Diel vertical distribution of fish larvae during the winter-mixing period in the Northwestern Mediterranean

A. Sabatés

The vertical distributions of the larvae of shelf and oceanic fish species that spawn during the winter-mixing period in the Mediterranean are described from 22 vertically stratified plankton tows. Diel differences in the vertical distribution patterns in relation to physical data and potential prey abundance throughout the water column were examined. Even in absence of stratification, the larvae of the various fish species showed different patterns of vertical distribution and diel changes. The larvae of shelf-dwelling species were found in the surface layers, mainly above 50-m depth, and with some exceptions, with very little diel variation in depth distribution. Therefore, the vertical distribution of the larvae of these species coincided with the maximum concentrations of their potential food, nauplii and copepodite stages of copepods. The larvae of mesopelagic fishes showed deeper distributions in the water column and most of these species were located closer to the surface during the day than at night. Given the homogeneity of the physical characteristics throughout the water column, except for light, this behaviour may be determined not only by the higher concentration of prey in the surface layers but also by adequate light levels for feeding.

Introduction

Marine fish larvae show a wide range of vertical distribution patterns that can be actively altered depending on various biotic and abiotic factors (Heath, 1992) and diel vertical migration is well documented (Neilson and Perry, 1990). Most species appear to ascend towards the surface at night (e.g. Kendall and Naplin, 1981; Lyczkowski-Shultz and Steen, 1991), although the opposite tendency has also been observed (e.g. Haldorson et al., 1993; Brodeur and Rugen, 1994). Some species do not show diel variations (Röpke, 1989) or else form aggregations during the daytime and disperse at night (e.g. Munk et al., 1989; Leis, 1991). The explanation for these migrations is controversial, but they have been related largely to following optimum light conditions (Heath et al., 1988), predator avoidance (Hunter and Sanchez, 1976) and suitable prey concentrations (Munk et al., 1989). It has been reported that fish larvae can concentrate in or above the thermocline, where the maximum concentrations of food are usually found (Ahlstrom, 1959; Kendall and Naplin, 1981; Coombs et al., 1983). Lasker (1981) proposed that persistence of vertical stratification allowed the development of suitable prey concentrations for anchovy larvae. In addition, it has been suggested that haddock larvae from stratified waters were in better condition than those from well-mixed areas (Frank and McRuer, 1989). Although the presence and position of the thermocline has been considered to be an important interface in the vertical distribution of fish larvae, other studies make it clear that it only has a limited role in the vertical distribution patterns of fish larvae (Gray, 1996; Conway et al., 1997).

The Mediterranean has a marked seasonality, as is to be expected given its geographical situation in mid-latitudes, with alternating periods of mixing and stratification. The summer is characterized by a marked stratification of the water column. Under these conditions, nutrients are gradually depleted in the mixed layer above the thermocline, and production in the water column becomes limited to the deep chlorophyll maximum (Estrada, 1985). In winter, the low temperatures, together with the effect of the wind, break down stratification and nutrients from deeper waters reach the surface layers. Therefore, during the winter period the absence of strong vertical gradients means...
that the water column is well mixed. This absence of vertical stability could favour a situation where fish larvae would not show stratified distributions and also allows movements of larvae along the water column. Without the physical constraints derived from stratification, larvae would seek those levels with the most suitable environmental conditions.

Although most fish species in the Mediterranean spawn during the spring and summer, some species that inhabit the continental shelf and slope, such as the sardine, *Sardina pilchardus* and some gadoids, reproduce in winter, while the mesopelagic species spawn throughout the year. Information on the vertical distribution of fish larvae in the Mediterranean is limited to the spring–summer period (Palomera, 1991; Olivar and Sabatés, 1997; Coombs et al., 2003) and there is no information available during the winter period, with the exception of certain species, such as the sardine (Olivar et al., 2001). This study describes the vertical distribution of larvae of both shelf and mesopelagic fish species, during the period of winter mixing in the Mediterranean. Diel differences in their vertical distribution patterns in relation to physical environment and food availability are examined.

**Material and methods**

This work was undertaken in the Catalan Sea (Northwestern Mediterranean Sea) in February 1997. A 25-nautical mile long transect, perpendicular to the bathymetry, and centred approximately on the 1000-m isobath was sampled twice. The transect comprised 11 stations, spaced 2.5 miles apart (Figure 1). Therefore, a total of 22 stations were consecutively sampled (nine during the day and 13 during the night). A CTD cast and a plankton tow were performed at each station. The vertical profiles of the basic hydrographic parameters (temperature, salinity, and fluorescence) were obtained with a SeaBird 25 CTD probe equipped with a SeaTech fluorometer. Vertically stratified zooplankton samples for fish larvae (45-cm mouth diameter, 300-μm mesh) and microzooplankton (9-cm diameter, 53-μm mesh) were collected simultaneously using a double Longhurst–Hardy Plankton Recorder net (LHPR; Williams et al., 1983). Tows were taken obliquely from the surface down to a depth of 300 m, with a sampling time of 10 min per stratum and a vertical resolution of 20 m in the first 100 m and 50 m for the remainder of the sampling interval. The towing speed was 3.5 knots and so every tow spanned a distance of approximately 9 km and it took about 48 h to complete each transect. The volume of water filtered by each net was recorded by a flowmeter attached to the mouth of the net. The average volume of water filtered for each sample was 67 m³ (34 s.d.) for the coarse net, while the fine mesh filtered 0.65 m³ (0.16 s.d.).

Zooplankton samples were fixed in 5% formaldehyde buffered with sodium tetraborate. All fish larvae were extracted from the 333-μm samples in the laboratory and identified to species level. Larval density was standardized to number per 1000 m³. For the microzooplankton aliquots were made for counting nauplii and the copepodite stages of copepods. Two aliquots were taken from each sample, and at least 300 individuals in each aliquot were counted. Mean concentration in the aliquots was expressed as number of individuals per m³.

**Results**

**Hydrography**

The temperature was virtually homogeneous throughout the water column, ranging between 12.8 and 13.8°C, which is a typical situation in winter for this zone (Figure 2). The salinity was lower in the first 30 m of the column, due to the influence of freshwater outflows from the River Ebro. This gave way to a slight pycnocline between 20 and 40 m. Fluorescence profiles showed highest values at the surface and between 30 and 40 m, slightly below the pycnocline (Figure 2).

**Microzooplankton and fish larvae**

The mean abundance of nauplii and copepodite stages of copepods in the various depth strata were higher in the first 40 m of the water column and decreased gradually with depth (Figure 3). No clear diel differences were observed in the distribution patterns.

Fish larvae belonging to a total of 21 taxa were identified, 13 corresponded to species that live on the continental shelf as adults and eight were mesopelagic,
open-sea, species. The mean concentrations of the different species collected in the different depth strata sampled are shown in Table 1. Abundance levels were higher for the mesopelagic group, which was dominated mainly by myctophid species (Table 1), although one shelf species, the sardine was also quite abundant. In general, most larvae of the different species collected, except the sardine, were small in size, less than 5-mm SL.

Figure 2. The mean vertical profiles, for all stations, of temperature (°C), salinity (psu), density (ρt), and fluorescence (arbitrary units) during the study period (horizontal lines indicate standard deviation).

Figure 3. The vertical distribution of nauplii and copepodite stages of copepods in daytime (light shading) and night-time (dark shading). The values correspond to the mean abundance at all stations for each depth stratum.
Table 1. Mean densities (No. per 1 000 m$^3$) and standard deviation of fish larvae at each depth stratum, all stations combined.

<table>
<thead>
<tr>
<th>Depth (m)</th>
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<td>Shelf species</td>
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<tr>
<td><em>Argyrostoma laterna</em></td>
<td>30 ± 44</td>
<td>79 ± 138</td>
<td>39 ± 71</td>
<td>28 ± 25</td>
<td>25 ± 59</td>
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<td><em>Callionymus</em> spp.</td>
<td>21 ± 33</td>
<td>13 ± 27</td>
<td>27 ± 39</td>
<td>28 ± 32</td>
<td>54 ± 102</td>
<td>43 ± 66</td>
<td>7 ± 8</td>
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<td>Carapidae</td>
<td>9 ± 11</td>
<td>14 ± 21</td>
<td>7 ± 9</td>
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<td><em>Dicentrarchus</em> labrax</td>
<td>12 ± 9</td>
<td>20 ± 19</td>
<td>8 ± 13</td>
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<td>13 ± 18</td>
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<td><em>Gaidropsarus</em> spp.</td>
<td>10 ± 7</td>
<td>12 ± 16</td>
<td>9 ± 11</td>
<td>22 ± 29</td>
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<td>3 ± 7</td>
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<td>Gobiidae</td>
<td>4 ± 6</td>
<td>61 ± 70</td>
<td>18 ± 21</td>
<td>6 ± 8</td>
<td>33 ± 43</td>
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<td><em>Helicolenus dactylopterus</em></td>
<td>3 ± 5</td>
<td>15 ± 15</td>
<td>10 ± 17</td>
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<td><em>Merluccius merluccius</em></td>
<td>3 ± 7</td>
<td>7 ± 10</td>
<td>5 ± 7</td>
<td>12 ± 13</td>
<td>28 ± 38</td>
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<td>Pagellus bogaraveo</td>
<td>18 ± 12</td>
<td>13 ± 17</td>
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<td><em>Sardina pilchardus</em></td>
<td>252 ± 553</td>
<td>671 ± 1674</td>
<td>392 ± 922</td>
<td>104 ± 177</td>
<td>148 ± 310</td>
<td>120 ± 234</td>
<td>3 ± 2</td>
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<td><em>Scomber scombrus</em></td>
<td>17 ± 3</td>
<td>54 ± 60</td>
<td>14 ± 24</td>
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<td>Triglidae</td>
<td>21 ± 21</td>
<td>28 ± 44</td>
<td>9 ± 14</td>
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<td><em>Trisopterus luscus</em></td>
<td>5 ± 8</td>
<td>11 ± 20</td>
<td>8 ± 13</td>
<td>16 ± 17</td>
<td>49 ± 59</td>
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<td><em>Argyropelecus hemigymnus</em></td>
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<td><em>Benthosema glaciale</em></td>
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<td><em>Ichthyococcus ovatus</em></td>
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<td><em>Maurolicus muelleri</em></td>
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<td><em>Myctophum punctatum</em></td>
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<td><em>Notolepis rissoi</em></td>
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<td><em>Notoscopelus elongatus</em></td>
<td>20 ± 26</td>
<td>46 ± 58</td>
<td>54 ± 33</td>
<td>55 ± 59</td>
<td>41 ± 50</td>
<td>39 ± 60</td>
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<td><em>Symbolophorus veranyi</em></td>
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The vertical distribution patterns for larvae of shelf species are shown in Figure 4. In general, the larvae of these species were located in the surface levels of the water column. The larvae of *Arnoglossus laterna* were mainly found between the surface and 60 m with fewer at the surface at night and a deeper extension during the day. The larvae of *Callionymus* spp. were located during the day mainly between the surface and 60 m, whereas at night they were more concentrated between 40 and 80 m. *Dicentrarchus labrax* larvae were distributed relatively close to the surface, with higher concentration between 10 and 20 m day and night. The larvae of *Merluccius merluccius* and *Trisopterus luscus* were collected between depths of 10 and 80 m during the day, whereas at night they showed greatest concentrations between 60 and 80 m. Larvae of the sardine *Sardina pilchardus* were mainly distributed between the surface and 80 m, although the greatest abundance were found between 10 and 30 m, both by day and by night. Given the high abundance of sardine larvae collected and their wide size range, two size ranges were plotted separately. Figure 5 shows the distribution for larvae <10-mm SL and >10-mm SL. The smallest larvae were mainly distributed in the upper 30 m, both day and night, whereas the largest larvae were relatively evenly dispersed, especially during the day (Figure 4).

The vertical distribution patterns for mesopelagic fish larvae are shown in Figure 6. In general, they showed wide distributions in the water column, although different species were confined to distinct depth zones. Among the Myctophidae, the larvae of *Notoscopelus elongatus* had a more surface distribution, mainly between 10 and 60 m during the day and 30-100 m at night. *Benthosema glaciale* showed an intermediate distribution between 20 and 100 m during the day but it was slightly deeper during the night, between 40 and 100 m. *Myctophum punctatum* showed a deeper distribution between 40 and 150 m, with the highest concentration between 60 and 80 m during the night and deeper, between 100 and 150 m, during the day. The larvae of *Maurolicus muelleri* were mainly located between 30 and 150 m, both day and night, with some evidence of a shift towards the surface at night. The larvae of *Notolepis rissoi* showed a marked change in distribution day and night, situated between 30 and 80 m during the day and between 60 and 200 m at night. *Argyropelecus hemigymnus* were mainly located below 100 m, both day and night but shifted towards a shallower distribution during the day. Although most of the larvae collected were of a small size,
the distribution throughout the column for larvae <5-mm SL and >5-mm SL for the most abundant species, *B. glaciale* (Figure 7), showed that there were only slight diel differences in the distribution of the smallest larvae, whereas the larger larvae were located much deeper at night than during the day.

**Discussion**

The winter period in the Mediterranean is characterized by well-mixed waters, but even in the absence of thermal stratification, the vertical distributions of larvae of different fish species were structured throughout the water column.

![Figure 5](https://academic.oup.com/icesjms/article-abstract/61/8/1243/629260)

Figure 5. The vertical distribution of *Sardina pilchardus* larvae by size class in daytime (light shading) and night-time (dark shading). The percentages calculated are based on the mean abundance at all stations for each depth stratum.

![Figure 6](https://academic.oup.com/icesjms/article-abstract/61/8/1243/629260)

Figure 6. The vertical distribution of larvae of six mesopelagic fish in daytime (light shading) and night-time (dark shading). The percentages calculated are based on the mean abundance at all stations for each depth stratum.
This is consistent with the vertical distribution patterns previously observed for assemblages of fish larvae from both coastal and oceanic waters (e.g. Ahlstrom, 1959; Leis, 1991; Röpke, 1993). The potential food organisms, nauplii and copepodite stages of copepods, showed a marked reduction in abundance with depth. The same pattern has been described both in vertical-mixing conditions (Mediterranean and North Atlantic; Hillgruber and Kloppmann, 2000; Olivar et al., 2001) and stratification (Mediterranean; Coombs et al., 2003). Nevertheless, in the North Atlantic other authors pointed out a more dispersed distribution down the water column under mixed conditions than when stratified (Coombs et al., 1992). In the present study, the abundance values of potential food particles were comparable with other estimates from elsewhere in the Mediterranean for the same period (Calbet et al., 2001; Sabatés et al., 2001; Coombs et al., 2003).

The larvae of shelf-dwelling species were found in the surface layers, mainly above 50-m depth, and there was very little diel variation in their depth distribution. Therefore, the vertical distribution of the larvae of these species coincided with the maximum concentrations of their potential food, nauplii and copepodite stages of copepods. Sardine larvae were located mainly between 50–80 m, but they also occur at depths to 150 m (Coombs and Mitchell, 1982; Röpke, 1989; Motos et al., 2000). Although the vertical distribution observed in the present study coincided with the above mentioned studies, during the day the distribution of the larvae extended more towards the surface. The larvae of Callionymus spp. were located slightly deeper at night than during the day as also noted by Olivar and Sabatés (1997) during the summer period in the Mediterranean. Nevertheless, in the North Atlantic Ocean, no evidence of diel variation has been described in the larvae of this genus (Röpke, 1989; Conway et al., 1997), while Southward and Bary (1980) found indications that they migrated upwards at night. The vertical distribution range detected in Arnoglossus laterna is broadly similar to that observed in previous studies conducted in the Mediterranean and in the North Atlantic Ocean (Röpke, 1989; Olivar and Sabatés, 1997) and, as described in these studies, larvae were less abundant at surface during the night.

In general, the larvae of mesopelagic fish showed deeper distributions in the water column than the shelf-dwelling species, which had already been indicated from other geographical areas (e.g. Ahlstrom, 1959; Moser and Pommeranz, 1999; Cass-Calay, 2003). In the northeastern Atlantic Ocean, the larvae of M. merluccius are mainly located between 50–80 m, but they also occur at depths to 150 m (Coombs and Mitchell, 1982; Röpke, 1989; Motos et al., 2000). The vertical distribution range detected in Benthosema glaciale is broadly similar to that observed in previous studies conducted in the Mediterranean and in the North Atlantic Ocean (Röpke, 1989; Olivar and Sabatés, 1997) and, as described in these studies, larvae were less abundant at surface during the night.

In general, the larvae of mesopelagic fish showed deeper distributions in the water column than the shelf-dwelling species, which had already been indicated from other geographical areas (e.g. Loeb, 1979; Boehlert et al., 1992; Röpke, 1993). It has been reported for the Lampanctinae, a subfamily of the Myctophidae, that the vertical distribution of the larvae is shallower than that of the larvae of the Myctophinae subfamily (Ahlstrom, 1959; Loeb, 1979; Moser and Smith, 1993). In our study, the larvae of N. elongatus, the only representative of the Lampanctinae subfamily, showed a more surface distribution, whereas the larvae of M. punctatum, belonging to the Myctophinae subfamily, had a deeper distribution. Nevertheless, the larvae of B. glaciale, also belonging to the Myctophinae

Figure 7. The vertical distribution of Benthosema glaciale larvae by size class in daytime (light shading) and night-time (dark shading). The percentages calculated are based on the mean abundance at all stations for each depth stratum.
subfamily, showed a relatively near-surface distribution. Röpke (1989) indicated a similar distribution range in the Celtic Sea for the larvae of this species. In addition, Röpke (1993) observed that the larvae of Benthosema pterotum in the Arabian Sea were clearly associated with the upper part of the pycnocline, especially during the day. The vertical distribution range of the larvae of Maurolicus muelleri found in the present study is similar to that described in the Mediterranean (Maso and Palomera, 1984) and in the North Atlantic (Röpke, 1989). It is worth mentioning that John and Kloppmann (1989), in a detailed study of the vertical distribution of larvae of this species conducted in the North Atlantic, indicated that recently hatched larvae were found at 100–400-m depth, the same zone as the highest abundance of eggs. Afterwards, the preflexion larvae with functional eyes, which would correspond to most of the larvae collected in the present exercise, were in the upper 100 m of the water column, being especially abundant in the first 50 m, just as observed here. As they grow, however, the tendency is to move deeper towards the deeper habitat of the adults. The larvae of A. hemigymnus showed deep distributions, both day and night, as was indicted by Olivar et al. (1998) during the stratified period of the summer in the Mediterranean.

With regard to the diel variations in the vertical distribution, the tendency shown by most of the species is for a more surface distribution during the day than at night. This is even more evident in most of the larvae of the mesopelagic species. The absence of a thermocline and strong density gradients, less than 0.5 eut units, were factors encouraging the vertical movements of larvae. The relationship between light and vertical distribution of fish larvae does not follow a clear pattern as it depends on the species and ontogenetic stages. Some species ascend to the surface at night (Neilson and Perry, 1990) while the opposite pattern, although less frequent, has been observed in larvae of various fish species (e.g. Boehlert et al., 1985; Brodeur and Rugen, 1994). The preference for a certain depth range has been related to various environmental, physical, and biological parameters, which ensure optimum survival for larval fish (Heath, 1992). It has also been argued that fish larvae have a preferred light level that determines their diurnal distributions and diel changes in the vertical distribution are simply a dispersal of larvae once the light stimulus disappears (Brewer and Kleppel, 1986; Leis, 1991). In the present study, given the homogeneity of the physical characteristics throughout the water column, except for light, it could be speculated that during the day the fish larvae are situated towards the surface, where they find high concentrations of food. Röpke (1993) concluded that prey densities seem to be more critical in the vertical distribution of fish larvae than physical gradients.

Food availability for larvae is determined not only by the concentration of prey items but also by the light intensity (Munk et al., 1989). Fish larvae are visual predators and they need an adequate level of light in the water column to detect and capture prey (Blaxter, 1986; Batty, 1987). Additionally, it has been noted that at intermediate turbulence levels, light intensity had a significant positive effect on prey-attack rate (Utne-Palm and Stiansen, 2002). Consequently, the vertical distribution of larvae will be determined by the exponential decrease in the light intensity by depth and the lower limit will be determined by the minimum light intensity at which feeding is possible. If the feeding of the larvae depends on a minimum light intensity, the distribution patterns observed might be partially explained by the feeding response of the larvae. Thus, it would be beneficial for the larvae to be in the upper water levels during the day where the light levels are high. At night, a period in which they do not feed, the larvae become relatively inactive and gradually sink to greater depths (Yamashita et al., 1985). Though in the present study the mesopelagic species were located below the maximum concentrations of potential food both day and night, they migrated to the relatively illuminated layers during the day to feed. In this respect, Sabatés et al. (2003) described a clear relationship between the light intensity and the feeding behaviour in larvae of B. glaciale and M. punctatum.

In summary, the present study has shown that even in the absence of stratification, the larvae of the various fish species have different patterns of vertical distribution and diel changes. The patterns displayed are similar to those reported in species of the same genus in other geographical areas, which indicates that the selection of a certain depth range is independent of local environmental conditions (Röpke, 1993). In general, most species are located closer to the surface during the day than at night. Since the abiotic variables, except light, vary very little throughout the water column this behaviour will be determined not only by the high concentrations of prey existing in the most surface layers but also by the existence of adequate light levels for feeding.

Acknowledgements

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References


