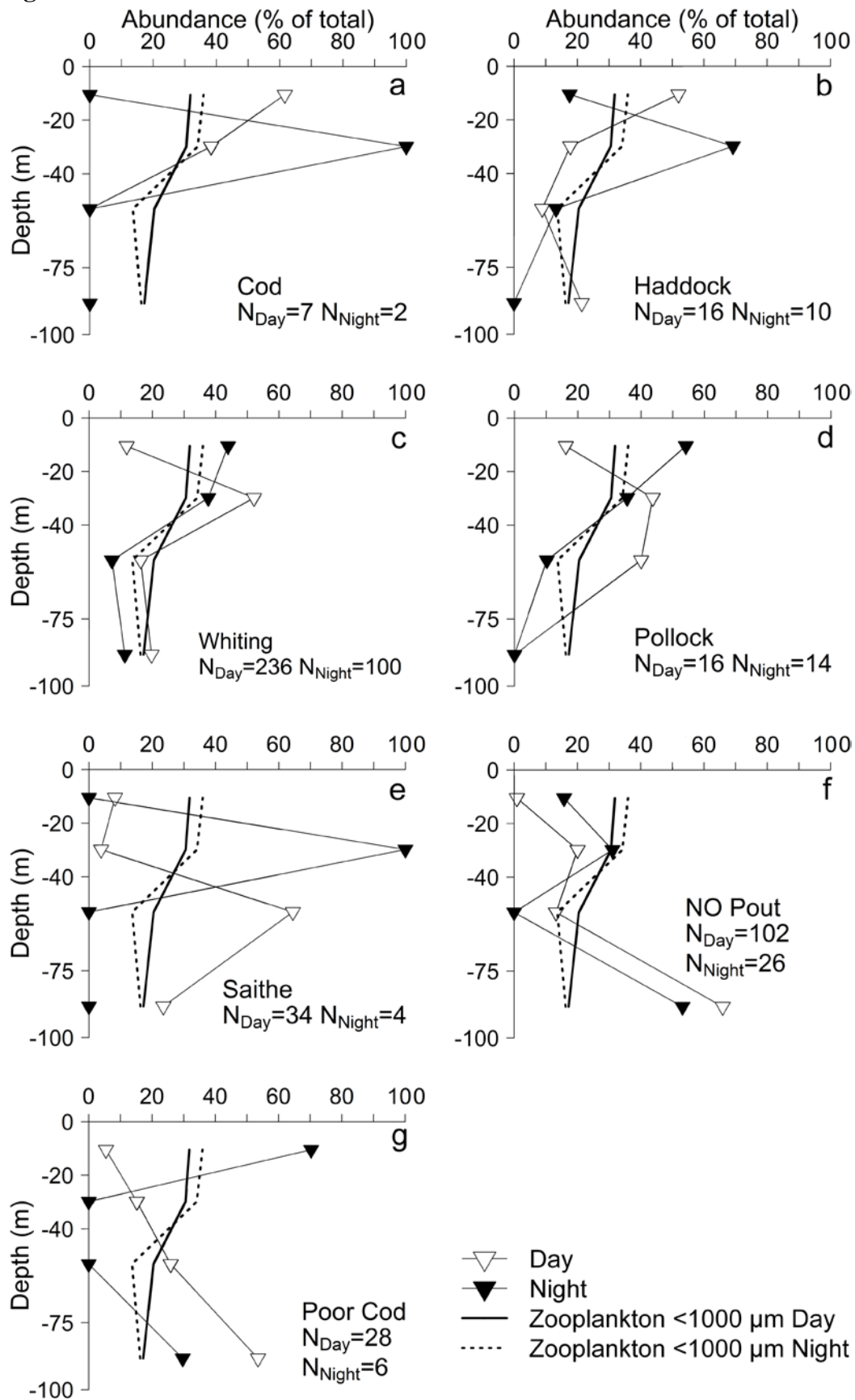


Figure 5:

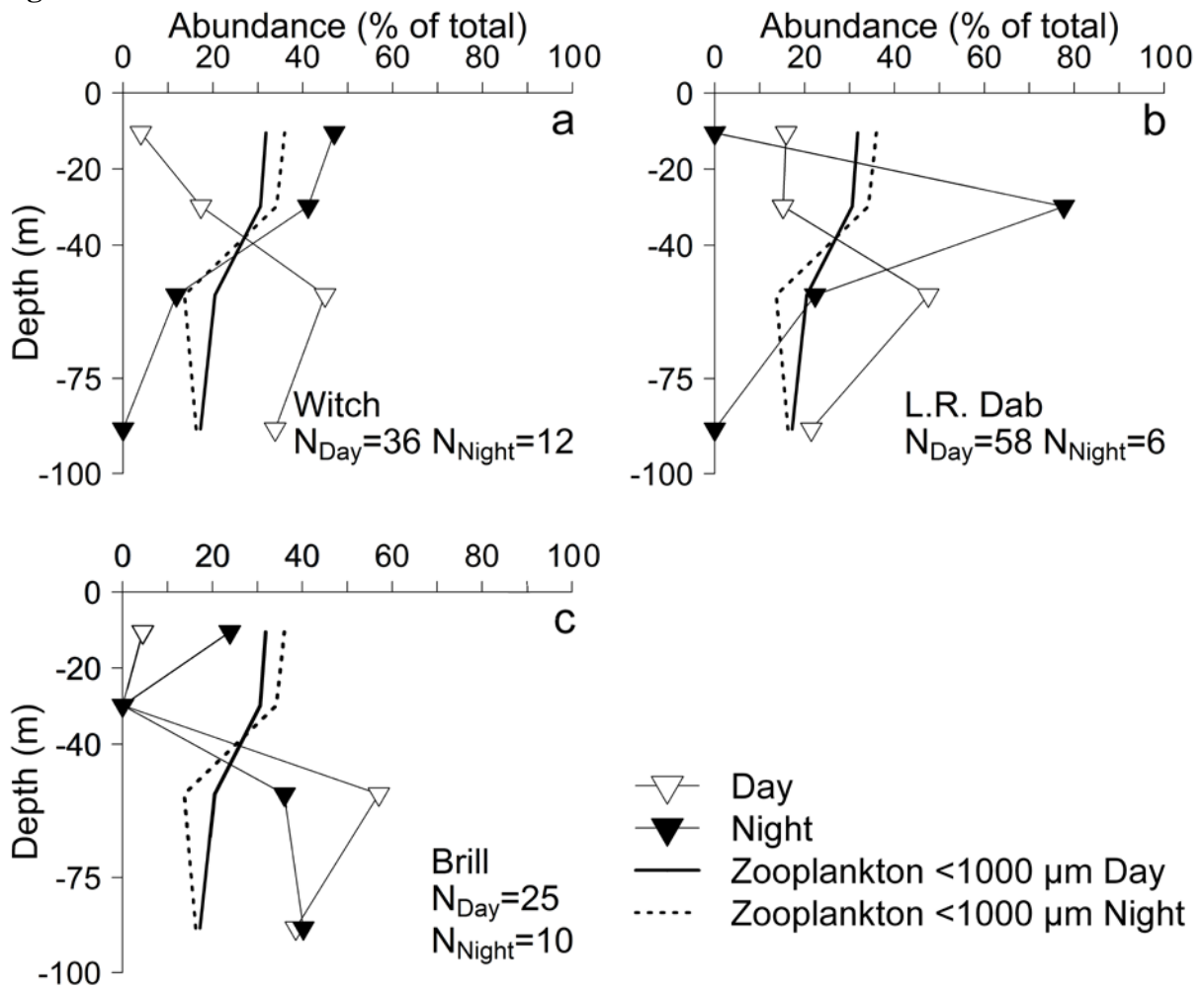


Figure 6:

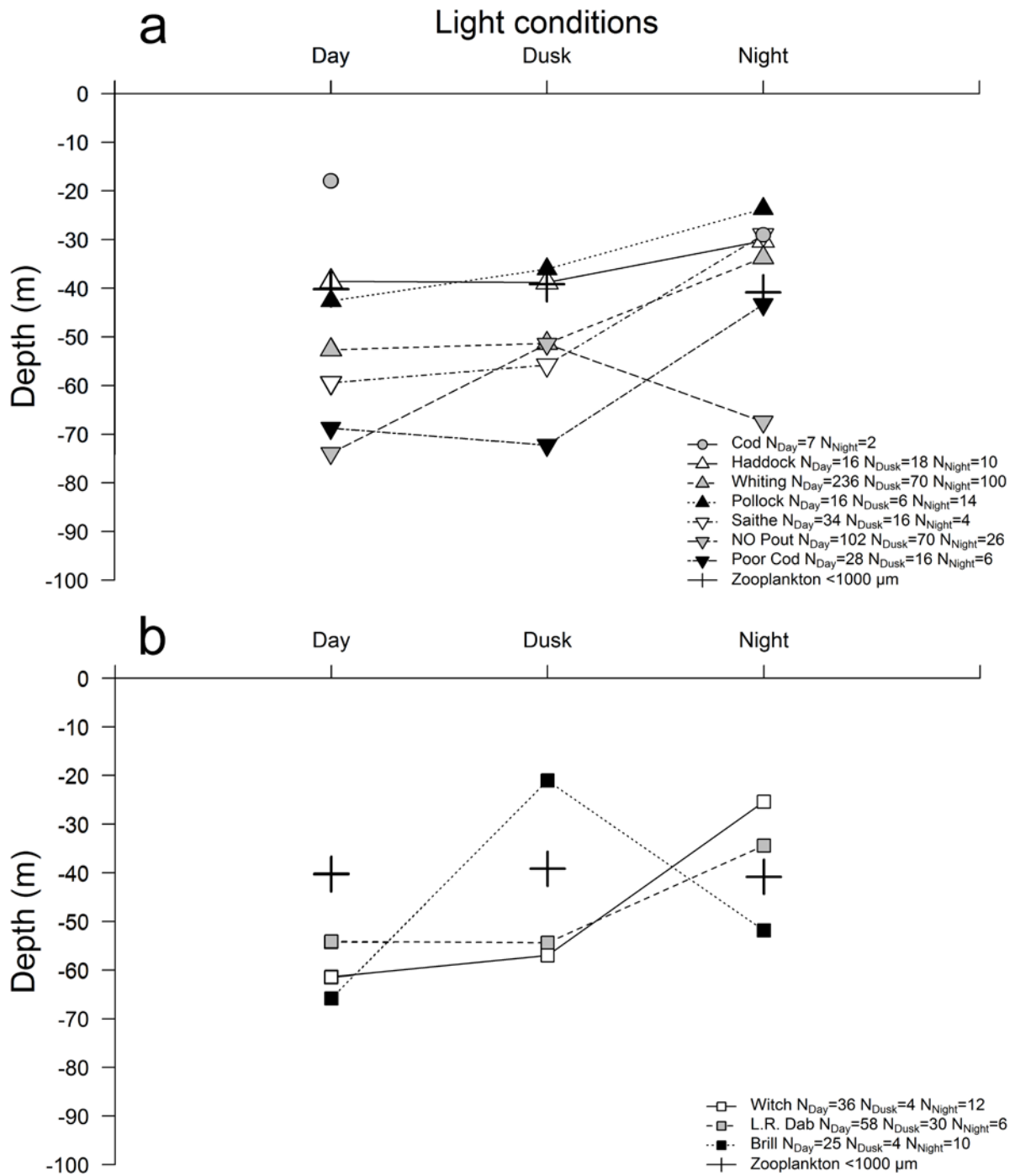


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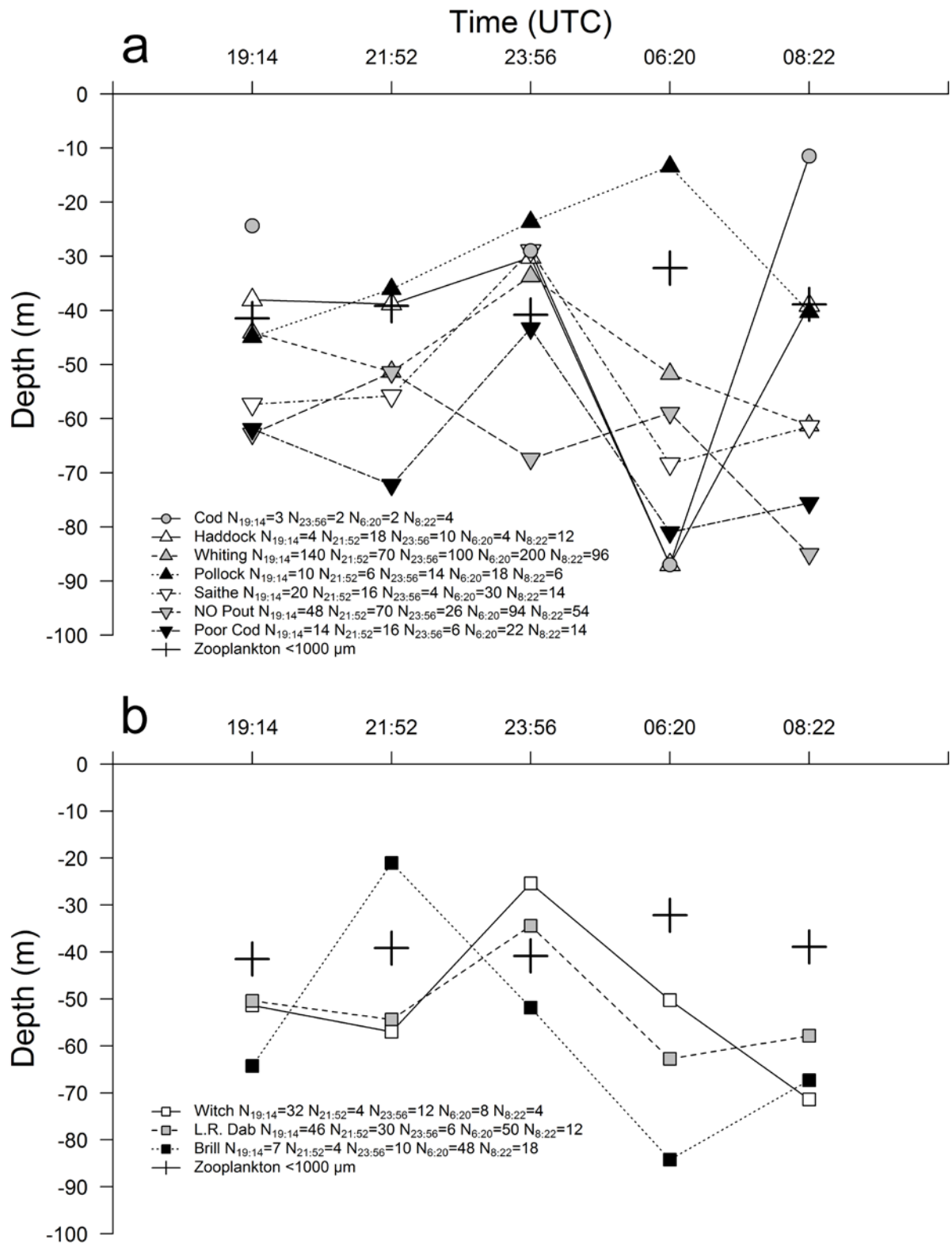


Figure 8:

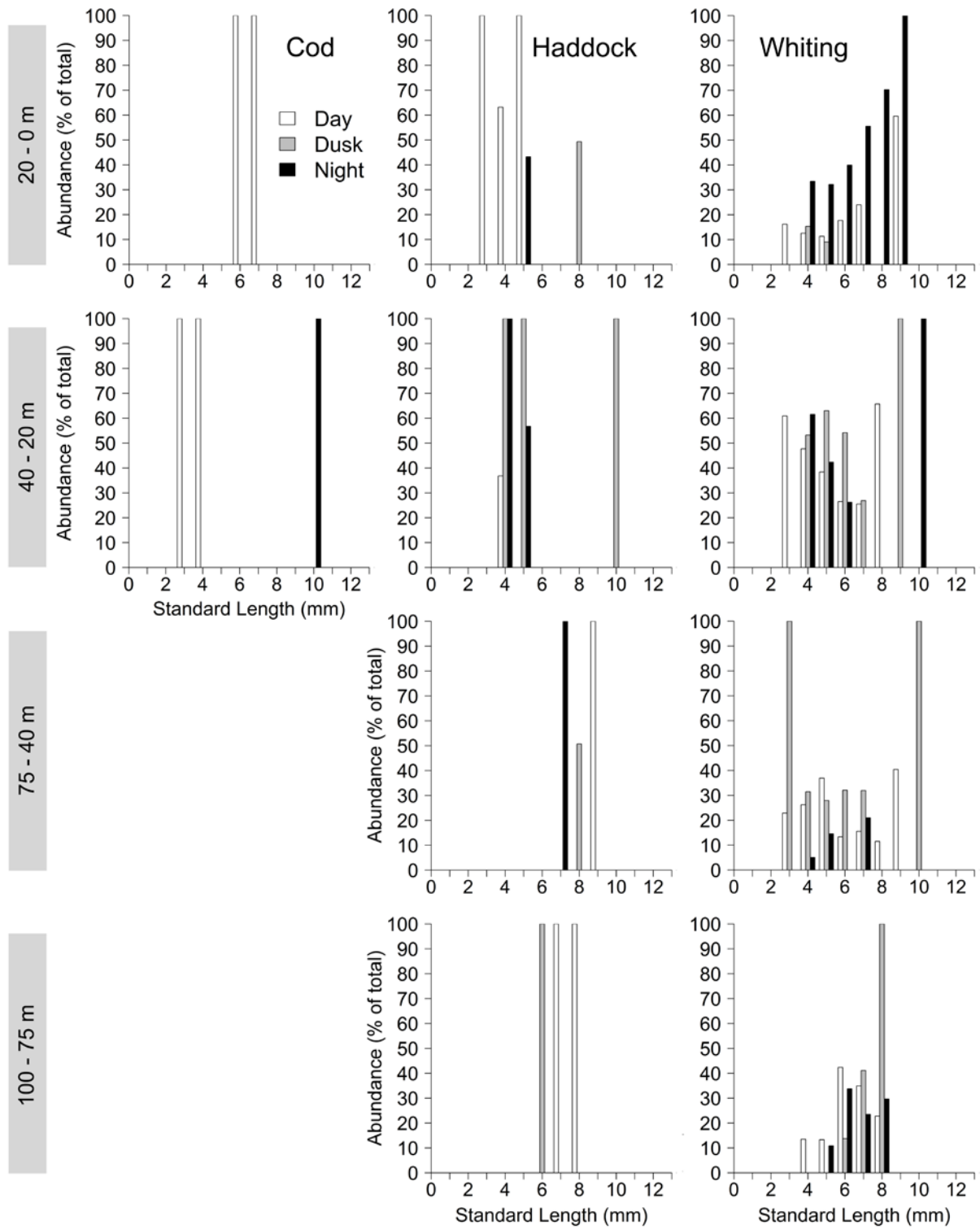


Figure 9:

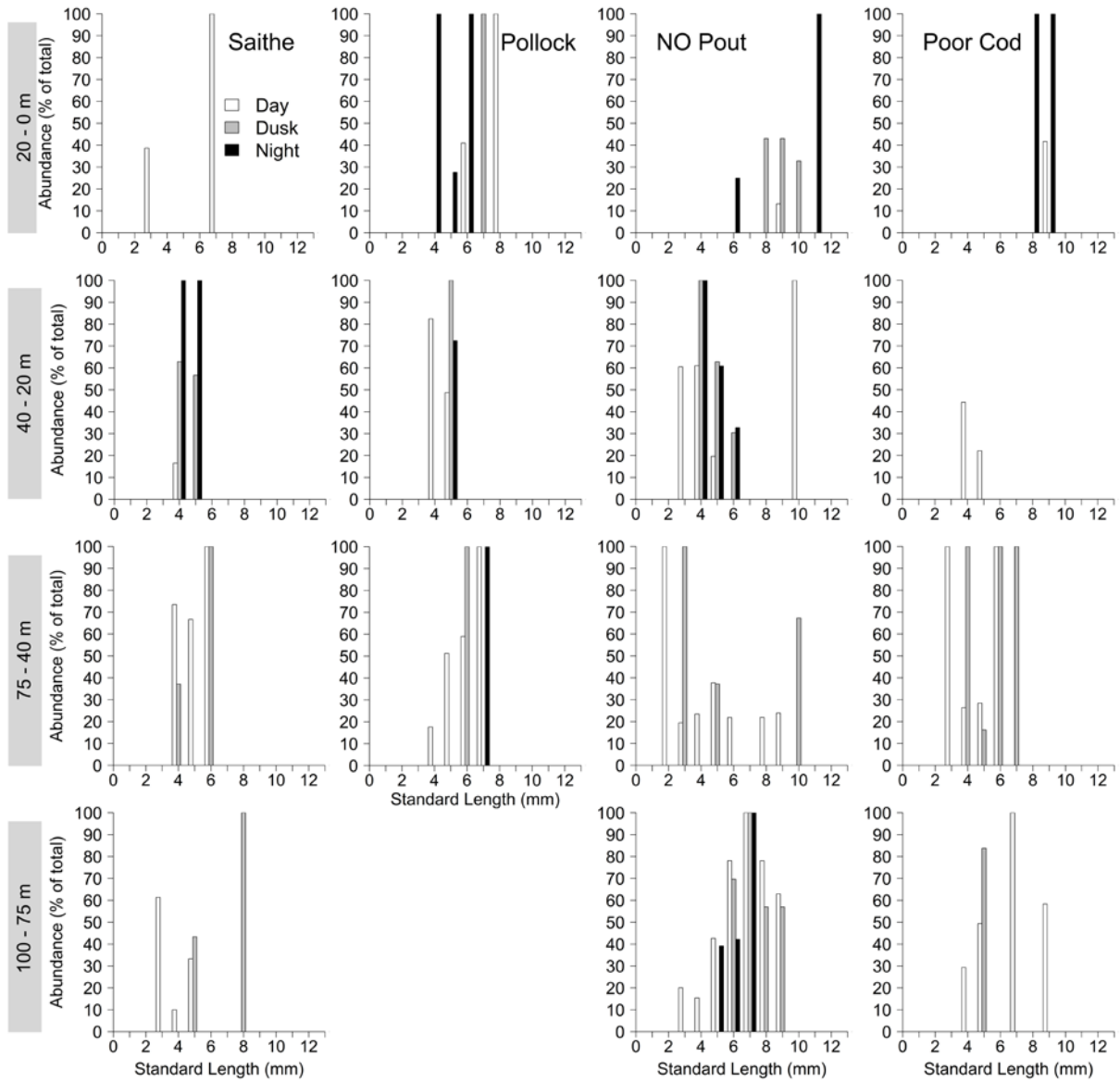


Figure 10:

