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Diel-depth distributions of fish larvae off the Balearic Islands (western Mediterranean) under two environmental scenarios

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ABSTRACT

The diel vertical distribution of fish larvae off the Balearic Islands during late autumn and summer was analysed in relation to the environmental conditions. Four fixed sampling stations, located in the outer shelf and slope zones, were sampled during both the day and night by means of oblique hauls at different water depths. In autumn the first 60 m were characterised by vertical mixing and relatively higher fluorescence values, while summer was characterised by strong near-surface stratification and the presence of a Deep Fluorescence Maximum (DFM). The fish larval community was dominated by mesopelagic species, myctophiforms and stomiiforms, with some differences in species composition and their relative contribution between periods. A higher number of species was observed to reproduce in summer. The diel vertical distribution patterns differed among species and, within species, some differences were detected between the day and night. Although their relative depth preferences were similar between surveys, seasonal comparisons for the most abundant species showed that in autumn larvae presented both a shallower distribution during the day and a deeper distribution during the night than in the summer period. The larvae of all species, except for *Argyropelecus hemigymnus*, were absent from layers below 200 m. In these deeper layers, only *A. hemigymnus* larvae and juvenile stages of myctophiforms and stomiiforms were found. Another group of species, including *Hygophum benoiti, Ceratoscopelus maderensis, Cyclothone braueri* and *Lampanyctus crocodilus*, characterised the surface assemblage, mainly appearing in the first 50 m during the day, while at night their distribution was wider, extending to deeper layers. *Benthosema glaciale*, *Symbolophorus veranyi* and *Myctophum punctatum* were located at intermediate levels (mostly 50–100 m). Larval size stratification was evident for the most abundant species, with younger stages being found at shallower depths in the water column, while postflexion stages presented a wide distribution at night, undergoing vertical displacement to the near-surface layers during the day. The roles of the position of the thermocline, the availability of food and light intensity as factors modulating these differences are discussed.

1. Introduction

The studies addressing the first developmental stages of teleostean fishes are crucial for understanding the recruitment processes that condition their population dynamics. In addition, they can be used to infer key biological traits of adult stocks and provide information about their biomass, structure and spatial distribution. This is especially useful in the case mesopelagic communities, which, despite being key elements of oceanic food webs (Cherel et al., 2008; Williams et al., 2001), are not as well known as coastal and exploited species because of the lack of fishing interest and the intrinsic difficulty of sampling them.

Knowledge of the vertical distributions of larval fishes is necessary to analyse the processes that affect their survival (Ahlstrom, 1959; Kendall and Naplin, 1981), as the vertical dimension of the ocean shows significant gradients of physical, chemical and biological parameters.

Although most neritic and oceanic fish larvae are located in the upper part of the water column, i.e., in the surface mixed layer, above the thermocline (Boehlert and Mundy, 1994; Olivar and Sabatés, 1997; Palomera, 1991; Smith and Suthers, 1999), vertical distribution ranges and preferred depths as well as migration patterns differ among species (Cha et al., 1994; Loeb, 1980; Röpke, 1989; Sogard et al., 1987) and can vary during ontogenetic development (Fortier and Harris, 1989; Fortier and Leggett, 1983, 1984; Heath et al., 1991; Loeb, 1979).

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 is also observed (e.g., Brodeur and Rugen, 1994; Haldorson et al., 1993). Some species do not show diel variations (Röpke, 1989), while others form aggregations during the day and are more dispersed at night (e.g., Leis, 1991; Munk et al., 1989).

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The vertical distributions of the larvae of each fish species and variations of these are expected to be regulated via endogenous mechanisms (Neilson and Perry, 1990), but modulated by biological and hydrographic parameters (Heath, 1992). Abiotic environmental factors, such as light (Heath et al., 1988), or biotic factors, such as predator (Hunter and Sanchez, 1976) and prey densities (Munk et al., 1989), have been found to be linked to larval migrations. It has been reported that the larvae of some fish species can adjust their vertical distributions at scales of several metres to forage on prey peak abundances (De Lafontaine and Gascon, 1989; Fortier and Harris, 1989; Fortier and Leggett, 1983, 1984).

It has been demonstrated that thermoclines and haloclines influence the vertical structure of fish larval assemblages (Kendall and Naplin, 1981; Röpke, 1993; Sameoto, 1982; Southward and Bary, 1980) and vertical larval displacements, either directly (frontal boundary, buoyancy effect) (Ferreira et al. (2012) or through their effect on the location of prey (Lasker, 1975). Nevertheless, when the intensity of thermocline signature is low or in coastal waters of dynamic nature this factor plays a limited role in the vertical distribution patterns of fish larvae (Gray, 1996; Conway et al., 1997; Rodríguez et al., 2006).

Among the taxonomic groups whose larvae show more complex vertical distribution patterns, several orders of the aforementioned mesopelagic fishes must be noted, such as Myctophiforms and Stomiiforms, which usually dominate offshore larval assemblages around the world (Holliday et al., 2011; Koslow et al., 2011; Olivar and Beckley, 1994; Rodríguez et al., 2009a,2009b; Sassa et al., 2002) and constitute the most abundant fish component of the oceanic waters of all temperate and tropical regions in the world (Gjøsaeter and Kawaguchi, 1980).

Variations in the horizontal patterns of fish larval distributions in the Balearic Sea have been studied in relation to hydrographic characteristics, mainly in the summer season (Alemany et al., 2006, 2010; Torres et al., 2011; Álvarez et al., 2012; Rodriguez et al., 2013). However, an in-depth analysis of the vertical distribution of fish larvae has not previously been carried out in this area, although some preliminary data are available (Alemany, 1997) and several studies have been carried out in nearby zones of the western Mediterranean (Olivar and Sabatés, 1997; Olivar et al., 2010; Sabatés, 2004).

The Balearic Islands represent the natural limit between two subbasins of the western Mediterranean Sea (WMED), the Algerian and the Ligur-Provencal, playing a key role in water mass dynamics by conditioning the water mass exchange between the two basins (López-Jurado et al., 1995; Pinot et al., 2002). The upper layers of the water column, from the surface to approximately 200 m, are occupied by waters with a recent Atlantic origin (recent AW) in the Algerian sub-basin and by waters that have remained longer in the Mediterranean (resident AW) in northern areas. In summer, when atmospheric forcing decays, surface Atlantic Waters flow northwards from the Algerian Basin, leading to a complex hydrographic situation. Several mesoscale oceanographic features, such as fronts, filaments and eddies, are found in the Balearic Sea (Millot, 1994).

The waters surrounding the Balearic Islands, as in all of the Mediterranean Sea, are considered oligotrophic (Estrada, 1996; Fernández de Puelles et al., 2007). During summer, when the water column is stratified due to the presence of a well-defined thermocline, biological production is mainly associated with mesoscale oceanographic features, such as fronts and eddies (Alcaraz et al., 2007; Jansà et al., 1998, 2004). The vertical distribution of chlorophyll shows a deep chlorophyll maximum (DCM) located below the thermocline (Estrada et al., 1993; Fernández de Puelles et al., 2007; Jansà et al., 1998), where the maximum concentration of zooplankton is also found (Alcaraz et al., 2007; Saiz et al., 2007). The winter mixing period is characterised by an absence of strong vertical gradients. Under this situation, the vertical distributions of chlorophyll and zooplankton are quite homogeneous in the photic layer (Olivar et al., 2010; Sabatés et al., 2007). This marked seasonality, with alternating periods of mixing and stratification, could strongly affect the vertical distribution patterns of fish larvae throughout the yearly cycle.

The aim of the present study was to analyse the vertical distribution of early developmental stages of fishes on the shelf and slope in the Balearic region, under two different environmental scenarios: mixing and stratified conditions. Our objective was to identify ontogenetic and diel patterns for the species that constitute the main larval assemblages in relation to the biotic and abiotic factors in each situation.

2. Materials and methods

2.1. Sampling

Two surveys, the first in late autumn (December 2009) and the second in summer (July 2010), were carried out off Mallorca Island (western Mediterranean). To determine the vertical distribution of plankton, samples were obtained at four fixed locations in 48 h sampling cycles in two zones: to the southeast (Cabrera) and northeast (Sóller) of the island. In each zone, two sampling locations, placed on the outer shelf (200 m) and slope (900 m), were intensively sampled in both the day and night (Fig. 1). A grid of hydrographic stations covering a larger area than the plankton was used to characterise the region. Vertical casts with a CTD SBE911 with an attached fluorometer were performed from the surface to the bottom, and the obtained temperature, salinity, density and fluorescence profiles were averaged at 1 m intervals to depict the vertical structure of the water column. The horizontal distribution of fluorescence in the studied zone was calculated as integrated values for the first 150 m of the water column.

Depth-stratified plankton hauls were conducted from near the bottom to the surface using multiple opening and closing nets. In autumn, a total of 17 stations were sampled (8 by day and 9 by night) using a HYDRO-BIOS net with a 0.25 m^2 mouth opening consisting of 5 nets with a 333 μm mesh size, obtaining a total of 85 samples. In summer, 26 fixed sampling stations were examined (16 by day and 10 by night) with a MOCNESS net with a 1 m^2 mouth opening consisting of 7 nets with a 333 μm mesh size, collecting a total of 182 samples. These two types of gears are widely used in ichthyoplankton collections and although catchability of larger larvae may be lower for the 0.25 m^2 net, due to the larger net avoidance, this would only affect to direct abundance comparisons between surveys, but not the vertical distribution patterns of larvae. The depth strata sampled by each multi-net were chosen according to the number of available nets in each device, the vertical hydrographic profile during each period and the bottom depth,

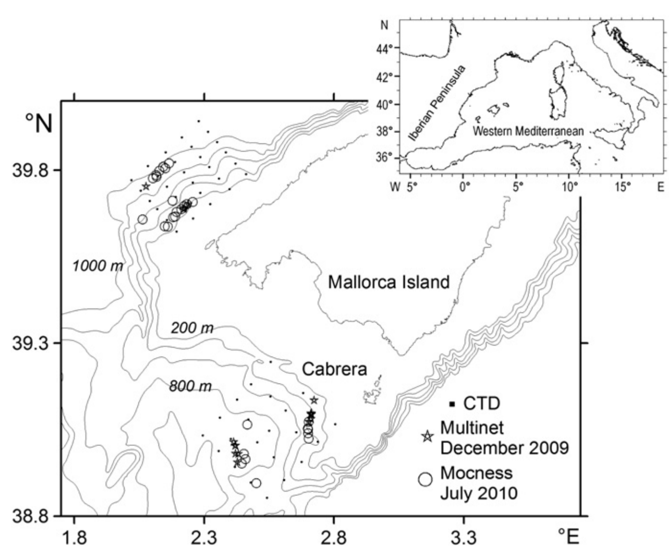

Fig. 1. Study area showing the location of plankton sampling stations (stars for autumn and circles for summer surveys). Dots denote the positions of the CTD casts.