

Coexistence of larvae of tuna species and other fish in the surface mixed layer in the NW Mediterranean

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Received December 1, 2010; accepted in principle August 5, 2011; accepted for publication August 8, 2011

Corresponding editor: Roger Harris

To analyze the potential trophic interactions among tuna larvae and other fish species, we studied the larval fish assemblages inhabiting the surface mixed layer around the Balearic Islands using data from two surveys carried out in summer 2006 and 2008. Despite the high diversity, *Thunnus alalunga*, *Auxis rochei*, *Cyclothone pygmaea* and *Ceratoscopelus maderensis* clearly dominated the catch in both years. The spatial distribution of several larval fish assemblages, in which tuna larvae were among the dominant species, was related to the presence of fronts and mixed Atlantic waters (AW). Different developmental stages of tuna were found in similar hydrographical scenarios. Smaller tuna larvae and plausible piscivorous tuna were found in the areas with mixed AW. Later in the season, potential piscivorous tuna were found together with small larvae from other non-tuna species that had been spawned later and transported by the fresh AW flow to offshore stations. That the different life stages of tuna co-occur with mesopelagic species in the mixed layer reveals the interesting possibility of ecological interactions between the different larvae.

KEYWORDS: tuna larvae; Mediterranean; oceanography; mixed surface layer; dominance; coexistence; Balearic Islands; mesopelagic; fish larvae

INTRODUCTION

Tuna have been studied extensively as they are a key-stone species in many marine ecosystems (Smale, 1992; Kitchell *et al.*, 1999) and have special biological traits (Block and Donald Stevens, 2001). Moreover, tuna fisheries are among the most important in the world, both due to the volume of landings and their high economic value. Several international organizations have been created specifically for managing the tuna and other large pelagic stocks. Unfortunately, neither the available scientific knowledge nor the management measures of these organization have impeded

the total collapse or striking decline in some populations, such as the western stock of the Atlantic bluefin tuna in the 1970s (Safina and Klinger, 2008) and the eastern stock in the 1990s (Ravier and Fromentin, 2001). Concern for the sustainability, or indeed survivorship, of this emblematic species, exploited and studied since ancient times (Doumenge, 1998; Fromentin, 2009), led the Standard Committee of Research and Statistics of ICCAT (International Commission for the Conservation of Atlantic Tuna) to recommend studying in greater depth the reproductive biology and other biological parameters of this species (Anonymous, 1999).

In line with this recommendation, and bearing in mind that the planktonic phase of teleosts is a critical period that largely determines the recruitment strength, and hence the evolution of the biomass of the population (Peterson and Wroblewski, 1984; Bradford, 1992; Hsieh *et al.*, 2006), in 2001 the Spanish Institute of Oceanography initiated a research program on tuna larvae ecology in the Balearic Sea, a recognized spawning area of this species (Mather *et al.*, 1995; Alemany *et al.*, 2006; Rooker *et al.*, 2007). The results of the first ichthyoplankton surveys carried out within the framework of this program (García *et al.*, 2005; Alemany *et al.*, 2006, 2010) confirmed that the Balearic Sea is an important spawning ground not only for Atlantic bluefin tuna (*Thunnus thynnus*) but also for other tuna and large pelagics inhabiting the Mediterranean Sea during summer. The outputs of individual-based models developed with field data from this research program (Reglero *et al.*, 2011) suggest that piscivory, even cannibalism, among tuna larvae may be a crucial process that affects tuna larval survivorship in the study area. It is well known that food availability and predation are among the main factors affecting fish larval mortality (Cowan *et al.*, 1993; Houde, 1997; Esteves *et al.*, 2000), and it has also been demonstrated that Scombridae larvae become piscivorous during the planktonic stages (Young and Davis, 1990; Miyashita *et al.*, 2001; Shoji and Tanaka, 2006). Some previous studies have been carried out using larvae sampled in the Balearic Sea (Catalán *et al.*, 2007, 2011) or nearby areas (Morote *et al.*, 2008). In order to interpret the data obtained from the stomach content analysis properly, and thus understand better the trophic ecology of tuna larvae, mainly in relation to piscivorous behavior, it is necessary to determine in detail the specific composition of the larval assemblages of which tuna larvae are a part. Several studies have described larval assemblages in which tuna larvae are present, even as dominant species (Miller, 1979; Alemany *et al.*, 2006; Richardson *et al.*, 2010), but this is not always enough to reveal the potential prey field of larger piscivorous tuna larvae. It is also necessary to determine the spatio-temporal overlapping of these piscivorous larvae and other fish larvae during the daytime, when tuna larvae feed (Morote *et al.*, 2008).

Unfortunately, most studies investigating tuna larvae report abundances for Scombridae but do not include other species (Miller, 1979; Davis *et al.*, 1990; Boehlert and Mundy, 1994; Beckley and Leis, 2000; Alemany *et al.*, 2010). Only a few studies provide information on the entire ichthyoplankton community in which tuna larvae are a major component or even the dominant

species (Somarakis *et al.*, 2002; Alemany *et al.*, 2006). In some cases, the analyses are limited to the pelagic species (Richardson *et al.*, 2010). However, these studies describe the ichthyoplankton assemblages in samples taken at the surface or with oblique tows that sample water layers below those where tuna larvae are distributed, since tuna larvae are usually only found in the upper water column occupying the mixed layer above the thermocline (Davis *et al.*, 1990; Boehlert and Mundy, 1994; Morote *et al.*, 2008; Satoh, 2010). These sampling strategies can show a biased view of the fish larvae community. Hence, the actual proportion of tuna larvae compared with other fish larvae in the mixed layer where tuna larvae are distributed is still unknown in most tuna spawning areas. This gap in knowledge is an important constraint against determining the possible links within the tuna larvae community and with fish larvae at lower to intermediate trophic levels, especially if potential competition and predation scenarios are to be understood.

To determine these potential interactions, it is also necessary to understand the size spectra of larval populations, as well as larval morphologies and growth rates, both in terms of length and biomass. The rate of increase in weight by length can vary between larval morphologies. Therefore, the dominant species within the larval assemblages in terms of biomass can change over short periods of time, even though relative abundances among these species do not vary greatly. However, changes in larval length during ontogenetic development are usually linked to increasing foraging abilities. Tuna larvae hatch at 2–4 mm and in a few days they reach the flexion stage (Kendall *et al.*, 1984). They finally reach the post-flexion stage at around 6.5 mm at which they can feed on fish larvae (Kaji *et al.*, 1996, 1999). Studies aimed at combining all this information would provide insight into larval growth strategies and energy allocation patterns (Díaz *et al.*, 2009).

The present study has been designed as a first step to fill some of the gaps in knowledge about potential trophic interactions among tuna larvae and other fish larvae in the Balearic Sea. This area is a suitable location for estimating the proportion of tuna larvae compared with larvae of other fish species in the mixed layer because it is a recognized spawning ground for all the tuna found in the Mediterranean Sea. The spatial coexistence of larvae of different tuna species in summer is enhanced by mesoscale hydrographic features resulting from interactions between Mediterranean and Atlantic waters (AW; Alemany *et al.*, 2010), which favor encounters among more coastal spawning species,

such as *Auxis* spp., and offshore spawners, such as *Thunnus* spp.

Therefore, the specific objective in this study was to describe the larval fish assemblages in the upper layers of the open sea pelagic ecosystem around the Balearic Islands, focusing on the spatial coexistence of tuna larvae and those of other abundant species. To achieve this objective, we first characterized the extent and hydrographical characteristics of the surface mixed layer. Second, we described the larval assemblages that coexist in the mixed layer during the day, when tuna larvae feed, by analyzing the species composition, the abundances and the spatial distributions of the larvae of tuna and the species that coexist with them. Third, we explained the horizontal patterns of the larval associations in terms of the environmental data and determined the size structure of the more abundant fish larvae populations present in the tuna larvae dominated ichthyoplankton assemblages. Differences in the diet and foraging traits among the species are described based on data from the literature.

METHOD

Hydrographic scenario

The Balearic Islands are the natural limit between two sub-basins of the western Mediterranean (WMED), the Algerian and the Balearic Basins (Fig. 1). In the southern part, the Algerian sub-basin receives fresh surface water from the Atlantic (AW), and its dynamics are mainly driven by density gradients. To the north, the Balearic sub-basin contains colder and more saline surface AW that has remained longer in the Mediterranean (resident AW), and its dynamics are affected by notable atmospheric forcing, mainly wind. The Mallorca and Ibiza channels play an important role in the regional circulation of this area and their topographies condition the exchanges between these two sub-basins (Pinot *et al.*, 2002). As a consequence, there are significant differences between the general hydrodynamic conditions that affect the north and the south of the islands.

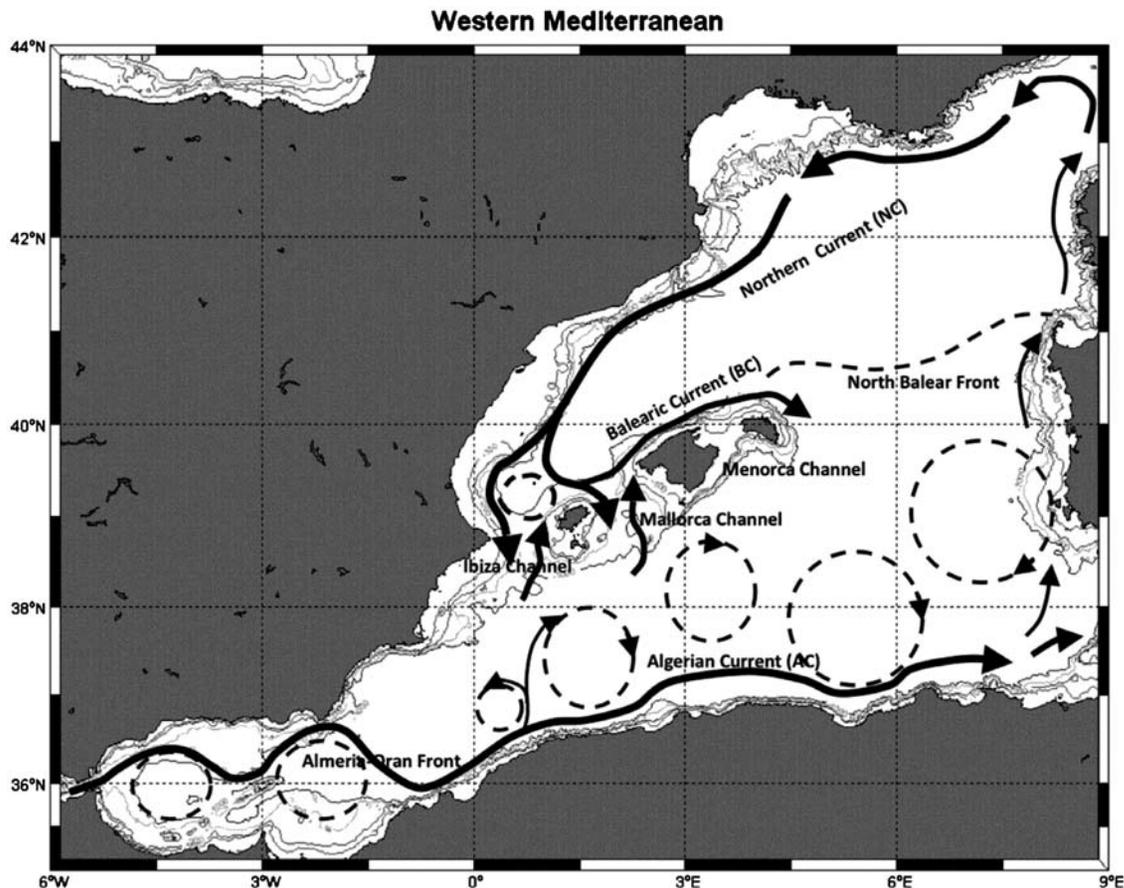


Fig. 1. The study area and main hydrographic features. The Mallorca and Ibiza channels, the Northern and Balearic Currents, and the Algerian Gyres are indicated.

This study was carried out in Balearic surface waters with Atlantic origin that have different residence times in the Mediterranean. The confluence of fresher and older AW in the channels causes ocean fronts that affect the dynamics. The location and intensity of these fronts also depend on the seasonal and inter-annual variability (López-Jurado *et al.*, 2008). A salinity value of <37.0 is the criterion we used to identify the fresher AW, and that of >37.5 was used to identify resident AW. Intermediate values correspond to mixed AW. The mixed layer, in which active turbulence has homogenized the depth range, has waters with similar temperature and salinity values and is located between the surface and the top of the thermocline (transition zone where the temperature begins to decrease faster with depth).

Sampling

During summer 2006 and 2008, the Spanish Institute of Oceanography carried out two ichthyoplankton surveys on board the R/V Odon de Buen around the Balearic Islands (WMED, Fig. 1). A regular grid of 55 stations in 2006 and 48 in 2008, with a 5-mile and 10-mile separation between stations, was sampled from the 29 June to 14 July 2006 and from 31 July to 11 August 2008. Conductivity, temperature and pressure data were recorded at all stations by means of CTDs (Sbe911+ and Sbe25) lowered to a depth of 350 m, although at some deep stations the CTD was lowered to 650 m. Data at each station were processed at their original sampling frequency and reduced to a 1-m vertical resolution for analysis. The dynamic height at different isobaric surfaces was calculated by vertical integration of the specific volume anomaly from 600 m depth, which was chosen as the level of no motion (Pinot *et al.*, 1995).

Salinity, temperature and dynamic height distributions were interpolated onto a uniform grid of $0.01^\circ \times 0.01^\circ$ ($\sim 1 \times 1$ km) by using minimum error variance methods with a correlation length of 0.3° (~ 30 km) and a maximum allowed root mean square error for the interpolated field of 20%. The correlation length was chosen on a theoretical basis to be of the order or smaller than the Rossby deformation radius and does not depend on the way a variable is sampled but rather on the size of the dominant mesoscale structures (Gomis *et al.*, 2001). The geostrophic currents were estimated by first differencing the interpolated dynamic height field.

We used our CTD data and also the information provided by the Mediterranean Forecasting System (MFS) model to describe the general hydrographic context of

both surveys (Tonani *et al.*, 2008). MFS assimilates daily data such as the sea-level anomaly and sea surface temperature. The output of this model was used because it shows very good qualitative agreement with our temperature, salinity and geostrophic current observations and provides a broader perspective and a qualitative description of the local circulation and hydrographical conditions at the time of the surveys.

Biological samples

Fish larvae were collected at 39 stations each year by standard double-oblique hauls using Bongo nets (90 cm mouth diameter) equipped with 500 μm meshes down to 20 m depth, coinciding with the beginning of the transition zone determined from the CTD profiles (see below). All stations were sampled during the daytime. Plankton samples were quickly preserved in 4% seawater-buffered formalin and once in the laboratory the fish larvae from one of the replicates were sorted and identified to the lowest recognizable taxonomic level. The number of fish larvae caught at each station was standardized to individuals per 100 m^3 . The relative abundance and the frequency of occurrence of each species were calculated.

Size structure and morphological traits

The Scombridae larvae and the associated species grouped by the MDS analysis (see below) with an occurrence frequency of >0.6 and representing more than 2% of the total larval abundance were measured to the nearest 0.1 mm. Their standard length (SL) was measured from the tip of the jaw to the extreme of the urostyle using a stereomicroscope. No correction for shrinkage in formalin was applied. According to their SL, larvae were separated into four categories, considering the size ranges determined and applying a base-2 logarithmic scale to the observed total SL range: 0.8–1.6 (size class 1), 1.6–3.2 (size class 2), 3.2–6.4 (size class 3) and 6.4–12.8 (size class 4; Sheldon *et al.*, 1972; Blanco *et al.*, 1994). These size classes correspond to the different stages of tuna larval development since size classes 1–4 match well the yolk-sac stage, the pre-flexion, the flexion and the post-flexion ontogenetic stages, respectively (Kendall *et al.*, 1984). Tuna larvae included in the largest size class (6.4–12.8 mm) were considered to be potentially piscivorous larvae, whereas all the other size classes and species were considered to be zooplanktivorous (Catalán *et al.*, 2007; Morote *et al.*, 2008). Morphological differences between species within the scombrid assemblage were determined by estimating the relationship between SL and body depth

Table I: Relationships between dry weight and SL modified from published literature sources [Dry weight versus SL (mg versus mm)]

Species	Relationship	Species used	Reference
<i>Auxis rochei</i> ; <i>Thunnus alalunga</i>	$W = 0.000682 SL^{3.807}$	<i>Thunnus alalunga</i>	García <i>et al.</i> (2006)
<i>Ceratoscopelus maderensis</i>	$W = 0.0004 SL^{4.137}$	<i>Pagrus pagrus</i>	Mihelakakis <i>et al.</i> (2001) and Suzer <i>et al.</i> (2007)
<i>Chromis chromis</i>	$W = 0.0002 SL^{4.561}$	<i>Amphiprion melanopus</i>	Alshuth <i>et al.</i> (1998) and Arvedlund <i>et al.</i> (2000)
<i>Cyclotone pygmaea</i>	$W = 0.00002 SL^{4.394}$	<i>Engraulis encrasicolus</i>	García <i>et al.</i> (2003)

measured as the maximum linear dorso-ventral distance of the larvae (Scharf *et al.*, 1998). This was used as a proxy for tadpole-like or eel-like body types.

The role of tuna species in the assemblage in terms of abundance and biomass was estimated by calculating the proportion represented by tuna larvae compared with the abundance and biomass of other larval fish species within each size class at every station. To obtain biomass, larval SLs were converted into dry weights using the length–weight relationships taken from the literature detailed in Table I, referring to the same species or for species with similar body shapes. The relative abundance of the potential piscivorous larvae (largest tuna size class 6.4–12.8 mm) was estimated in relation to the abundance of the smaller sized groups of tuna and other species within the assemblage. The net avoidance capability of potentially piscivorous large tuna larvae is higher than that of the smaller larvae. This was taken into account when conclusions were made based on these comparisons, since the observed ratios between larger potentially piscivorous larvae and the rest of the smaller tuna larvae were assumed to underestimate larger larvae abundances.

Multivariate statistical analysis

Similarities among stations

The similarity among stations and species was analyzed with cluster analysis (Clarke, 1993) using the pair-group average clustering algorithm from the Bray–Curtis similarities of square-root transformed larval abundances (Field *et al.*, 1982). The crossing was chosen to obtain groups with similar species compositions (group-to-group) for 2 years in accordance with a logical relation to hydrography. The PRIMER software package was used for the multivariate analyses (Clarke and Gorley, 2006).

Since the aim of this analysis was to group together the stations showing similar absolute and relative abundances of the more widespread species, only species that appeared at more than 10% of the stations were considered. The specific composition of these meaningful

cluster groups was described and sampling stations assigned to each were plotted on a map.

Grouping of species

A multidimensional scaling (MDS) analysis was performed in order to explore inter-relationships among species, focusing on the fish larvae that coexist with the Scombridae larvae. Since very rare species were not relevant for the purposes of this study, and to make the plotted results more easily understandable, we only included species with an abundance percentage higher than 0.50%.

RESULTS

Hydrographic scenario

The average thicknesses of the mixed layer during the surveys of 2006 and 2008 were 12 and 15 m, respectively. Average mixed layer temperatures were close to 26°C, followed by a strong thermal gradient from the top of the thermocline, 15 m, down to 100 m, and followed by a zone with a constant temperature down to the bottom. Figure 2 shows that the mixed layer was slightly more superficial in July (2006) than in August (2008). The vertical salinity profiles showed inflows of mixed AW, with average salinities <37.5 in both surveys, and salinity increased with depth (Fig. 2). The lower surface layers generally consisted of typical resident AW (salinity > 37.5).

In this summer situation, in the absence of the winter atmospheric, the density gradient forcing becomes predominant and allows AW inputs to enter the Balearic area. Therefore, the waters surrounding the Balearic Islands were usually mixed waters. The surface temperature field in both surveys showed values within the tolerance range of the larvae of all the tuna species observed in the area (Alemany *et al.*, 2010); therefore, this was not a limiting factor for larval distribution. However, at this time of the year, surface heating is very intense in the entire sampling area, and since the measurements are not synoptic, the observed values do

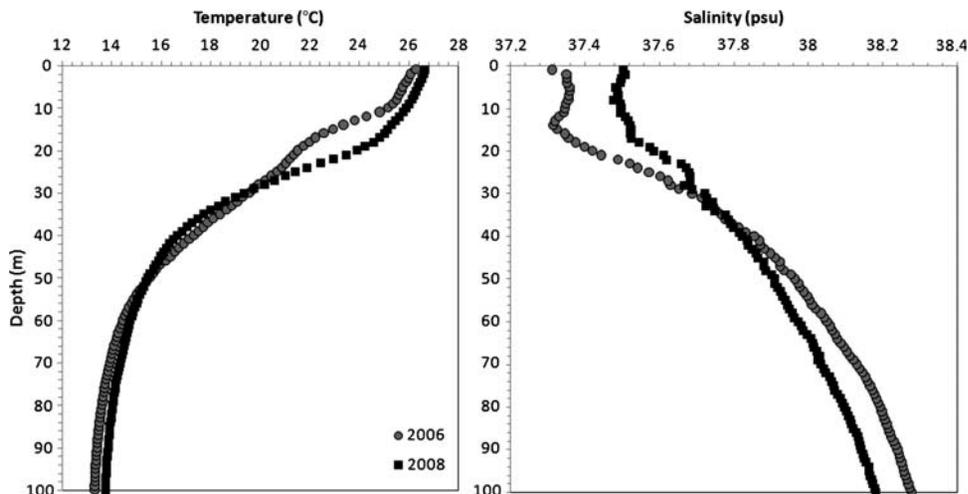


Fig. 2. Vertical profiles of average temperature and salinity for the stations sampled on the two cruises, grey dots (2006) and black squares (2008).

not depend on the geographical position but rather on the sampling date; thus, temperature is not useful for characterizing different surface water masses. For these reasons, although temperature is usually considered one of the main factors affecting tuna larval distribution (Kitagawa *et al.*, 2010), in this case salinity was considered the best parameter for characterizing the hydrographic scenario.

The horizontal hydrographic scenario is represented by two types of maps, one showing the dynamic topography with the geostrophic currents at 15 dbar and the other with the salinity distribution at the same depth. This level was used to describe the hydrography of the mixed layer where tuna larvae are found (Figs 3 and 4).

During July 2006, the salinity field (Fig. 3a) showed an input of fresh AW into the Mallorca channel that seemed to reinforce the Balearic Current, taking this AW along the northern insular slope toward Menorca Island. Figure 3a also shows low salinity values to the east of Mallorca and the south of Menorca, which suggests that these waters crossed the Menorca channel as geostrophic currents indicate (Fig. 3b). The south of Mallorca Island is occupied by mixed AW and the east of Menorca Island by resident AW. The MFS output showed that during July 2006, there was an intrusion of AW through the Ibiza channel that converged with the Northern Current and that partly reinforced the Balearic Current. The remaining waters re-circulated through the Mallorca channel out of our study area.

In August 2008, fresh AW was found at the southern limit of our study area between the islands of Mallorca and Menorca (Fig. 4a). Mixed AW occupied the rest of the area and an input of resident AW crossing the

channel southward was only found in the Mallorca channel. The south of Mallorca and east Menorca were occupied by mixed AW. Reanalysis of MFS showed good agreement and suggests that the fresh AW input is part of an anticyclonic gyre coming from the Algerian Basin, partly observed in the geostrophic currents in Fig. 4b.

Larval fish assemblages

A total of 3147 fish larvae, belonging to 38 different taxa, were identified in 2006: 25 classified to species level, 9 to genera and 4 to family level (Table II). In 2008, 9354 fish larvae were captured and a total of 54 different taxa classified: 39 to species level, 11 to genera, 3 to family and 1 to order level (Table II). Two Scombridae were among the most abundant and ubiquitous species in 2006 and 2008: the bullet tuna (*Auxis rochei*), with a mean density of 6.7 per 100 m³ in 2006 and 9.4 per 100 m³ in 2008, and the albacore (*Thunnus alalunga*), with 1.9 per 100 m³ in 2006 and 3 per 100 m³ in 2008. Larvae of other Scombridae were also sampled, but in lower abundance under 0.5 per 100 m³, such as those of Atlantic bluefin (*T. thynnus*), little tunny (*Euthynnus alletteratus*) and skipjack (*Katsuwonus pelamis*). *Katsuwonus pelamis*, which is considered a tropical tuna, was only found in 2008. Another very abundant and frequent species in both years was the mesopelagic Gonostomatidae *Cyclothone pygmaea* (4.6 per 100 m³ in 2006 and 21 per 100 m³ in 2008). Species present in high abundances in only one of the surveys included the damselfish (*Chromis chromis*; 3.3 per 100 m³) and the small pelagic round sardine (*Sardinella aurita*; 2.1 per 100 m³) in 2006 and a mesopelagic myctophid

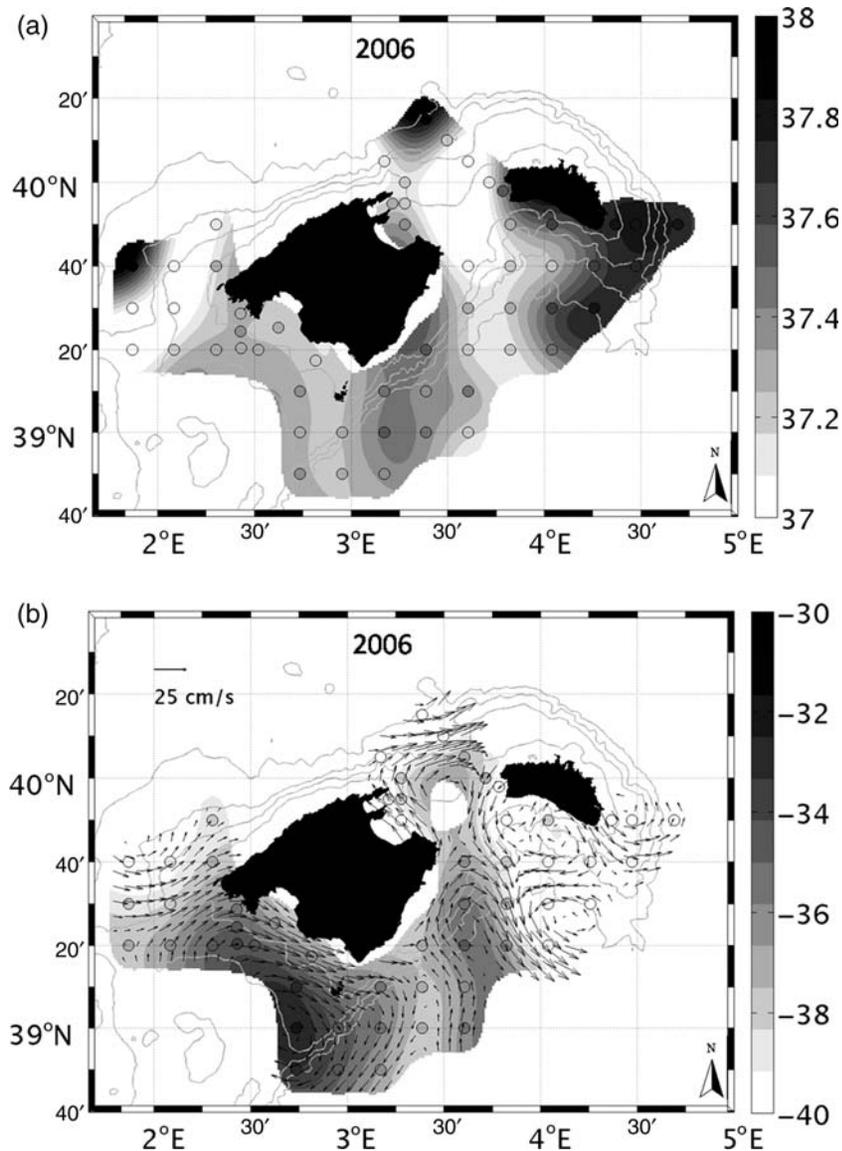


Fig. 3. Sampling stations and interpolated salinity field distribution (a) and interpolated dynamic height and derived geostrophic currents (b) at 15 dbar, during the 2006 cruise.

Ceratoscopelus maderensis (6.8 per 100 m³) in 2008 (Table II).

The larval stages of most of the species identified were non-piscivorous according to the larval gut content studies cited in Table III. The only exceptions were the Scombridae larvae *T. thynnus*, *T. alalunga*, *X. gladius*, *A. rochei*, *E. alletteratus* and *K. pelamis*, the carangid *Seriola dumerili* and the belonid *Belone belone*, which are reported to show piscivorous behavior when they reach certain sizes.

The species composition was similar in 2006 and 2008, as the three dominant taxa in both years were the Scombridae *A. rochei* and *T. alalunga* and the mesopelagic

Gonostomatidae *C. pygmaea*. However, the relative abundances of these species were rather different among the sampling stations (Table IV).

Similarity analysis among stations by year did not show well-defined, clearly separated groups. However, in both years, there were several meaningful clusters of stations related to mesoscale oceanographic features and/or as a result of the different spawning strategies of different species. In 2006, stations were grouped into two main clusters (Fig. 5a). The first group (6-1) was dominated by larvae of tuna and mesopelagic species, and the second group (6-2) contained these species but was characterized by higher abundances of coastal

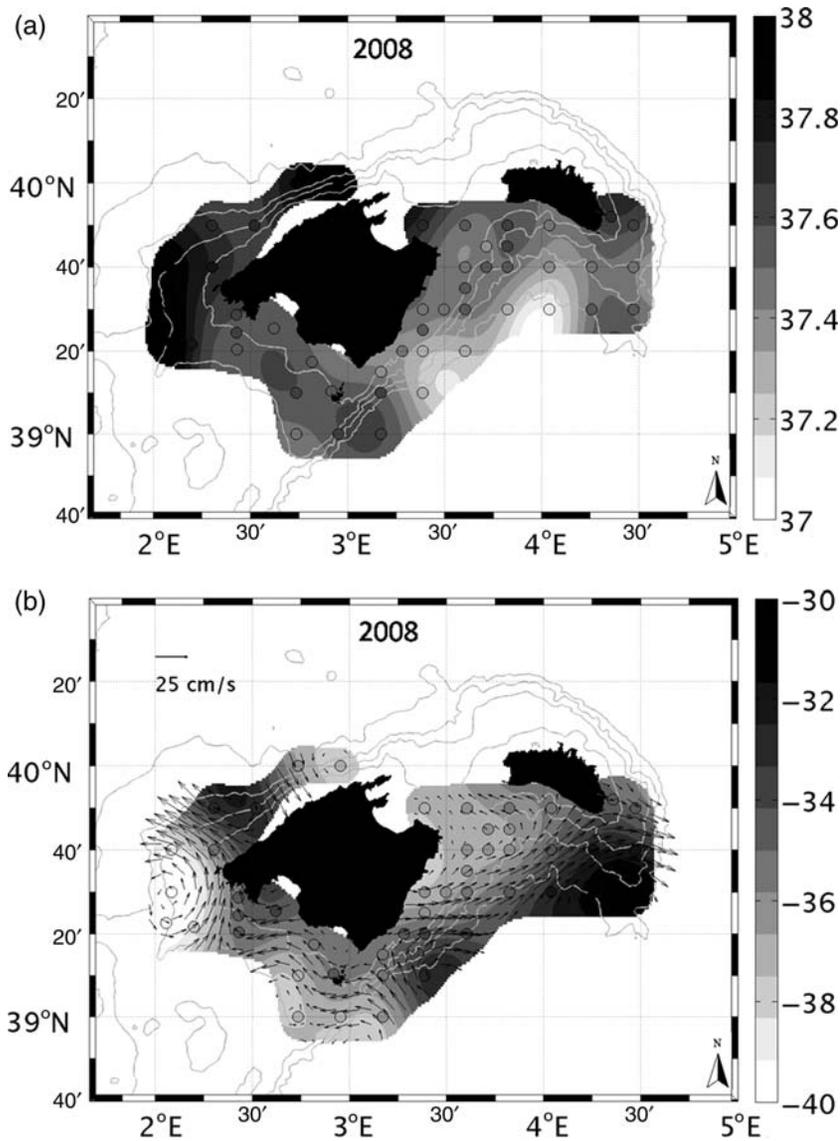


Fig. 4. Sampling stations and interpolated salinity field distribution (a) and interpolated dynamic height and derived geostrophic currents (b) at 15 dbar, during the 2008 cruise.

species, mainly *C. chromis* (Table IV). The first group (squares, Fig. 6a) clustered together stations that were generally located far from the coast and mainly occupied by mixed AW to the south of Mallorca Island and influenced by currents flowing from the open sea, which is compatible with the dominance of larvae of tuna and mesopelagic species at these stations. The dominance of coastal species in the second cluster (circles, Fig. 6a) could be explained by the stations being closer to the coast, and at the offshore stations, it could be related to the waters that flow from the Mallorca channel northwards crossing the Menorca channel and taking coastal species with them. The three stations to

the south of Mallorca that belonged to this second cluster corresponded well to the inner waters associated with the gyre related to the AW coming from the Ibiza channel (Fig. 6a).

In 2008, the overall similarity among stations was higher. Three groups were observed (Fig. 5b). One meaningful group, 8-3 (triangles, Fig. 6b), associated with a perturbation of the Balearic Current on the NW coast of Mallorca was characterized by low densities of a high diversity of coastal species, although the most abundant species was *C. pygmaea* (Table IV). However, the main group 8-1, which included seven stations located to the SE of Menorca (squares, Fig. 6b), was

Table II: Species composition in the catches

Species	N	F	%A	AA+	SD (AA+)	AAAt
2006						
<i>Apogon imberbis</i>	10	0.10	0.40	0.83	0.50	0.09
<i>Arnoglossus</i> spp.	1	0.03	0.03	0.24	—	0.01
<i>Atherina</i> spp.	6	0.03	0.19	1.56	—	0.04
<i>Auxis rochei</i> ^a	928	0.82	31.06	8.14	8.40	6.68
Blenniidae	10	0.15	0.32	0.45	0.49	0.07
<i>Bothus podas</i>	4	0.08	0.15	0.42	0.11	0.03
<i>Callionymus</i> spp.	6	0.08	0.22	0.62	0.32	0.05
<i>Ceratoscopelus maderensis</i>	67	0.44	2.24	1.10	1.30	0.48
<i>Chromis chromis</i> ^a	539	0.69	15.54	4.83	6.22	3.34
<i>Coryphaena hippurus</i>	3	0.08	0.10	0.28	0.01	0.02
<i>Cyclothone braueri</i>	11	0.15	0.37	0.52	0.21	0.08
<i>Cyclothone pygmaea</i> ^a	718	0.72	21.27	6.37	8.33	4.57
<i>Engraulis encrasicolus</i>	35	0.23	1.22	1.14	1.04	0.26
<i>Epinephelus</i> spp.	2	0.05	0.07	0.28	0.00	0.01
<i>Euthynnus alletteratus</i>	2	0.05	0.07	0.28	0.02	0.01
Gobiidae spp.	10	0.15	0.33	0.46	0.14	0.07
<i>Lepidorhombus</i> spp.	2	0.05	0.06	0.26	0.04	0.01
<i>Mullus</i> spp.	17	0.31	0.55	0.38	0.14	0.12
Ophidiidae	2	0.05	0.06	0.25	0.03	0.01
<i>Pagrus pagrus</i>	8	0.10	0.27	0.56	0.34	0.06
<i>Parablennius tentacularis</i>	1	0.03	0.03	0.29	—	0.01
<i>Pseudaphya ferreri</i>	1	0.03	0.03	0.26	—	0.01
<i>Sardinella aurita</i>	298	0.44	9.73	4.80	5.08	2.09
<i>Scorpaena</i> spp.	3	0.08	0.10	0.28	0.01	0.02
<i>Seriola dumerili</i>	36	0.36	1.20	0.72	0.68	0.26
<i>Serranus cabrilla</i>	5	0.08	0.17	0.48	0.35	0.04
<i>Serranus hepatus</i>	3	0.08	0.11	0.31	0.06	0.02
Sparidae	5	0.08	0.18	0.50	0.35	0.04
<i>Spicara smaris</i>	14	0.10	0.48	1.00	0.68	0.10
<i>Symphodus</i> spp.	1	0.03	0.03	0.28	—	0.01
<i>Taurulus bubalis</i>	2	0.05	0.07	0.31	0.02	0.02
<i>Thunnus alalunga</i> ^a	263	0.82	9.01	2.36	3.00	1.94
<i>Thunnus thynnus</i>	49	0.31	1.52	1.06	1.26	0.33
<i>Trachinus draco</i>	33	0.15	1.11	1.55	1.97	0.24
<i>Trachurus</i> spp.	22	0.28	0.74	0.57	0.43	0.16
<i>Uranoscopus scaber</i>	6	0.08	0.18	0.50	0.20	0.04
<i>Xiphias gladius</i>	21	0.31	0.69	0.48	0.38	0.15
<i>Xyrichthys novacula</i>	3	0.08	0.10	0.29	0.03	0.02
2008						
<i>Apoda</i>	7	0.13	0.08	0.32	0.17	0.04
<i>Apogon imberbis</i>	7	0.10	0.09	0.43	0.36	0.04
<i>Arnoglossus</i> spp.	5	0.13	0.06	0.24	0.07	0.03
<i>Auxis rochei</i> ^a	2027	1.00	19.12	9.37	13.24	9.37
<i>Belone belone</i>	1	0.03	0.01	0.24	—	0.01
<i>Benthoema glaciale</i>	1	0.03	0.01	0.26	—	0.01
Blenniidae	2	0.03	0.02	0.40	—	0.01
<i>Bothus podas</i>	21	0.33	0.25	0.37	0.23	0.12
<i>Brama brama</i>	1	0.03	0.02	0.31	—	0.01
<i>Callionymus</i> spp.	1	0.03	0.01	0.20	—	0.01
<i>Centracanthus cirrus</i>	1	0.03	0.01	0.15	—	0.00

Continued

Table II: Continued

Species	N	F	%A	AA+	SD (AA+)	AAAt
<i>Ceratoscopelus maderensis</i> ^a	1570	0.97	13.95	7.01	11.94	6.83
<i>Chromis chromis</i>	72	0.44	0.80	0.90	1.15	0.39
<i>Coris julis</i>	8	0.15	0.11	0.36	0.15	0.06
<i>Coryphaena hippurus</i>	2	0.05	0.02	0.21	0.02	0.01
<i>Cyclothone braueri</i> ^a	211	0.64	2.79	2.14	2.31	1.37
<i>Cyclothone pygmaea</i> ^a	3730	1.00	43.18	21.15	28.11	21.15
<i>Dactylopterus volitans</i>	75	0.44	0.84	0.94	0.71	0.41
<i>Diplodus</i> spp.	2	0.05	0.02	0.23	0.02	0.01
<i>Euthynnus alletteratus</i>	83	0.41	0.98	1.17	1.37	0.48
<i>Hygophum</i> spp.	95	0.13	1.39	5.30	6.87	0.68
<i>Katsuwonus pelamis</i>	8	0.13	0.10	0.37	0.24	0.05
<i>Lampanyctus crocodilus</i>	6	0.08	0.10	0.64	0.51	0.05
<i>Lampanyctus pusillus</i>	3	0.05	0.05	0.43	0.27	0.02
<i>Lebetus guilleli</i>	3	0.03	0.03	0.60	—	0.02
<i>Lepidorhombus</i> spp.	4	0.10	0.05	0.22	0.06	0.02
<i>Lestidiops jayakari</i>	1	0.03	0.02	0.38	—	0.01
<i>Lophotus lacepede</i>	1	0.03	0.01	0.26	—	0.01
<i>Luvarus imperialis</i>	12	0.21	0.14	0.33	0.10	0.07
<i>Merluccius merluccius</i>	2	0.05	0.03	0.25	0.01	0.01
<i>Micromesistius poutassou</i>	1	0.03	0.01	0.23	—	0.01
Myctophidae	1	0.03	0.01	0.26	—	0.01
<i>Mugil cephalus</i>	2	0.03	0.02	0.38	—	0.01
<i>Mullus barbatus</i>	1	0.03	0.02	0.30	—	0.01
<i>Mullus</i> spp.	1	0.03	0.02	0.29	—	0.01
Ophidiidae	14	0.15	0.17	0.55	0.44	0.08
<i>Pseudaphya ferreri</i>	20	0.21	0.23	0.56	0.47	0.11
<i>Sarda sarda</i>	2	0.03	0.02	0.45	—	0.01
<i>Sardinella aurita</i>	698	0.36	7.95	10.85	22.60	3.89
<i>Scorpaena porcus</i>	9	0.15	0.10	0.32	0.18	0.05
<i>Scorpaena</i> spp.	11	0.21	0.14	0.33	0.14	0.07
<i>Serranus cabrilla</i>	8	0.10	0.09	0.42	0.28	0.04
Sparidae	1	0.03	0.01	0.25	—	0.01
<i>Symphodus</i> spp.	2	0.05	0.02	0.21	0.04	0.01
<i>Symphurus nigrescens</i>	1	0.03	0.01	0.22	—	0.01
<i>Synodus saurus</i>	2	0.05	0.03	0.24	0.01	0.01
<i>Thunnus alalunga</i> ^a	552	0.82	6.09	3.63	6.04	2.98
<i>Thunnus thynnus</i>	16	0.23	0.22	0.46	0.19	0.11
<i>Trachinus draco</i>	7	0.08	0.09	0.54	0.27	0.04
<i>Trachinus</i> spp.	1	0.03	0.01	0.24	—	0.01
<i>Trachurus mediterraneus</i>	24	0.15	0.26	0.83	0.77	0.13
<i>Trachurus</i> spp.	2	0.05	0.02	0.16	0.01	0.01
<i>Uranoscopus scaber</i>	1	0.03	0.01	0.18	—	0.00
<i>Xiphias gladius</i>	8	0.13	0.09	0.33	0.11	0.04
<i>Xyrichthys novacula</i>	7	0.15	0.08	0.24	0.08	0.04

The number of larvae identified (*N*), frequency of occurrence (*F*), percentage of abundance (%A), average abundance considering only stations where larvae were caught (AA+), standard deviation [SD (AA+)] and mean abundance considering all stations (AAAt) are reported for each taxon and expressed as individuals per 100 m³.

^aSpecies chosen to be measured.

Table III: Literature review compiling information on larval feeding strategies (piscivorous, zooplanktivorous)

Species	Category	Piscivorous	Zooplanktivorous	Not known	Piscivorous	No reference found
<i>Apogon imberbis</i>	Demersal shelf/slope		X (Sampey <i>et al.</i> , 2007)			
<i>Arnoglossus</i> spp.	Demersal shelf/slope		X (Sampey <i>et al.</i> , 2007; Sánchez-Velasco, 1998)			
<i>Atherina</i> spp.	Small pelagics					X
<i>Auxis rochei</i>	Medium pelagics	X (Morote <i>et al.</i> , 2008)	X (Sampey <i>et al.</i> , 2007)			
<i>Belone belone</i>	Medium pelagics	X (Rosenthal, 1970)	X (Rosenthal, 1970)			
<i>Benthoosema glaciale</i>	Meso- and bathypelagics		X (Sabatés <i>et al.</i> , 2007)			
Blenniidae	Demersal shelf/slope		X (Sampey <i>et al.</i> , 2007)			
<i>Bothus podas</i>	Demersal shelf/slope		X (Sánchez-Velasco, 1998)			
<i>Brama brama</i>	Medium pelagics					X
<i>Callionymus</i> spp.	Demersal shelf/slope		X (Sampey <i>et al.</i> , 2007; Sánchez-Velasco, 1998)			
<i>Centracanthus cirrus</i>	Demersal shelf/slope					X
<i>Ceratoscopelus maderensis</i>	Meso- and bathypelagics		X (Conley and Hopkins, 2004; Sabatés <i>et al.</i> , 2007)	X		
<i>Chromis chromis</i>	Demersal shelf/slope		X (Sampey <i>et al.</i> , 2007)			
<i>Coris julis</i>	Demersal shelf/slope					X
<i>Coryphaena hippurus</i>	Medium pelagics					X
<i>Cyclothone braueri</i>	Meso- and bathypelagics					X
<i>Cyclothone pygmaea</i>	Meso- and bathypelagics					X
<i>Dactylopterus volitans</i>	Demersal shelf/slope					X
<i>Diplodus</i> spp.	Demersal shelf/slope		X (Llopiz, 2008; Sánchez-Velasco and Norbis, 1997)			
<i>Engraulis encrasicolus</i>	Small pelagics		X (Tudela <i>et al.</i> , 2002)			
<i>Epinephelus</i> spp.	Demersal shelf/slope		X (Fujii <i>et al.</i> , 2007)	X		
<i>Euthynnus alletteratus</i>	Medium pelagics	X (Sánchez-Velasco <i>et al.</i> , 1999)	X (Sánchez-Velasco <i>et al.</i> , 1999)			
Gobiidae	Demersal shelf/slope		X (Sampey <i>et al.</i> , 2007)			
<i>Hygophum</i> spp.	Meso- and bathypelagics		X (Conley and Hopkins, 2004; Sabatés <i>et al.</i> , 2007)			
<i>Katsuwonus pelamis</i>	Medium pelagics	X (Llopiz, 2008; Takasuka <i>et al.</i> , 2004; Young and Davis, 1990)	X (Llopiz, 2008; Young and Davis, 1990)			
<i>Lampanyctus crocodilus</i>	Meso- and bathypelagics		X (Conley and Hopkins, 2004; Sabatés <i>et al.</i> , 2007)			
<i>Lampanyctus pusillus</i>	Meso- and bathypelagics		X (Conley and Hopkins, 2004; Sabatés <i>et al.</i> , 2007)			
<i>Lebetus guilleti</i>	Demersal shelf/slope		X (Llopiz, 2008)			
<i>Lepidorhombus</i> spp.	Demersal shelf/slope					X
<i>Lestidiops jayakari</i>	Meso- and bathypelagics					X
<i>Lophotus</i> spp.	Meso- and bathypelagics					X
<i>Luvarus imperialis</i>	Medium pelagics					X
<i>Merluccius merluccius</i>	Demersal shelf/slope		X (Cass-Calay, 2003; Llopiz, 2008)			
<i>Micromesistius poutassou</i>	Demersal shelf/slope		X (Hillgruber and Kloppmann, 1999; Llopiz, 2008)			
Myctophidae	Meso- and bathypelagics		X (Llopiz, 2008)			
<i>Mugil cephalus</i>	Meso- and bathypelagics		X (Eda <i>et al.</i> , 1990)			
<i>Mullus barbatus</i>	Demersal shelf/slope		X (Llopiz, 2008)			
<i>Mullus</i> spp.	Demersal shelf/slope		X (Sampey <i>et al.</i> , 2007)	X		
Ophidiidae	Demersal shelf/slope		X (Sampey <i>et al.</i> , 2007)			
<i>Pagrus pagrus</i>	Demersal shelf/slope					X
<i>Parablennius tentacularis</i>	Demersal shelf/slope		X (Gaughan and Potter, 1997)			
<i>Pseudaphya ferreri</i>	Demersal shelf/slope					X
<i>Sardinella aurita</i>	Small pelagics		X (Sampey <i>et al.</i> , 2007)			
<i>Scorpaena porcus</i>	Demersal shelf/slope		X (Llopiz, 2008)			
<i>Scorpaena</i> spp.	Demersal shelf/slope		X (Sampey <i>et al.</i> , 2007)			

<i>Seriola dumerili</i>	Medium pelagics	X (Takasuka et al., 2007)		
<i>Serranus cabrilla</i>	Demersal shelf/slope		X (Llopiz and Cowen, 2009)	X
<i>Serranus hepatus</i>	Demersal shelf/slope		X (Llopiz and Cowen, 2009)	X
Sparidae	Demersal shelf/slope		X (Sánchez-Velasco and Norbis, 1997)	
<i>Spicara smaris</i>	Demersal shelf/slope		X (Llopiz and Cowen, 2009)	X
<i>Symphodus</i> spp.	Demersal shelf/slope			X
<i>Symphurus nigrescens</i>	Demersal shelf/slope			X
<i>Synodus saurus</i>	Demersal shelf/slope			X
<i>Taurulus bubalis</i>	Demersal shelf/slope			
<i>Thunnus alalunga</i>	Large pelagics	X (Sampey et al., 2007)		
<i>Thunnus thynnus</i>	Large pelagics	X (Miyashita et al., 1999)		
<i>Trachinus draco</i>	Demersal shelf/slope		X (Catalán et al., 2007; Sampey et al., 2007)	X
<i>Trachinus</i> spp.	Demersal shelf/slope		X (Arthur, 1976; Uotani et al., 1990; Miyashita et al., 1999)	X
<i>Trachurus mediterraneus</i>	Small pelagics		X (Arthur, 1976; Llopiz, 2008)	
<i>Trachurus</i> spp.	Small pelagics		X (Sassa et al., 2008)	
<i>Uranoscopus scaber</i>	Demersal shelf/slope		X (Govoni et al., 2003; Sampey et al., 2007)	X
<i>Xiphias gladius</i>	Large pelagics		X (Llopiz and Cowen, 2009)	
<i>Xyrichtys novacula</i>	Demersal shelf/slope			

The taxa were assigned to five categories according to their habitat when adults: small pelagic, medium pelagic, large pelagic, demersal shelf/slope and meso- and bathypelagic fish.

separated from the rest of the stations by a frontal area related to the anticyclonic gyre coming from the Algerian Basin and included almost exclusively tuna and mesopelagic species in high densities, of which *C. pygmaea* was the dominant species. The other group 8-2 (circles, Fig. 6b) was more heterogeneous and was not clearly related to any specific hydrographic structure.

The inter-relationships between species determined with the MDS analysis by year (Fig. 7a and b) showed four groups according to a similarity level over 30% in a cluster analysis of the species abundance data. Two of these groups in each year included Scombridae as the dominant species. Stress coefficients (goodness of fit) with values <0.15 indicate that the data are portrayed well (Clarke and Gorley, 2006). One of these groups in the 2 years, called, respectively, groups 6A and 8A, comprised an assemblage that included *T. alalunga* and *A. rochei* and the mesopelagics *C. pygmaea* and *C. maderensis*. The companion species were *C. chromis* in 2006 and *S. aurita* and *C. braueri* in 2008. The species *T. alalunga*, *A. rochei* and *C. pygmaea*, together with *C. chromis* in 2006 and *C. maderensis* in 2008, were clearly the most abundant and ubiquitously distributed across stations in both years. Other Scombridae defined a second group in both years. This group was formed exclusively by *T. thynnus* in 2006 (group 6B) and by *E. alletteratus* together with the coastal species *C. chromis* and *Dactylopterus volitans* (group 8B). Unlike groups 6A and 8A, the species included in groups 6B and 8B showed low total abundances and were restricted to a few stations. In both years, a third group was made up of larvae of small pelagic species: *S. aurita* in 2008 (group 8C) and *Engraulis encrasicolus* and *Trachurus* spp. together with the large pelagic *X. gladius* and the coastal species *T. draco* in 2006 (group 6C). The fourth cluster was very different in the 2 years, since in 2006 it included more coastal species, such as *S. dumerili* and *Mullus* spp. (group 6D), whereas in 2008 it was constituted only by the mesopelagic genera *Hygophum* spp. (group 8D). Therefore, these analyses showed that we should expect interactions between two tuna species, *A. rochei* and *T. alalunga*, and occasionally with other abundant larvae, such as *C. pygmaea* and *C. chromis* in 2006 and *C. maderensis* in 2008. These four species represented on average more than 80–85% of the total number of fish larvae.

Larval morphology and size structure of the species present in the larval assemblages characterized by high tuna larval abundances

The larval length and body depth measurements of the species in groups 6A and 8A (described above) showed that the main species could be grouped into two very different morphological types (Fig. 8; see Table V for

Table IV: Similarities among stations regarding taxon composition and average abundance (AA) of species that represent around 90% of the contribution (expressed as individuals per 100 m³) of each main cluster group (CG)

Year	CG	Ns	AS	Species	AA	%C				
2006	6-1	19	47.31	<i>Cyclotone pygmaea</i>	2.08	39.30				
				<i>Thunnus alalunga</i>	1.31	31.64				
				<i>Auxis rochei</i>	1.04	19.39				
	6-2	20	44.54	<i>Chromis chromis</i>	2.17	31.41				
				<i>Auxis rochei</i>	2.41	23.53				
				<i>Sardinella aurita</i>	1.36	11.08				
				<i>Cyclotone pygmaea</i>	1.08	9.33				
				<i>Thunnus alalunga</i>	0.87	7.53				
				<i>Seriola dumerili</i>	0.45	3.30				
				<i>Mullus</i> sp.	0.30	2.24				
				<i>Ceratoscopelus maderensis</i>	0.38	1.97				
				2008	8-1	7	66.38	<i>Cyclotone pygmaea</i>	7.73	40.00
								<i>Ceratoscopelus maderensis</i>	5.85	26.21
<i>Thunnus alalunga</i>	2.99	13.21								
8-2	29	55.57	<i>Auxis rochei</i>		2.36	12.32				
			<i>Cyclotone pygmaea</i>		3.52	35.44				
			<i>Auxis rochei</i>		3.23	28.75				
8-3	3	61.06	<i>Ceratoscopelus maderensis</i>	1.65	13.94					
			<i>Thunnus alalunga</i>	1.00	7.23					
			<i>Cyclotone braueri</i>	0.80	5.58					
			<i>Cyclotone pygmaea</i>	1.61	15.95					
			<i>Dactylopterus volitans</i>	1.38	12.51					
			<i>Auxis rochei</i>	1.70	11.66					
			<i>Thunnus alalunga</i>	1.55	11.20					
			<i>Chromis chromis</i>	1.30	7.81					
<i>Euthynnus alletteratus</i>	1.11	7.56								
<i>Sardinella aurita</i>	1.08	7.34								
<i>Bothus podas</i>	0.70	5.67								
<i>Ceratoscopelus maderensis</i>	0.73	4.20								
<i>Ophidiidae</i>	0.70	3.00								

The number of stations that make up the cluster (Ns), the average similarity in the group (AS) and the contribution percentage of each species from each cluster group (%C) are reported.

equations). The tuna species, *T. alalunga* and *A. rochei*, and the neritic *C. chromis* were characterized by a tadpole-like body with an enlarged head and wider body size. However, the two mesopelagic species *C. maderensis* and *C. pygmaea* showed an eel-like morphology characterized by a thin elongated body.

The horizontal distribution of potential piscivorous larvae (large tuna larvae between 6.4 and 12.8 mm in SL) compared with that of larvae of smaller tuna and other species (1.6–6.4 mm in SL) was related to the hydrography of the region. In general, small tuna were much more frequent than larger tuna larvae, but at the stations where the latter did appear their biomass was comparable with or even higher than that of the larvae of small tuna and other species (Fig. 9). In 2006 (Fig. 9a), large tuna were caught in locations

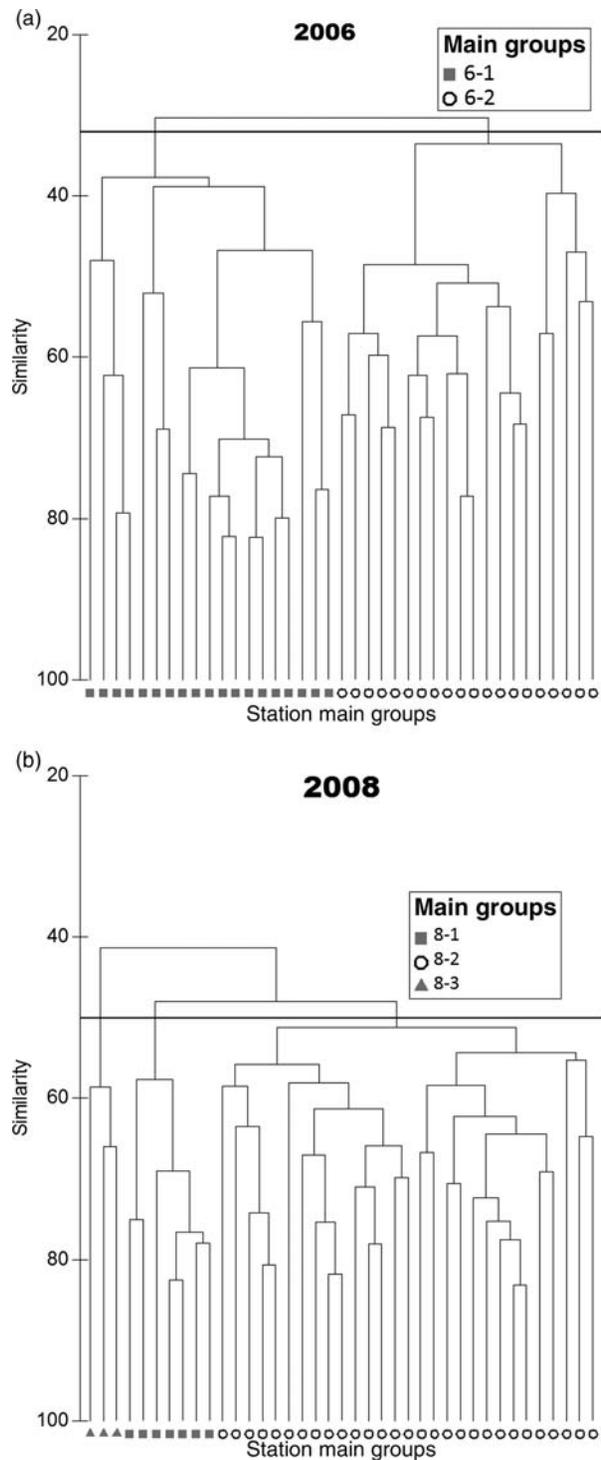


Fig. 5. Similarities among stations resulting from the cluster analysis based on the relative abundances of fish larval species and related to mesoscale oceanographic features in the 2006 (a) and 2008 (b) surveys. Station groups were plotted in grey squares (1), transparent circles (2) and for 2008 also in triangles (3). The x-axis corresponds to the station identification.

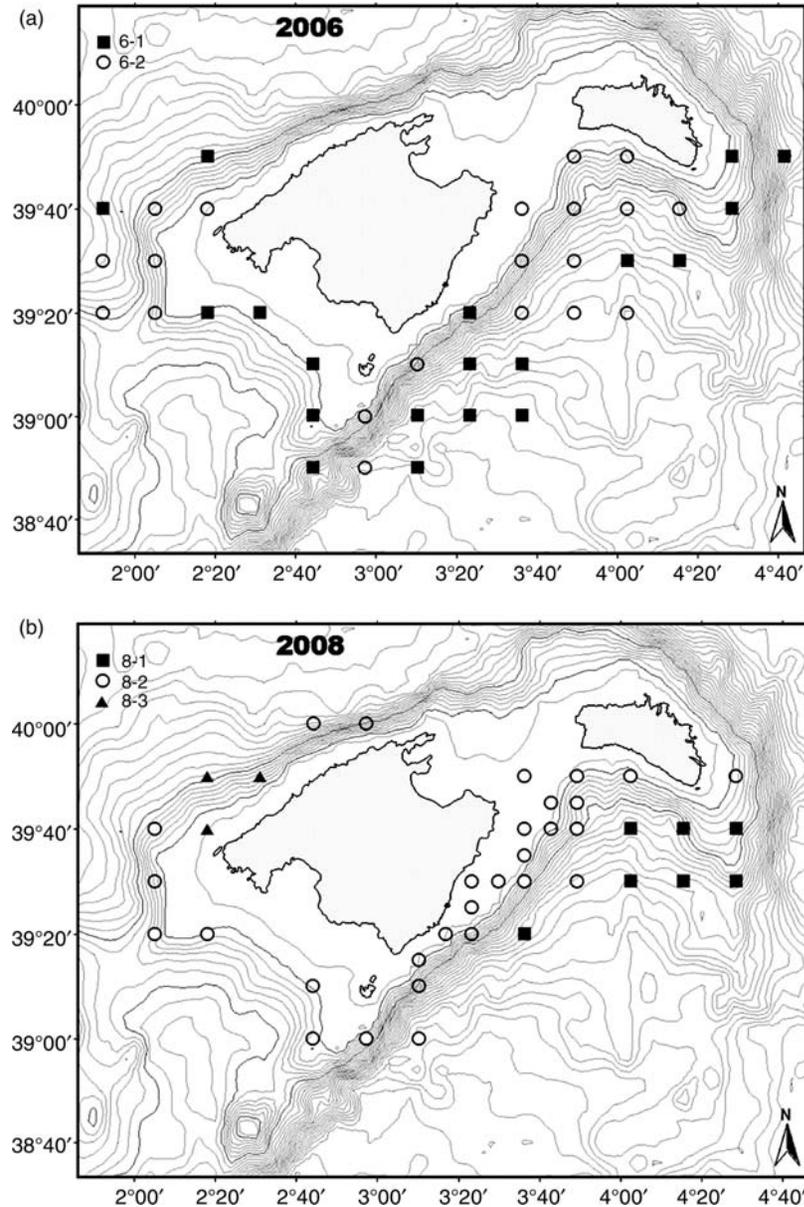


Fig. 6. Spatial distribution of sampling stations and main cluster group assigned to each (based on Fig. 5) in 2006 (a) and 2008 (b).

characterized by inputs of fresh AW in the Mallorca channel that flows northwards crossing the Menorca channel, except for the northeast station, which could be related to a local oscillation of the current. They coexisted mainly with small tuna larvae that followed similar hydrographical patterns in their distribution, whereas small larvae from other species were related more to the resident AW. The large and small tuna in 2008 (Fig. 9b) were located in the mixed AW that occupied most of the area, although small larvae of other species were also important at many stations. The higher abundance of small larvae of non-tuna species

compared with 2006 may be related to a later spawning peak in other species compared with tuna.

DISCUSSION

Horizontal distribution of fish larvae inhabiting the surface mixed layer in relation to hydrographic features

This study indicates that interactions between fresh and resident AW and the resulting mesoscale hydrographic

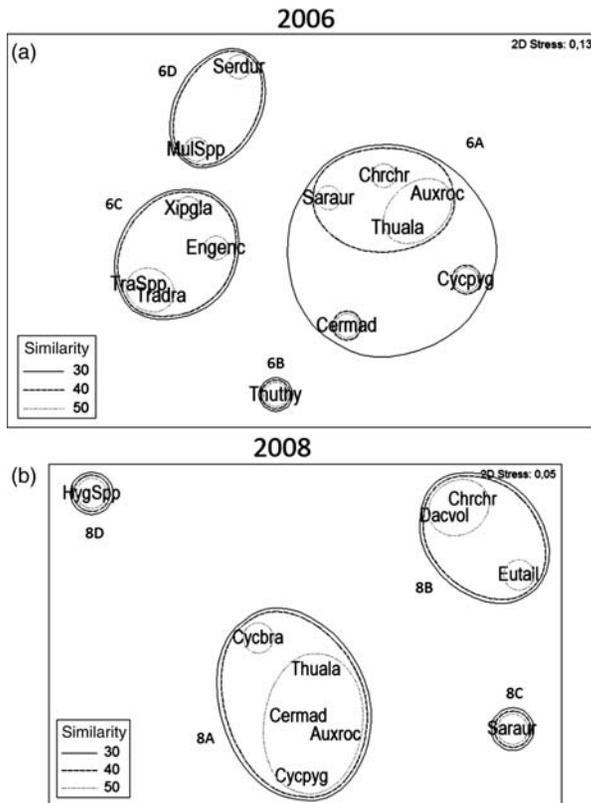


Fig. 7. Grouping of species analyzed with MDS analysis, in 2006 (a) and 2008 (b). Auxroc, *Auxis rochei*; Cermad, *Ceratoscopelus maderensis*; Chrchr, *Chromis chromis*; Cycbra, *Cyclothone braueri*; Cycpyg, *Cyclothone pygmaea*; Dacvol, *Dactylopterus volitans*; Engenc, *Engraulis encrasicolus*; Eutall, *Euthynnus alletteratus*; HypSpp, *Hypophum* spp.; MulSpp, *Mullus* spp.; Saraur, *Sardinella aurita*; Serdur, *Seriola dumerili*; Thuala, *Thunnus alalunga*; Thuthy, *Thunnus thynnus*; Tradra, *Trachinus draco*; TraSpp, *Trachinus* spp.; Xipgla, *Xiphias gladius*.

features are crucial in determining the distribution of tuna larvae in the Balearic Sea, as suggested in previous studies (Alemany *et al.*, 2006, 2010; Sabatés *et al.*, 2007). Consequently, depth usually explains only a small percentage of this spatial distribution (Alemany *et al.*, 2006). This phenomenon is favored by the narrowness of the continental shelf around the archipelago. Therefore, mesopelagic species can dominate larval assemblages in areas relatively near to the coast, as observed in 2008 with *C. pygmaea*. Moreover, larvae of coastal species are frequently present at offshore stations, as was the case of *C. chromis* larvae in 2006. This particular species is representative of a reproductive strategy followed by most neritic species in the Mediterranean, in which spawning takes place during the spring–summer period (Ancona *et al.*, 1931–1956). However, depth is still the major factor determining the distribution of some species that spawn near the coast, such as *S. aurita*, which dominates coastal stations

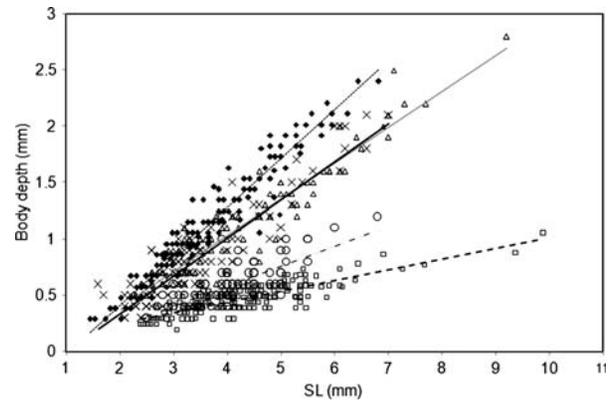


Fig. 8. Larval SL and body depth relationships for *Auxis rochei* (triangles), *Ceratoscopelus maderensis* (circles), *Chromis chromis* (rhomboids), *Cyclothone pygmaea* (squares) and *Thunnus alalunga* (crosses).

Table V: Relationships between SL and body depth (body depth = a + b SL a; all units in mm)

Species	a	b	r ²	N	SL range
<i>Auxis rochei</i>	-0.24	0.32	0.90	100	2.3–9.2
<i>Ceratoscopelus maderensis</i>	-0.13	0.18	0.57	108	2.5–6.8
<i>Chromis chromis</i>	-0.46	0.43	0.93	192	1.4–6.8
<i>Cyclothone pygmaea</i>	0.06	0.10	0.66	228	2.4–9.9
<i>Thunnus alalunga</i>	-0.34	0.34	0.85	94	1.6–7.0

occupied by saline Mediterranean waters on the Spanish mainland (Sabatés *et al.*, 2009) and around the Balearic Islands, as shown in our study.

We identified five tuna species. Atlantic bluefin tuna larvae were usually found at offshore stations, probably due to migrating spawners reaching the area associated with the fresh AW input, which usually flows outside the 200-m isobath. Other migrant species, such as *K. pelamis*, have also been found at stations occupied by fresh AW. The larvae of *T. alalunga* and *A. rochei* were dominant in various cluster groups that included both inshore and offshore stations, which agrees with previous results for the area (Dicenta *et al.*, 1975, 1983; Alemany *et al.*, 2006, 2010). We did not catch high abundances of bluefin tuna, *T. thynnus*, despite the Balearic Islands being one of the main spawning grounds of this species. This was because its spawning window is shorter than that of *A. rochei* and *T. alalunga* and spawning generally takes place in June–early July, which is before our sampling period. Therefore, bluefin tuna larvae are expected to dominate the larval assemblage earlier in summer. However, the sampling in the two study years was carried out in different months and the spawning peaks of the different tuna species

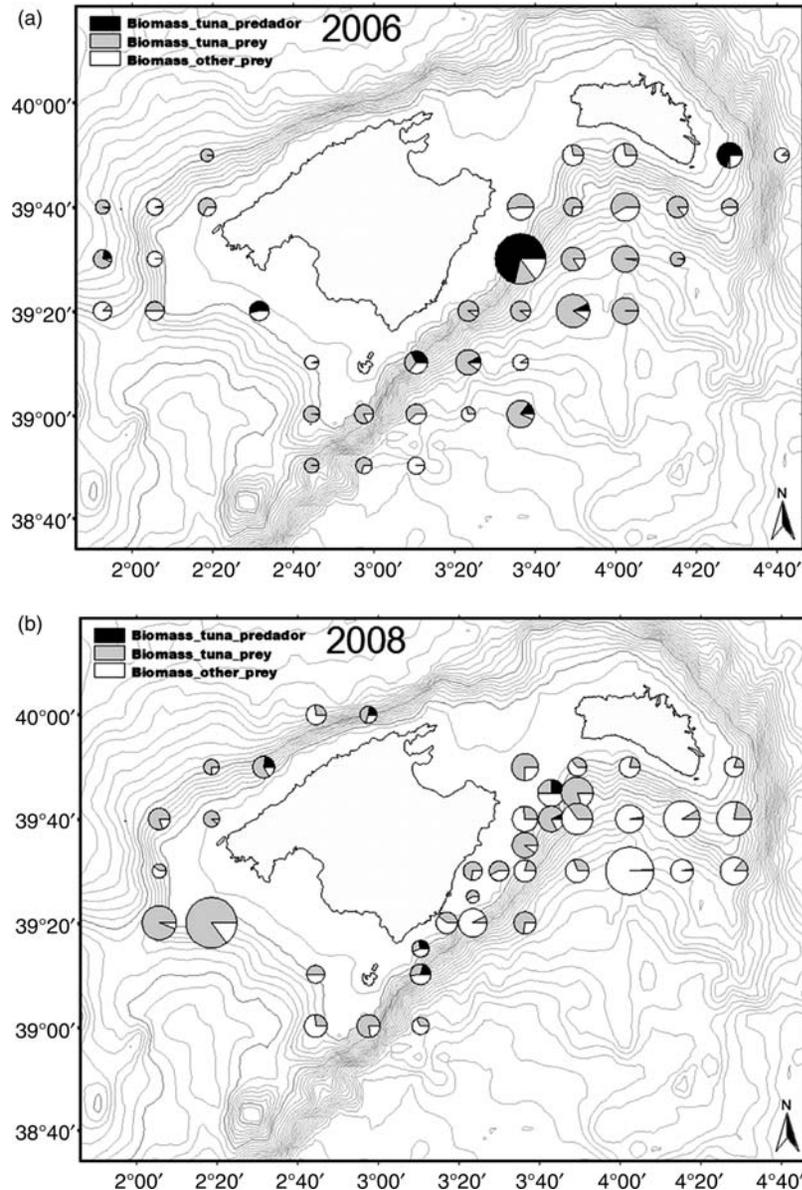


Fig. 9. Average proportion of the total biomass of large sized tuna larvae “predators” (6.4–12.8 mm in SL; black) compared with small sized tuna larvae “prey” (1.6–6.4 mm in SL; grey) and other species from assemblage “other_pre” (1.6–6.4 mm in SL; white) for 2006 (a) (“other_pre”: *C. pygmaea* and *C. chromis*) and 2008 (b) (“other_pre”: *C. pygmaea* and *C. maderensis*).

observed in the study area did not occur at exactly the same time (Alemany 1997; Alemany *et al.*, 2006, 2010); thus, part of the differences found between the 2 years in the absolute and relative larval abundances of the various tuna species and of tuna compared with the other species could be attributed to the disparity in sampling dates.

Our study supports the results from previous studies showing that the dominance of tuna larvae around the Balearic Islands during summer differs from the predominance of small pelagic fish in the nearby mainland

shelf areas, which is associated with river plumes (Sabatés *et al.*, 2007), as well as the dominance of larvae of meso- and bathypelagic species in offshore waters in other nearby areas of the WMED (Sabatés and Saiz, 2000; Vargas-Yañez and Sabatés, 2007; Olivar *et al.*, 2010). Tuna larvae are a major component of summer larval fish assemblages around other islands in the Mediterranean Sea (Kohno *et al.*, 1982; Somarakis *et al.*, 2002) and other islands worldwide (Miller, 1979; Leis *et al.*, 1991; Boehlert and Mundy, 1994; Sánchez-Velasco *et al.*, 1999; Beckley and Leis, 2000).

Specifically, the two most abundant and frequent species in our samples, *A. rochei* and *T. alalunga*, have also been reported as dominant species in tropical areas such as the Hawaiian Islands, with abundances up to 44 larvae per 100 m³, and in some cases *A. rochei* represents over 94% of all the Scombridae larvae found (Miller, 1979; Bochlert and Mundy, 1994). A similar pattern has been observed in east China (Okazaki and Nakata, 2007) and French Polynesia, the Marquesas Islands and the central Pacific (Leis *et al.*, 1991).

Our results improve what is known about tuna-dominated larval assemblages by showing that it is necessary to consider the vertical distribution of the larvae and the oceanography of the area to describe the horizontal spatial distribution of station groups and their dominant species. We carried out sampling in the mixed layer, whereas previous studies on the larval associations in tuna spawning grounds included samples obtained from depths below those where tuna are distributed (Somarakis *et al.*, 2002; Alemany *et al.*, 2006). Apart from the tuna larvae, the other abundant larvae in our samples were mainly those of meso- and bathypelagic species, although these are mainly distributed below the thermocline. Tuna and mesopelagics also dominate summer larval assemblages in other tuna spawning grounds, e.g. the Straits of Florida (Richardson *et al.*, 2010) and the Aegean Sea (Somarakis *et al.*, 2002). But the larval vertical distribution differs among mesopelagic species, since some species are mostly found in deeper layers under the mixed layer, whereas others mainly occupy the first 20 m of the water column (Olivar *et al.*, 2010) and become mesopelagic when they reach the juvenile stage. Therefore, tuna larvae can only potentially interact with these latter species. Mesopelagic species do not show clear vertical migrations and occupy similar water depths throughout the diel cycle depending on the species (Sassa *et al.*, 2004; Olivar *et al.*, 2010). Similarly, tuna larvae usually remain in the upper layers during both the day and the night (Satoh, 2010). Therefore, large pelagic species coexist only with the mesopelagic species that occupy the mixed layer during the larval stage and not with those showing a deeper distribution. Specifically, in our samples, the abundant larvae of meso- and bathypelagic species in the upper layers were those of *C. pygmaea* and *C. braueri* (family Gonostomatidae) and also larvae of *C. maderensis* and *Hygophum* spp. (family Myctophidae) and tuna larvae.

Our second main result is that the hydrography in the mixed layer determines the spatial distribution of the species that move with the AW flow. Tuna larvae are often found around islands associated with frontal areas and eddies that could act as convergence and retention

areas (Bakun, 2006; Satoh, 2010), and hence high ichthyoplankton abundances could be expected. We suggest that these could be mechanisms that lead to greater accumulations of small and large larvae as well as higher food availability, depending on the morphology and feeding habits of the larvae.

Composition and structure of surface mixed layer larval assemblages: implications for the trophic ecology of tuna larvae

Our results on the dominant biomass of tuna larvae showed that the coexistence of small and large tuna larvae was linked to the location of the mixed AW earlier in the season when small tuna are some of the most abundant larvae in the entire assemblage, whereas later in the season abundances of other larval species are higher. Among the specimens identified in our study, only the larger tuna larvae have been reported in the literature to be piscivorous. Therefore, these larger tuna co-occurring with smaller larvae could result in potential feeding areas, with larger tuna acting as predators both of smaller tuna, which would have a higher biomass and calorific content, and larvae of small mesopelagic species, with a lower biomass and calorific content.

The different morphologies of tuna and Gonostomatidae may also indicate differences in feeding habits, since the Gonostomatidae larvae found in our study probably feed on smaller prey than do the tadpole-shaped tuna larvae of similar and even smaller sizes. Data in the literature describing the diet of the more abundant species found in our samples, the tuna *A. rochei* and *T. alalunga*, the mesopelagics *C. pygmaea* and *C. maderensis* and the more coastal *C. chromis*, indicate that tuna larvae gain the capacity to capture larger prey earlier than mesopelagic–bathypelagic species (Fig. 10). However, similarities in the prey size spectrum among the species considered suggest that there could be competition for prey among tuna species at similar larval sizes (Fig. 10). In addition, there is no literature on prey selectivity for any Gonostomatidae, including *Cyclothone*. Therefore, we used data reported for anchovy (*E. encrasicolus*) as this species has a similar body type and its vertical and horizontal distributions overlap those of tuna and Gonostomatidae larvae (Olivar *et al.*, 2010). That these species are all found in NW Mediterranean waters in summer can be explained by the influence of eddies that transport oceanic larvae from the shelf break to the shelf (Olivar *et al.*, 2010) and also by the spawning strategy of anchovy, which spawns

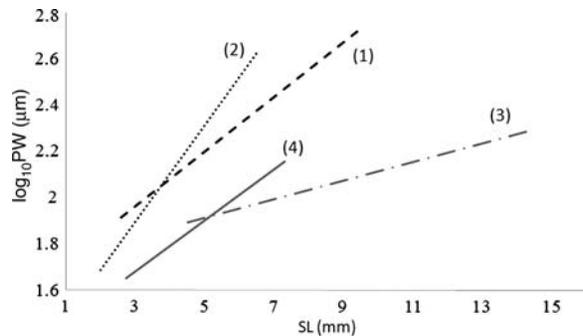


Fig. 10. Relationship of mean prey width (PW) and SL for *Ceratoscopelus maderensis*, tuna-like and eel-like. 1, *T. alalunga* (Catalán *et al.*, 2007); 2, *A. rochei* (Morote *et al.*, 2008); 3, *E. encrasicolus* (Morote *et al.*, 2010); 4, *C. maderensis* (Sabatés and Saiz, 2000).

mainly near the shelf break (Huret *et al.*, 2010) so that it spreads over open waters beyond the shelf break.

There are few potential prey items for smaller tuna larvae in offshore oligotrophic surface waters, such as those around the Balearic Islands or in other tropical tuna spawning or nursery grounds (Nishimura *et al.*, 1999), and the micro- and mesozooplankton density is too low to guarantee that fish larvae do not starve; therefore, the spawning strategies of the tuna species considered cannot be explained as a strategy for optimizing larval feeding opportunities. On the contrary, the main reason that tuna spawn in these poor areas could be to avoid predators (Bakun, 2006). Therefore, Scombridae larvae would take advantage of their special adaptations, such as high visual capacity, relatively large mouths and high swimming speed (Margulies, 1997; Masuda *et al.*, 2002; Catalán *et al.*, 2007), to survive in these low prey density scenarios. From a certain size, the change to a piscivorous diet would permit some larvae to survive until juvenile stages. Our results support this hypothesis, since the spatial coexistence of larger and smaller tuna larvae or other tadpole-like larvae, such as those of *C. chromis*, as well as post-flexion tuna larvae and smaller larvae of meso- or bathypelagic species, would permit these trophic interactions. It could also be hypothesized that larger tuna larvae would prey preferentially on other tadpole-like larvae, such as smaller tuna or *C. chromis* larvae, since this would be a way of optimizing their feeding strategy.

However, our results do not allow us to confirm these hypotheses at present. More information on the ontogenetic and diel patterns of the vertical distribution of gonostomatid and myctophid larvae, which have a wider distribution in the water column than tuna larvae, and stomach content or isotopic analysis of the prey of large tuna larvae would be necessary to improve our understanding of the possible interactions among these species

in the Balearic Sea. This extends to the coastal species *C. chromis*, for which there is very little information. These further studies would allow us to make sound inferences about diet overlap, trophic ecologies and competition and predator–prey relationships among the four dominant species within the offshore open sea larval assemblage characteristic of the waters around the Balearic Islands during summer. Moreover, it would be necessary to improve our knowledge of the ecology of all the zooplankton communities in the area to achieve a better understanding of the biological processes affecting the survival rates of tuna larvae in this spawning ground.

CONCLUSION

The complex surface water circulation pattern around the Balearic Islands can modify the larval fish distribution to the point that the initial spatial pattern resulting from the distribution of spawners, which is generally closely related to the depth gradient, becomes blurred. The area occupied by the mixed AW and the location of the frontal areas related to the anticyclonic gyres coming from the Algerian Basin sets the hydrographic scenario for tuna larvae to dominate the larval associations and for the coexistence of different tuna species and two other mesopelagic species, mainly *C. pygmaea* and/or *C. maderensis*. Tuna occur in similar hydrographic scenarios during their different developmental stages; therefore, potential feeding areas for plausible piscivorous tuna that depend on the abundance of smaller tuna larvae are likely to be located in the areas with mixed AW. Later in the season, when the tuna spawning activity slows down, potential feeding areas for piscivorous tuna could depend more on the abundance of small larvae of non-tuna species that are spawned later and transported by the fresh AW flow to offshore stations.

Therefore, the co-occurrence of tuna and mesopelagic larval species in the mixed layer reported in our study cannot be assumed to represent direct interactions of either competition or predation. However, by describing the Scombrid dominated summer larval associations in the Balearic Sea, this study sets the foundations for further studies on the main ecological interactions that could be established among tuna larvae and larvae of other fish in this important tuna spawning ground.

ACKNOWLEDGEMENTS

We would like to thank the scientific personnel and the crew participating in the surveys on board the R/V

Odón de Buen; 2 anonymous reviewers; Catherine Stonehouse reviewed the English; Jose Luis López Jurado and Raúl Laiz provided helpful discussions; Aurora Alcover and Clara Cánovas helped identify and measure the larvae. We are grateful to I. A. Catalán and A. Sabatés for providing their data for Figure 10.

FUNDING

This study was partly financed by the Spanish Ministry of Science and Innovation (BALEARES, CTM 2009-07944 MAR). A.P.T. was partly supported by a scholarship from the Conselleria d'Agricultura i Pesca of Balearic Government.

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