

The influence of mesoscale physical processes on the larval fish community in the Canaries CTZ, in summer

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Abstract

We have studied the relation between the hydrography, the composition and horizontal structure of the larval fish community, and the horizontal distribution patterns of larval fish abundances in an area characterised by strong mesoscale oceanographic activity, located between the Canary Islands and the African coast (the Canaries Coastal Transition Zone), during August 1999. Upwelling, upwelling filaments, cyclonic and anticyclonic eddies and island wakes are typical mesoscale features of the northwest African coast in summer. A single upwelling filament off Cabo Juby was joined in mid-August by a second that originated about 100 km to the north. The two filaments flowed together and merged 100 km offshore. The merged filament was partially entrained around a cyclonic eddy, trapped between the Canary Islands and the African coast, and interacted with cyclonic and anticyclonic eddies shed from Gran Canaria. Mesoscale oceanographic features strongly influenced the horizontal distributions of fish larvae. Eddies acted as a mechanism of concentration, while upwelling filaments were

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dispersive, transporting larvae from the African neritic zone into oceanic areas and towards the Canary archipelago. This transport was the major cause of the predominance of neritic larvae in the composition of the larval fish community of the area. The results also suggest (1) that anchovy larvae are good indicators of the offshore displacement of upwelled water, (2) that the alternation between anchovy and sardine as species dominant in the larval fish community of the area during summer depends upon the water temperature in the African upwelling region, anchovy dominating at higher temperature, and (3) that a coupling of anchovy and sardine spawning with the mesoscale oceanographic structure formed by the upwelling filaments and trapped eddy overcomes the negative effect that Ekman transport has on their populations.

Contents

1. Introduction	3
2. Materials and methods.....	5
2.1. Ichthyoplankton sampling.....	5
2.2. Laboratory analysis.....	6
2.3. Data analysis.....	6
3. Results	7
3.1. Hydrographic conditions	7
3.2. Taxonomic composition of the larval fish community	8
3.3. Horizontal distributions	9
4. Discussion	13
Acknowledgements	19
References	19

1. Introduction

Mesoscale oceanographic processes play a major role in determining the horizontal distribution pattern of larval fish abundance and the horizontal structure of the larval fish community. Structures such as eddies and fronts can work as mechanisms of retention and concentration (Iles & Sinclair, 1982; Bolz & Lough, 1984; Lobel & Robinson, 1986, 1988; Kioerboe, Munk, Richardson, Christensen & Paulsen, 1988; Sabates & Maso, 1990, 1992; Sournia, 1994). On the other hand, other mesoscale phenomena, such as the Ekman transport associated with coastal upwelling, upwelling filaments and even eddies may work as mechanisms of dispersion (Wroblewski & Cheney, 1984; Flierl & Wroblewski, 1985; Fiedler, 1986; Myers & Drinkwater, 1989; Roy, 1998; Smith & Suthers, 1999). Upwelling filaments can transport neritic larvae into the oceanic region (Rodriguez, Hernández-León & Barton, 1999), far away from their birthplace. The fact that fish larvae aggregate mainly in the upper 200 m makes them an ideal group to observe the coupling between hydrodynamic events and the structure of planktonic populations (Sabates & Maso, 1992). Biological factors, such as the location and strategy of spawning (Parrish, Nelson & Bakun, 1981; Norcross & Shaw, 1984; John, 1985; Kim & Bang, 1990), the vertical distribution of fish larvae in the water column (John, 1985; Frank, Loder, Carscadden, Leggett & Taggart, 1992; Olivar & Sabates, 1997) and their migratory behaviour (Parrish *et al.*, 1981; Gorbunova, Evseenko & Garetovsky, 1986; Myers & Drinkwater, 1988) are also involved in the horizontal distribution of fish larvae. However, in plankton communities, biological-physical interactions are more important in determining patterns of horizontal distributions than purely biological forcing mechanisms (Mackas, Denman & Abbot, 1985).

The Canaries Coastal Transition Zone (The Canaries CTZ) is an area of strong mesoscale oceanographic activity. The Canary Islands, acting as a barrier to the Trade Winds and the Canary Current, introduce a strong variability in the atmospheric and oceanic flows. This gives rise to mesoscale oceanographic features, such as eddies and warm wakes leeward of the islands (Mittelstaedt, 1991; Van Camp, Nykjaer, Mittelstaedt & Schlittenhardt, 1991; Hernández-Guerra, Arístegui, Cantón & Nykjaer, 1993; Arístegui, Sangrá, Hernandez-Leon, Cantón, Hernández-Guerra & Kerling, 1994; Arístegui, Tett, Hernández-Guerra, Basterretxea, Montero, Wild *et al.*, 1997; Barton, Arístegui, Tett, García-Braun, Hernández-León, Nikjær *et al.*, 1998). On the other hand, the upwelling filaments associated with the NW African upwelling can transport upwelled water masses (Barton *et al.*, 1998; Navarro-Pérez & Barton, 1998) and their load of chlorophyll (Hernández-Guerra *et al.*, 1993; Basterretxea, 1994; Arístegui *et al.*, 1997), mesozooplankton (Hernández-León, Almeida, Portillo-Hahnefeld, Gómez, Rodríguez & Arístegui, 2002) and neritic fish larvae (Rodríguez *et al.*, 1999) to open ocean waters and toward the Canary Islands. *In situ* measurements carried out by Arístegui *et al.* (1997) showed evidence of water masses originating in the African upwelling close to the east coast of Gran Canaria. Moreover, remote sensing studies of sea surface temperature and ocean colour of the northwest African upwelling have shown that the upwelling filaments, found between Cape Juby and Cape Bojador, are recurrent mesoscale oceanographic structures affecting the Canaries CTZ (Barton *et al.*, 1998; Navarro-Pérez & Barton, 1998).

In this paper we study the relationship between mesoscale oceanographic structures and fish larvae in an area of strong mesoscale oceanographic activity, the Canaries CTZ, located between the Canary archipelago and the African coast. More specifically, we demonstrate that the composition and the horizontal structure of the larval fish

community, and horizontal distribution patterns of larval fish abundances can be explained in the light of the mesoscale oceanographic processes operating in the area at the time of the sampling.

2. Materials and methods

The data presented here were obtained during the cruise He56 of R/V *Hesperides*, carried out from 5 to 27 August 1999 in the Canaries CTZ, located between the Canary Islands and the African coast (Fig. 1). Hydrographic conditions were measured at every station by means of a CTD (Barton, Arístegui, Tett & Navarro-Pérez, this volume). In total, 37 stations were sampled for ichthyoplankton; these stations were arranged in a long section, seven short transects and two isolated stations (Fig. 1). Five of the short transects (S, F, Q, -a repeat of F-, W and Y) cut the upwelling filaments detected in the satellite images (Barton, Arístegui, Tett & Navarro-Pérez, this volume) perpendicularly at different distances from the African coast. The three transects were arranged with one station north of an upwelling filament, one (two for transect S) in the filament itself and one south of the filament. Transect V crossed filament F2 and the anticyclonic eddy (A7) located southwest of Fuerteventura; transect Z crossed the anticyclonic eddy (A6) located south-southeast of Gran Canaria (Fig. 1). The two isolated stations, D2 and D4, corresponded to 24-hour samplings following surface drifters.

2.1. Ichthyoplankton sampling

Zooplankton samples were collected at various times of day and night with a Longhurst-Hardy Plankton Recorder (LHPR) (Williams, Collins & Conway, 1983) fitted with a calibrated flow meter. The 200 μm mesh screen in the sampler was programmed to increment at 2 minute intervals during the descent of the net. Tows were oblique to 200

m depth or to 10 m above the bottom at shallower stations. On recovery of the gear, the plankton was removed from the meshes and the resulting samples were preserved in a buffered 4% solution of formalin and seawater.

2.2. *Laboratory analysis*

In the laboratory, all fish eggs and larvae were sorted. The number of individuals collected in the different sampling strata was integrated to obtain abundances, number of individuals per $(10 \text{ m})^2$ of sea surface (Smith & Richardson, 1979). The fish larvae were identified to the lowest taxonomic level possible and grouped into three categories, 'neritic', 'oceanic' and 'other', according to Rodriguez *et al.* (1999). The taxonomic organization of the larval fish community follows Whitehead et al (1984). The number of larval fish taxa recorded at each station is taken as a measure of the taxonomic diversity.

2.3. *Data analysis*

The horizontal structure of the larval fish community was addressed through multivariate analysis. Hierarchical agglomerative clustering was used to group stations into several larval fish assemblages (Richardson, Laroche & Richardson, 1980; Smith, Gibbs, Middleton & Suthers, 1999). Only taxa present in at least 10% of the samples were included in the analysis; the others, rare taxa, carry little classificatory information (Boesch, 1973). The Bray-Curtis measure of similarity (Bray & Curtis, 1957) was applied to the square-root transformed data of larval fish abundances. The station classification was performed by applying the UPGMA (Unweighted Pair Group Using Arithmetic Average) method (Sokal & Michener, 1958) to the Bray-Curtis matrix. Finally, the station groupings produced by this analysis were geographically represented (Sabates & Olivar, 1996).

3. Results

3.1. Hydrographic conditions

The hydrography of the study area during the sampling period, described by Barton *et al.* (this volume), was characterised by different mesoscale oceanographic structures whose location at the time of *in situ* sampling is indicated in Fig. 1. These included an anticyclonic eddy (A1) shed from Tenerife, anticyclonic (A6) and cyclonic (C2) eddies shed from Gran Canaria, an eddy spinning anticyclonically south of Fuerteventura (A7) and an upwelling filament (F1), partially entrained at its end around a cyclonic eddy (C7). Moreover, the characteristic warm regions in the lee of Gran Canaria and Fuerteventura were evident. Fig. 1 is an idealised sketch of the situation because eddies and filaments are structures that change in space and time. For example, cyclonic and anticyclonic eddies are continuously shed from Gran Canaria to drift southward with the general flow of the Canary Current (Arístegui *et al.*, 1994; Arístegui *et al.*, 1997; Barton *et al.*, 1998) and filaments, as discussed later, are also changing structures.

Anticyclone A1, with its core situated west of station LS10, and cyclone C2, both crossed by the Long Section, were evident in the vertical temperature profile of this transect (Fig. 2a). Eddies A7 and A6 were also apparent in the vertical temperature profiles of transects V and Z (Figs. 2b and 2c, respectively). These eddies distorted the warm lee region of the islands.

The single upwelling filament (F1), observed in early August, had its origin on the continental shelf at approximately 27.2° N and extended almost to the east coast of Gran Canaria. A second filament (F2) developed in mid-August near 28.3° N and flowed southwest from the shelf to merge with F1 some 100 km offshore (Fig. 1). Associated

with the development of F2, a pair of counter-rotating eddies (cyclonic C8 and anticyclonic A8) formed between the two filaments and the African coast (Fig.1). The single upwelling filament and later the merged filament were partially entrained around C7 and interacted with both cyclonic and anticyclonic eddies shed from Gran Canaria. The upwelling filaments are a recurrent mesoscale feature in this area, and C7 is seemingly a quasi-permanent feature topographically trapped between the eastern islands of the Canary Archipelago and the African coast (Barton *et al.*, 1998; Navarro-Pérez & Barton, 1998). Barton *et al.* (1998) suggested that a significant part of the offshore flow in the filament is entrained around the trapped cyclonic eddy and returned to the coastal zone.

3.2 Taxonomic composition of the larval fish community

In total, 3183 fish larvae belonging to 44 families were captured. A total of 109 taxonomic groups were identified, 81 to species level and the rest to genera and families (Table I).

The identifications carried out at species level included two categories. One of them comprised those whose genera and species were recognised (74 cases); the other (7 cases) included those whose genera were recognised and the different species were distinguished with the notation sp, or with this notation followed by a number. The early stages of *Cyclothone pallida* and *Cyclothone pseudopallida*, and of the three species of the genus *Vinciguerria*, some young larvae from the four species of the genus *Gonostoma* and from two species of the genus *Tetragonurus* were grouped due to difficulties in differentiating them. These four groups were not included in the taxonomic recount.

Of the 44 families of larval fish caught, only 8 exceeded 1% of the total of larval fish catches. The three most frequent captured families, Engraulidae (29.3% of total fish

larvae), Myctophidae (28.7%), and Serranidae (13.5%), accounted for 71.5% of total fish larvae. The most diverse family was Myctophidae (22 species identified). Six families were represented by only one species with only one specimen. As a whole, the neritic larvae, with 50.4% of the total catch, dominated the larval fish community, 43.5% were oceanic, 1.1% belonged to the group “other”, and the rest, 5.0%, remained as unidentified. The relatively high percentage of unidentified larvae resulted partly from damage during collection. Most of the neritic larvae (97.4%) were caught beyond what can be considered the limit of the neritic region, the 200 m isobath. In contrast, only 0.3% of the oceanic larvae were caught in the neritic region.

The structure of the larval fish community (Table I) was quite similar to that exhibited by the community inhabiting the area in August 1993 (Rodriguez *et al.*, 1999). The most outstanding difference is that this time anchovy, not sardine, was the dominant species. In August 1993, sardine and anchovy represented 27.6% and 7.5%, respectively, of the total larval fish catches.

3.3. Horizontal distributions

The number of taxa clearly increased with distance from the African coast and towards the core of the anticyclonic eddies. The opposite tendency was observed for cyclonic eddies (Fig. 3a). The lowest diversity was recorded at the neritic station D2. A relatively low number of species was also registered at the stations located within the filaments. Higher diversities were recorded at stations located on the north side of the upwelling filaments.

The horizontal distribution of larval fish abundances followed a pattern similar to that of the total number of species (Fig. 3b). Low abundances were recorded at the neritic stations, and the highest abundances were associated with group B stations established by the classification technique discussed later. Larval fish abundances tended to

increase from the edge towards the core of the anticyclonic eddies, while the opposite tendency was observed for the cyclonic eddies. Higher concentration of fish larvae was also observed at the stations located on the north side of the upwelling filaments. Larval fish abundances in the sites north, inside and south of the filaments were significantly different (Kruskal-Wallis test, $p < 0.05$).

The horizontal distributions of larvae of selected species, representative of the different patterns of distribution shown by the most abundant taxa, are presented in Fig. 4. The horizontal distribution of anchovy larvae (Fig. 4a) was characterised by their presence at almost all stations sampled and by highest abundance outside the African shelf region, between the upwelling front and the island of Fuerteventura. A relatively high abundance was also recorded at station LS17, located on the edge of the trapped cyclonic eddy (C7). It is emphasized that the hauls carried out on the African shelf, the only spawning area for anchovy and sardine in the northwest African upwelling region (Furnestin & Furnestin, 1959; FAO, 1980; Blackburn & Nellen, 1976), produced relatively high numbers of anchovy eggs. An important concentration of spawning with almost 15000 eggs $(10 \text{ m})^{-2}$ was detected at station D2, near the origin of F2, and more than 700 eggs $(10 \text{ m})^{-2}$ were recorded at the other neritic station (LS24). This contrasts strongly with the situation found on the African continental shelf in August 1993, when no anchovy eggs were collected, and anchovy spawning was supposedly taking place north of the sampled area (Rodriguez *et al.*, 1999). At that time, relatively strong sardine spawning was indicated by a density of more than 5000 $(10 \text{ m})^{-2}$ sardine eggs at the only neritic station sampled (Rodriguez, 1998). In neither cruise were any anchovy or sardine eggs collected outside the African shelf region.

The highest abundances for *Anthias anthias* (family Serranidae, “Swallowtail sea perch”) larvae were recorded at the stations situated south-southeast of Fuerteventura

(Fig. 4b). They were absent from the stations located in the African neritic region, and presented low abundances or were also absent from the offshore stations in the region of influence of the African upwelling and associated filaments. The significant centre of abundance located south-southeast of Fuerteventura included the stations situated north of F2 and stations in the anticyclonic eddy A7.

All of the most frequently caught oceanic species belonged to the mesopelagic habitat, and all of them, except *Myctophum punctatum*, presented a similar pattern of horizontal distribution. Fig. 4c shows the horizontal distribution of *Cyclothone braueri*. The larvae of this species were absent from the stations on the African shelf and presented low or zero abundances at the offshore stations near the shelf and under the influence of the African upwelling and associated filaments. Their absence from some oceanic stations was probably due to sampling variability.

The horizontal distribution pattern of *M. punctatum* larvae (Fig. 4d) was quite different from the other mesopelagic oceanic species and showed some similarities to that displayed by *Engraulis encrasicolus* (Fig. 4a). Its most striking feature was that it was the only species of oceanic larval fish caught at the stations situated on the African shelf. The highest abundance for all the stations sampled was recorded at station F5, located at the core of filament F1.

The classification technique established three larval fish assemblages (groups of stations) that we have named after their horizontal location and their relationship with the upwelling filaments (Fig. 5) as ‘neritic assemblage’ (A), ‘transitional or filament related assemblage’ (B) and ‘oceanic assemblage’ (C). The remaining stations remained as ungrouped because either they were dissimilar or they formed small incoherent groups. The geographic location of the stations groupings produced by the classification analysis is shown in Fig. 1.

The *neritic assemblage* occurred at stations situated in the African neritic region (labelled A in Fig. 1). It was characterised by low diversity (Fig. 3a), low abundances (Fig. 3b) and the predominance of neritic larvae (Table II). The most abundant species of this assemblage was *Engraulis encrasicolus*; the other taxa presented very low abundances. The only oceanic species caught in the region occupied by this assemblage, as already mentioned, was *Myctophum punctatum*.

The *transitional or filament-related assemblage* (stations B in Fig. 1) appeared within and north of the two filaments, as well as at station LS17 where the merged filament was entrained around the eddy C7. It also included stations within anticyclone A7 south of Fuerteventura, which interacted with filament F2 near its origin. That is to say, this assemblage occupied the region beyond the shelf, under the influence of the upwelling filaments. The most abundant species in this assemblage were *Engraulis encrasicolus* and *Anthias anthias* (Table II), which were responsible for the relatively high larval fish abundance recorded in the area occupied by this assemblage, the highest for the entire sampling area (Fig. 3b). Other taxa making up this assemblage were the mesopelagic, oceanic species such as *Cyclothone braueri* and *Myctophum punctatum* and the neritic Gobidae and *Sardina pilchardus*. Diversity was, in general, quite high and constant (Fig. 3a).

The *Oceanic assemblage* (stations C in Fig. 1) essentially occupied the region outside the upwelling and upwelling filaments, and was mainly made up by mesopelagic oceanic species like *Cyclothone braueri* and *Ceratoscopelus maderensis*, the most abundant. *Engraulis encrasicolus* was also present and ranked third (Table II). This assemblage was characterised by the highest diversity (Fig. 3a).

In summary, the larval fish community was horizontally structured in three assemblages characterised by a decrease in the influence of neritic larvae from the coastal to the oceanic assemblage.

4. Discussion

Our results suggest a close relationship between the horizontal distribution of fish larvae and the mesoscale oceanographic processes of the area prevailing at the time of sampling. The composition of the larval fish community, the horizontal structuring of this community into three assemblages, and the horizontal patterns of larval fish abundances suggest that the primary factor controlling the horizontal distribution of fish larvae in the area was the transport of neritic larvae from the African shelf into the oceanic region by the upwelling filaments.

This offshore transport resulted in the predominance of neritic larvae in the composition of the larval fish community inhabiting the Canaries CTZ. It also contributed to the relatively high larval abundances at oceanic stations under the influence of the upwelling filaments and possibly to the low abundances and taxonomic diversity recorded on the African shelf. However, both low larval abundances and low taxonomic diversity in this area could also be related to a reproductive strategy followed by many fish species in upwelling regions. These species avoid reproduction during strongest upwelling to prevent the offshore transport of their offspring (Parrish *et al.*, 1981). Off NW Africa north of 25° N, the upwelling is strongest in summer and autumn (Van Camp *et al.*, 1991).

The European anchovy *Engraulis encrasicolus*, the most frequently caught larva, is an example of a neritic species being transported by the upwelling filaments far away from

its origin over the African shelf. Anchovy larvae have their highest concentrations in relatively shallow depths, between 20 and 50 m (Rodriguez, Hernandez-Leon & Barton, unpublished data), within the surface Ekman layer. This is between 20 and 60 m deep in this area (Mittelstaedt, 1983), and comprises the bulk of the surface water mass transported offshore by filaments. The shelf origin of the anchovy is confirmed by three observations. First, the strongest spawning was recorded on the African shelf where F2 had its root. Then, the horizontal distribution of larval abundances was strongly related to the filaments, with highest concentrations occurring on the northern side of the filament, in association with the strongest current (Barton *et al.*, 1998; Navarro-Pérez & Barton, 1998). Third, according to Brito (1991), the European anchovy is at most an occasional species in Canary archipelago waters. The observed lack of either anchovy eggs or larvae in this region during several cruises carried out there (Rodriguez & Lozano-Soldevilla, 1993; Rodriguez, 2000; Rodriguez, Braun & Garcia, 2000; Rodriguez, Barton, Eve & Hernandez-Leon, 2001; Rodriguez, unpublished data) supports Brito's observation. Moreover, the pattern of horizontal distribution shown by anchovy larvae (Fig. 4a) was very similar to that displayed by sardine larvae in August 1993 (Rodriguez *et al.*, 1999). At that time, sardine dominated the larval fish community, and significant spawning of this species was recorded on the African shelf. The similarity between these distributions included the relatively high abundances at the stations in the filaments wrapped around the outer edge of the trapped cyclonic eddy C7 (e.g. St 80 in 1993 and LS 17 in 1999). The maximum abundance for sardine larvae in this study was also recorded at the same location, at station LS17. The horizontal distribution pattern of anchovy larvae also suggests that these larvae are good indicators of offshore displacement of upwelled waters.

The substitution of sardine by anchovy as the most captured species may be related to the higher temperatures registered in the shelf spawning area in 1999 as compared to 1993. The average temperature of the surface layer (0-30 m) in August 1999 was 18.6 °C at station D2, where maximum anchovy egg concentration was found, and 17.8 °C at station LS24, where the second highest concentration was detected. In contrast, in August 1993 the average temperature for the surface layer (0-30 m) over the shelf was 17.1 °C. According to Furnestín and Furnestín (1959), the 1999 temperatures were in the optimum range (18-23 °C) for anchovy spawning, while those in 1993 were in the optimum range (16-18 °C) for sardine spawning. The situation found during the 1999 cruise, with important anchovy spawning would be the normal one, since the anchovy would be at its spawning peak in the area at the time of the sampling, and the sardine would be at the period of minimum spawning (Furnestín & Furnestín, 1959; Roy, Cury, Fontana & Belvèze, 1989).

The horizontal distribution of anchovy larvae (Fig. 4a) also supports the idea (Rodríguez *et al.*, 1999) that neritic larvae are transported by upwelling filaments from the African shelf towards the Canary Islands. Upwelling filaments frequently interact with eddies shed from Gran Canaria and Fuerteventura (Barton *et al.*, this volume), and can transfer part of their load of larvae to them. The presence of both, anchovy and sardine larvae, within the cyclonic and anticyclonic eddies shed from these islands (Figs. 1 and 4a) would give support to this idea. Because similar eddies are shed from all of the islands of the archipelago (Arístegui *et al.*, 1994; Arístegui *et al.*, 1997; Barton *et al.*, 1998; Barton *et al.*, this volume), and because adjoining eddies can interact for some portion of their life span, the neritic larvae that reach the eastern islands would be spread throughout the archipelago by eddies. Moreover, the relatively significant concentrations of anchovy and sardine larvae in the merged filament entrained around

the cyclonic eddy C7 (station LS17) would agree with the idea (Rodriguez *et al.*, 1999) that another part of the African neritic larvae could return to the African shelf around this eddy, which also would provide them a nursery area.

On the other hand, the association of anchovy and sardine larvae with the Cabo Juby filaments and their related cyclonic eddy (C7) suggests a coupling between spawning of these species and these mesoscale oceanographic features, permitting these fish to avoid the negative effect that offshore Ekman transport would have on their populations (Parrish *et al.*, 1981; Norcross & Shaw, 1984). This is strongly supported by the relatively high abundance of fish eggs of the two species, sardine in 1993 and anchovy in 1999, found in the neritic region, just where the upwelling filaments had their origin. The coupling between fish spawning and mesoscale eddies and the functioning of eddies as mechanisms of retention and nursery have already been suggested (Parrish *et al.*, 1981; Norcross & Shaw, 1984; Lobel & Robinson, 1986, 1988; Lobel, 1989). It has even been found that sardine larvae in the California current had better survival rates when they were associated with eddies (Logerwell & Smith, 2001). Such a coupling would imply that the combined filament and trapped eddy is a predictable structure for these species. The characteristic of ‘predictability’ agrees with the ‘recurrent’ character of filaments and with the ‘permanent’ character of the trapped eddy.

Neritic larvae are also contributed to the system from the Canary Islands, a complementary source of the area’s larval fish community. These larvae are advected away from the islands by the general flow of the Canary Current and by eddies generated downstream of the islands. A neritic species representative of those from the Canary Islands is *Anthias anthias*, a common species in the Canarian archipelago waters (Brito, 1991). The island origin for the larvae of this species is apparent in the horizontal distribution of its larvae (Fig. 4b), which were absent from the African shelf

stations and from the area directly influenced by the African upwelling and upwelling filaments. Larvae of this species have been found in very littoral waters of Tenerife Island (Rodríguez & Lozano-Soldevilla, 1993), in samples collected around Gran Canaria (Rodríguez *et al.*, 2001) and in samples collected at the outer edge of a cyclonic eddy located directly south of Gran Canaria (Rodríguez, 1998) when no influence of the African neritic larvae on the taxonomic composition of the larval fish community of the area was detected (Rodríguez *et al.*, 2000).

The two different patterns of horizontal distribution displayed by oceanic larvae seemed to be related to the birthplace of the larvae and to their vertical distribution in the water column. The horizontal distribution of *Cyclothone braueri* would be typical of an oceanic species with relatively shallow vertical distribution. Its maximum density was recorded between 20 and 66 m (Rodríguez *et al.* unpublished data). This shallow distribution would allow offshore surface advection, associated with coastal upwelling and filaments, to maintain these larvae outside the region of coastal upwelling (Fig. 4c). It would also prevent them from being transported to the shelf by the onshore compensation flow, below the surface Ekman layer, at a depth of more than 60 m offshore (Mittelstaedt, 1983).

The pattern of horizontal distribution displayed by the larvae of *M. punctatum* could be explained by the association between the horizontal distribution of the adults, and consequently their spawning place, and the vertical distribution of its larvae in the water column. *M. punctatum* is a North Atlantic mesopelagic species, whose southernmost limit of occurrence is in the NW African upwelling region (Bolin, 1959), and is an oceanic to slope spawning-species (John, 1986). The location of the spawning on the slope and the vertical distribution of the larvae, with the highest density at the 66-82 m depth stratum (Rodríguez *et al.*, unpublished data), would place these larvae within

reach of the onshore compensation flow, which would trap and transport shoreward the larvae of this species. According to Hamann, John & Mittelstaedt (1981), the presence of *M. punctatum* larvae at shelf stations is evidence of an onshore transport. The maximum abundance for this species recorded at the core of F1 suggests that these larvae could also be trapped and transported offshore by the upwelling filaments. That is to say, the horizontal distribution of this species suggests that these more deeply distributed larvae are also apparently tracers of water movements in the region.

The accumulation of fish larvae at the core of anticyclonic eddies and at the edge of cyclonic eddies would be produced by surface layer divergent or swirling outward flow to the periphery of cyclonic eddies and convergent or swirling inward flow to the core of anticyclonic eddies (Chopra & Hubert, 1965; Owen, 1981; Olson & Backus, 1985). This divergent or convergent circulation could lead to the accumulation of planktonic particles, including fish larvae, at the edge and at the core of cyclonic and anticyclonic eddies, respectively. An increase in food supply in relation to surrounding waters (Beckmann, Auras & Hemleben, 1987; Lobel, 1989) could also be implied. The concentration of fish larvae at the edge of cyclonic eddies has already been documented (Lobel & Robinson, 1986, 1988), as has the accumulation of fish larvae on the north side of the filament studied in the area in 1993 (Rodriguez *et al.*, 1999).

It can be concluded that the horizontal distribution of fish larvae in the Canaries CTZ depended on the interaction between mesoscale oceanographic features and two biological factors: the spawning place of the adults and the vertical distribution of the larvae in the water column. This interaction led to the predominance of neritic larvae in the larval fish community and to the horizontal structuring of this community into three assemblages. Future research must be carried out to elucidate the importance that the

transport of African neritic larvae by filaments has on the populations of small pelagic fish species (sardine and anchovy) of the Canary archipelago.

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Figure legends

Fig 1. Geographic location of the study area, sampling stations, eddies and filaments discussed in the text and of groups of stations as established by the classification technique.

Fig 2. Vertical profiles of temperature for a) long section; b) transect V and c) transect Z. The location of the different eddies discussed in the text is indicated.

Fig. 3. a) Number of taxa recorded at every station, b) larval fish abundances (no. per 10 m²) -circle size is proportional to the abundance (or number or taxa) recorded at each sampling station-.

Fig. 4. Horizontal distribution of larval fish abundances (no. per 10 m²) of a) *Engraulis encrasicolus*; b) *Anthias anthias*; c) *Cyclothone braueri* and d) *Myctophum punctatum* - circle size is proportional to the abundance recorded at each sampling station-.

Fig. 5. Dendrogram showing classification of ichthyoplankton stations.

Table I. Taxonomic list of fish larvae caught, their origin (N neritic, O other and Oc oceanic) and their numeric percentage.

Species	Origin	%
Family Clupeidae		
<i>Sardina pilchardus</i> (Walbaum, 1792)	N	2.10
<i>Sardinella aurita</i> Valenciennes, 1847	N	0.16
<i>Sardinella maderensis</i> (Lowe, 1838)	N	0.03
Family Engraulidae		
<i>Engraulis encrasicolus</i> (Linnaeus, 1758)	N	29.26
Family Gonostomatidae		
<i>Cyclothone acclinidens</i> Garman, 1899	Oc	0.16
<i>Cyclothone braueri</i> Jespersen and Tåning, 1926	Oc	6.29
<i>Cyclothone pallida</i> Brauer, 1902	Oc	0.76
<i>Cyclothone pseudopallida</i> Mukhacheva, 1964	Oc	0.92
<i>Cyclothone pallida</i> and/or <i>pseudopallida</i> ¹	Oc	0.13
<i>Cyclothone</i> spp	Oc	0.10
<i>Gonostoma atlanticum</i> Norman, 1930	Oc	0.06
<i>Gonostoma denudatum</i> Rafinesque, 1810	Oc	0.13
<i>Gonostoma</i> sp 1	Oc	0.10
<i>Gonostoma</i> sp 2	Oc	0.10
<i>Gonostoma</i> spp ²	Oc	0.10
<i>Pollichthys maui</i> (Poll, 1953)	Oc	0.03
Unidentified spp	Oc	0.44
Family Sternoptychidae		
<i>Argyropelecus hemigymnus</i> Cocco, 1829	Oc	0.32
<i>Argiropelecus</i> spp	Oc	0.06
<i>Sternoptyx diphana</i> Hermann, 1781	Oc	0.03
<i>Sternoptyx</i> spp	Oc	0.19
<i>Valenciennellus tripunctulatus</i> (Esmark, 1871)	Oc	0.03
Family Photichthyidae		
<i>Vinciguerria attenuata</i> (Cocco, 1838)	Oc	0.35
<i>Vinciguerria nimbaria</i> (Jordan and Williams, 1895)	Oc	0.32
<i>Vinciguerria poweriae</i> (Cocco, 1838)	Oc	0.73
<i>Vinciguerria</i> spp ³	Oc	0.35
Family Chauliodontidae		
<i>Chauliodus sloani</i> Schneider, 1801	Oc	0.03
Family Stomiidae		
<i>Eustomias</i> sp	Oc	0.03
Family Melanostomiidae		
Unidentified spp	Oc	0.19
Family Argentinidae		
<i>Microstoma microstoma</i> Risso, 1810)	Oc	0.03
Family Bathylagidae		
Unidentified spp	Oc	0.16
Family Synodontidae		
<i>Synodus saurus</i> (Linnaeus, 1758)	N	0.10
Unidentified spp	N	0.03
Family Chlorophthalmidae		
<i>Chlorophthalmus agassizi</i> Bonaparte, 1840	Oc	0.13
Family Myctophidae		
<i>Benthoosema suborbitale</i> (Gilbert, 1913)	Oc	0.06
<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	Oc	3.94
<i>Ceratoscopelus warmingii</i> (Lütken, 1892)	Oc	0.70

¹ Include small sized larvae from both species.

² Include larvae from the four species of the genus *Gonostoma*

³ Include small sized larvae from the three Species of *Vinciguerria*

Table I (continued)

Species	Origin	%
<i>Diaphus holti</i> Tåning, 1918	Oc	1.05
<i>Diaphus metopoclampus</i> (Cocco, 1829)	Oc	0.51
<i>Diaphus rafinesquei</i> (Cocco, 1838)	Oc	0.51
<i>Diaphus</i> sp 1	Oc	0.06
<i>Diaphus</i> spp	Oc	1.72
<i>Diogenichthys atlanticus</i> (Tåning, 1928)	Oc	3.49
<i>Hygophum hygomii</i> (Lütken, 1892)	Oc	0.03
<i>Hygophum macrochir</i> (Günther, 1864)	Oc	0.32
<i>Hygophum reinhardtii</i> (Lütken, 1892)	Oc	0.60
<i>Hygophum taaningi</i> Bekker, 1965	Oc	0.54
<i>Lampanyctus crocodilus</i> (Risso, 1810)	Oc	0.19
<i>Lampanyctus pusillus</i> (Johnson, 1890)	Oc	0.10
<i>Lampanyctus</i> spp	Oc	4.10
<i>Lepidophanes gaussi</i> (Brauer, 1906)	Oc	0.19
<i>Lobianchia dofleini</i> (Zugmayer, 1911)	Oc	0.03
<i>Loweina rara</i> (Lütken, 1892)	Oc	0.06
<i>Myctophum nitidulum</i> Garman, 1899	Oc	0.29
<i>Myctophum punctatum</i> Rafinesque, 1810	Oc	3.21
<i>Myctophum selenops</i> Tåning, 1928	Oc	0.13
<i>Notolychnus valdiviae</i> (Brauer, 1904)	Oc	1.84
<i>Notoscopelus</i> (Not.) <i>resplendens</i> (Johnson, 1863)	Oc	0.22
<i>Notoscopelus</i> spp	Oc	0.15
<i>Symbolophorus</i> spp	Oc	1.14
Unidentified spp	Oc	3.56
Family Scopelarchidae		
<i>Benthalbella infans</i> Zugmayer, 1911	Oc	0.29
Family Paralepididae		
<i>Lestidiops jayakari</i> (Boulenger, 1889)	Oc	0.57
<i>Paralepis atlantica atlantica</i> Krøyer, 1868	Oc	0.03
<i>Sudis hialina</i> Rafinesque, 1910	Oc	0.06
Unidentified spp	Oc	0.19
Family Nettastomatidae		
<i>Nettastoma melanurum</i> Rafinesque, 1810	N	0.19
Family Congridae		
Unidentified spp	N	0.25
Family Derichthyidae		
<i>Derichthys serpentes</i> Gil, 1884	Oc	0.10
Family Ophichthidae		
Unidentified spp	N	0.06
Family Scomberosocidae		
<i>Scomberosox saurus</i> (Walbaum, 1792)	Oc	0.06
Family Macroramphosidae		
<i>Macroramphosus scolopax</i> (Linnaeus, 1758)	Oc	0.06
Family Melamphaidae		
<i>Melamphaes simus</i> Ebeling, 1962	Oc	0.06
<i>Melamphaes thylops</i> (Lowe, 1843)	Oc	0.03
<i>Melamphaes</i> sp	Oc	0.03
Family Serranidae		
<i>Anthias anthias</i> (Linnaeus, 1758)	N	13.02
<i>Serranus cabrilla</i> (Linnaeus, 1758)	N	0.48
Family Cepolidae		
<i>Cepola macrophthalma</i> (Linnaeus, 1758)	N	0.03

Table I (continued)

	Species	Origin	%
Family	Carangidae		
	<i>Trachurus</i> sp	N	0.13
	Unidentified spp	O	0.32
Family	Sciaenidae		
	Unidentified spp	N	0.10
Family	Sparidae		
	<i>Pagrus pagrus</i> (Linnaeus 1758)	N	0.06
	Unidentified spp	N	0.13
Family	Pomacentridae		
	<i>Chromis chromis</i> (Linnaeus, 1758)	N	0.51
Family	Labridae		
	<i>Coris julis</i> (Linnaeus, 1758)	N	0.03
	<i>Thalassoma pavo</i> (Linnaeus, 1758)	N	0.32
	<i>Xyrichtys novacula</i> (Linnaeus, 1758)	N	0.10
	Unidentified spp	N	0.13
Family	Scaridae		
	<i>Sparisoma (Euscarus) cretense</i> (Linnaeus, 1758)	N	0.03
Family	Trachinidae		
	<i>Trachinus draco</i> Linnaeus, 1758	N	0.25
Family	Gempylidae		
	<i>Diplospinus multistriatus</i> Maul, 1948	Oc	0.25
	<i>Gempylus serpens</i> Cuvier, 1829	Oc	0.03
	Unidentified spp	Oc	0.10
Family	Chiasmodontidae		
	Unidentified spp	Oc	0.03
Family	Scombridae		
	<i>Auxis</i> sp	O	0.22
Family	Gobiidae		
	Unidentified spp	N	1.52
Family	Blennidae		
	Unidentified spp	N	0.03
Family	Ophidiidae		
	<i>Parophidion vassali</i> (Risso, 1810)	N	0.03
	Unidentified spp	N	0.03
Family	Tetragonuridae		
	<i>Tetragonurus atlanticus</i> Lowe, 1939	Oc	0.25
	<i>Tetragonurus cuvieri</i> Risso, 1810	Oc	0.03
	<i>Tetragonurus</i> spp ⁴	Oc	0.22
Family	Scorpaenidae		
	Unidentified spp	O	0.51
Family	Bothidae		
	<i>Arnoglossus imperialis</i> Rafinesque, 1810	N	0.16
	<i>Arnoglossus</i> spp	N	0.35
	<i>Bothus podas maderensis</i> (Lowe, 1834)	N	0.60
Family	Soleidae		
	<i>Buglossidium luteum</i> (Risso 1810)	N	0.03
	Unidentified spp	N	0.03
Family	Cynoglossidae		
	<i>Symphurus nigrescens</i> Rafinesque, 1810	N	0.06
Family	Monacanthidae		
	<i>Stephanolepis hispidus</i> (Linnaeus, 1766)	N	0.06
Family	Melanocetidae		
	<i>Melanocetus murrayi</i> Günther, 1887	Oc	0.03
	<i>Melanocetus</i> spp	Oc	0.03

⁴ Include larvae from the two species of the genus *Tetragonurus*

Table II. Mean abundance (no. per 10 m²) (Mean), standard deviation (SD) and frequency of occurrence (%) of the most common species by groups of stations as established by the classification technique.

	Group A			Group B			Group C		
	Mean	SD	%	Mean	SD	%	Mean	SD	%
<i>Sardina pilchardus</i>	-	-	-	32.6	63.9	50	12.5	11.7	66.7
<i>Sardinella aurita</i>	3.0	4.3	50.0	0.6	2.4	7	0.6	2.1	8.3
<i>Engraulis encrasicolus</i>	100.9	23.2	100.0	631.6	531.2	100	32.0	28.2	83.3
<i>Cyclothone acclinidens</i>	-	-	-	0.6	2.4	7	2.6	5.1	25.0
<i>Cyclothone braueri</i>	-	-	-	52.7	35.8	86	65.6	59.6	91.7
<i>Cyclothone pallida</i>	-	-	-	-	-	-	18.5	31.5	33.3
<i>Cyclothone pseudopallida</i>	-	-	-	8.9	16.1	29	1.6	4.1	16.7
<i>Argyropelecus hemig.</i>	-	-	-	2.4	4.9	21	4.6	4.3	50.0
<i>Vinciguerria nimbaria</i>	-	-	-	0.6	2.4	7	2.1	5.3	16.7
<i>Vinciguerria poweriae</i>	-	-	-	0.6	2.4	7	2.5	3.9	33.3
<i>Ceratoscopelus maderensis</i>	-	-	-	36.0	25.0	86	53.4	45.1	83.3
<i>Ceratoscopelus warmingii</i>	-	-	-	3.1	5.6	29	12.1	15.5	58.3
<i>Diaphus holti</i>	-	-	-	13.2	21.6	50	5.3	8.8	25.0
<i>Diaphus metopoclampus</i>	-	-	-	5.4	9.2	36	4.5	13.4	16.7
<i>Diaphus rafinesquii</i>	-	-	-	7.2	10.1	50	2.2	4.0	16.7
<i>Diogenichthys atlanticus</i>	-	-	-	47.3	50.5	100	23.7	17.5	83.3
<i>Hygophum reinhardtii</i>	-	-	-	7.6	12.4	36	7.1	13.8	33.3
<i>Hygophum taaningi</i>	-	-	-	10.0	12.1	50	9.6	13.9	41.7
<i>Myctophum nitidulum</i>	-	-	-	2.3	4.8	21	1.7	4.6	16.7
<i>Myctophum punctatum</i>	13.6	6.4	100.0	51.0	53.0	86	8.4	20.7	41.7
<i>Myctophum selenops</i>	-	-	-	2.5	5.4	21	0.7	2.3	8.3
<i>Notolychnus valdiviae</i>	-	-	-	13.3	16.8	64	17.1	20.4	50.0
<i>Notoscopelus (Not) resplendens</i>	-	-	-	2.7	5.9	21	3.7	7.7	25.0
<i>Symbolophorus spp</i>	-	-	-	14.9	11.5	79	5.5	6.3	50.0
<i>Benthalbella infans</i>	-	-	-	3.6	6.4	29	5.2	16.6	16.7
<i>Lestidiops j. pseudospiraenoides</i>	-	-	-	6.1	8.1	43	3.1	6.4	25.0
<i>Nettastoma melanurum</i>	-	-	-	2.1	5.7	14	3.9	7.7	25.0
Congridae	-	-	-	3.6	6.6	29	2.2	5.2	16.7
<i>Anthias anthias</i>	-	-	-	289.9	492.7	57	12.3	15.6	41.7
<i>Serranus cabrilla</i>	-	-	-	3.9	9.8	21	0.4	1.5	8.3
<i>Trachurus sp</i>	-	-	-	1.4	5.3	7	2.3	5.4	16.7
<i>Chromis chromis</i>	-	-	-	1.3	4.8	7	5.0	10.9	25.0
<i>Thalassoma pavo</i>	-	-	-	1.8	3.6	21	4.7	7.2	41.7
<i>Trachinus draco</i>	3.0	4.3	50.0	-	-	-	2.2	6.0	16.7
<i>Diplospinus multistriatus</i>	-	-	-	4.6	8.5	29	4.6	7.4	25.0
<i>Auxis sp</i>	4.5	6.4	50.0	1.0	3.8	7	-	-	-
Góbiidae	9.0	12.8	50.0	23.3	34.9	50	8.2	17.9	41.7
<i>Arnoglossus spp</i>	3.0	4.3	50.0	1.0	2.6	14	3.2	7.0	25.0
<i>Bothus podas maderensis</i>	-	-	-	3.9	14.7	7	7.1	17.1	16.7

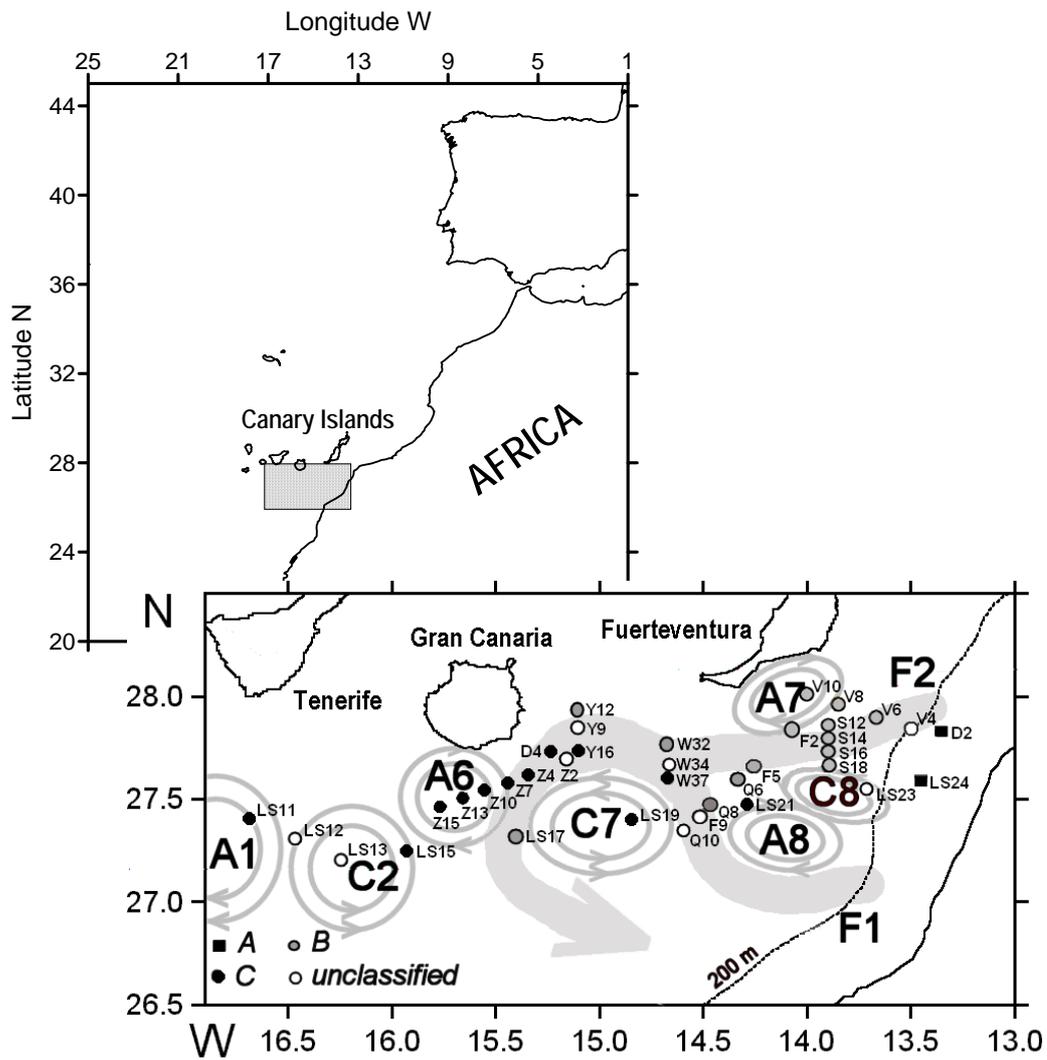


Fig 1. Geographic location of the study area, sampling stations, eddies and filaments discussed in the text and of groups of stations as established by the classification technique.

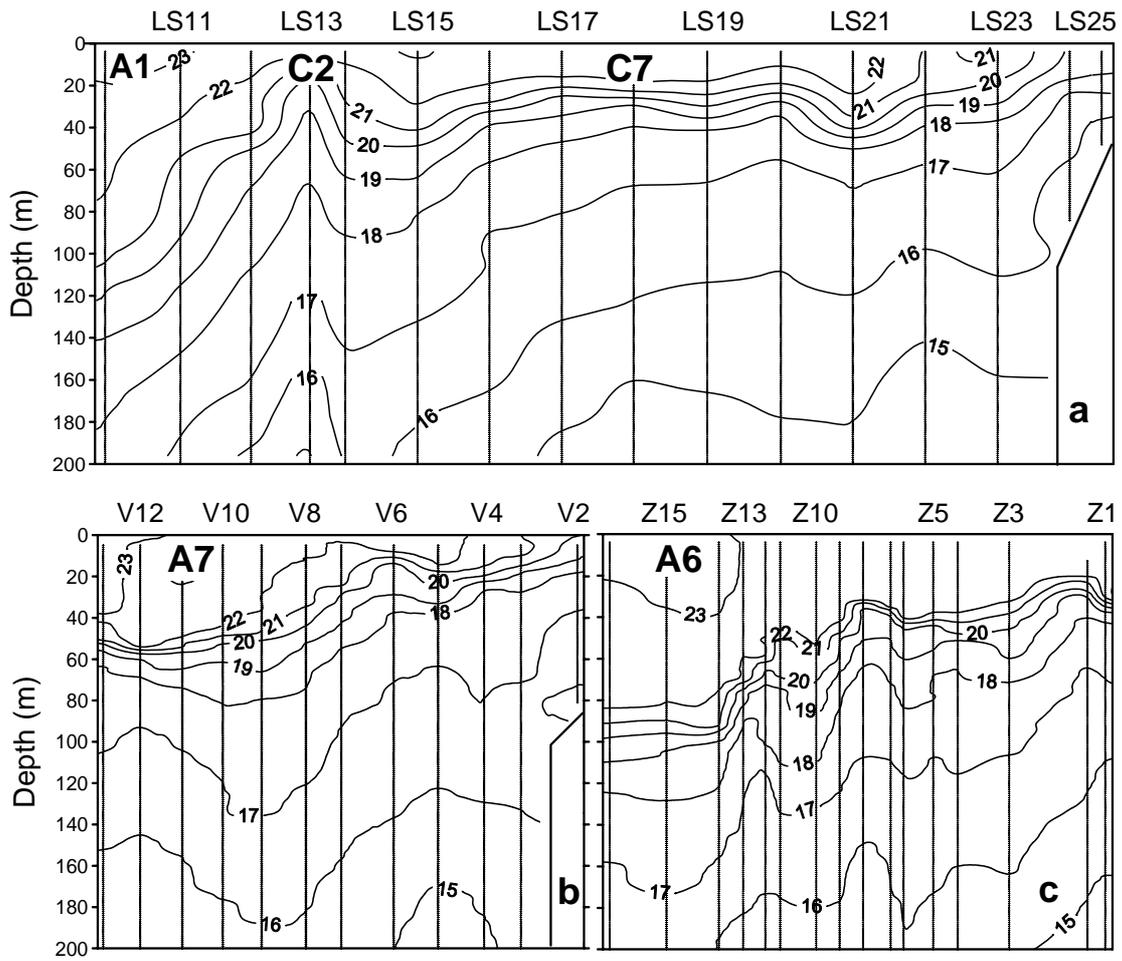


Fig 2. Vertical profiles of temperature for a) long section; b) transect V and c) transect Z. The location of the different eddies discussed in the text is indicated.

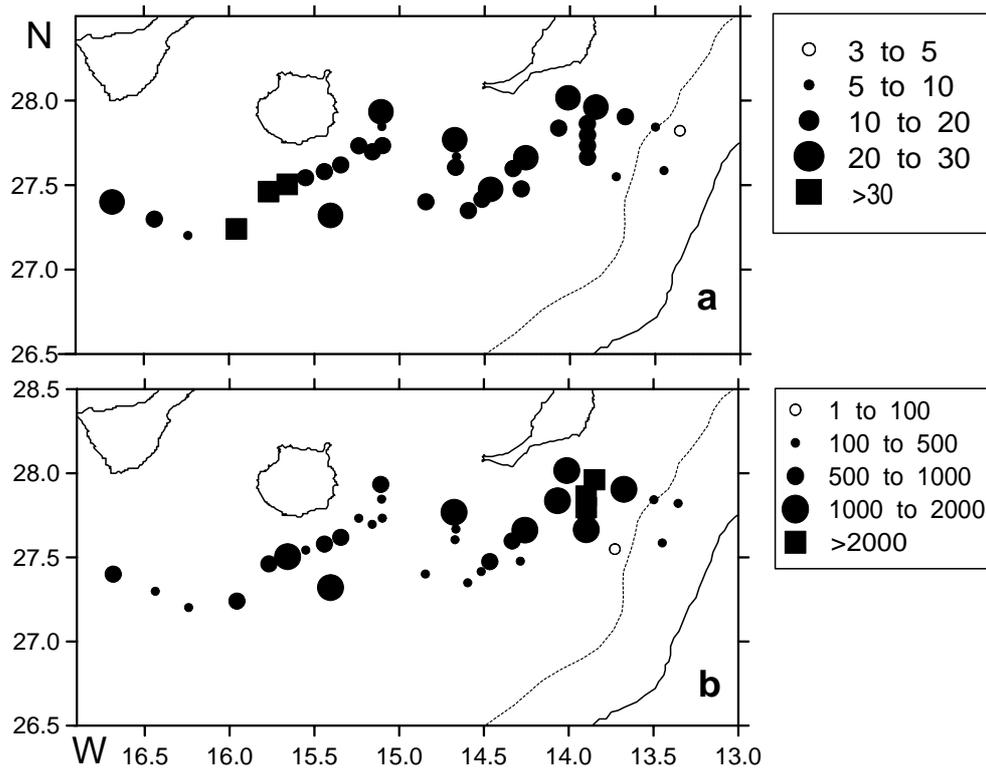


Fig. 3. a) Number of taxa recorded at every station, b) larval fish abundances (no. per 10 m²) -circle size is proportional to the abundance (or number of taxa) recorded at each sampling station-.

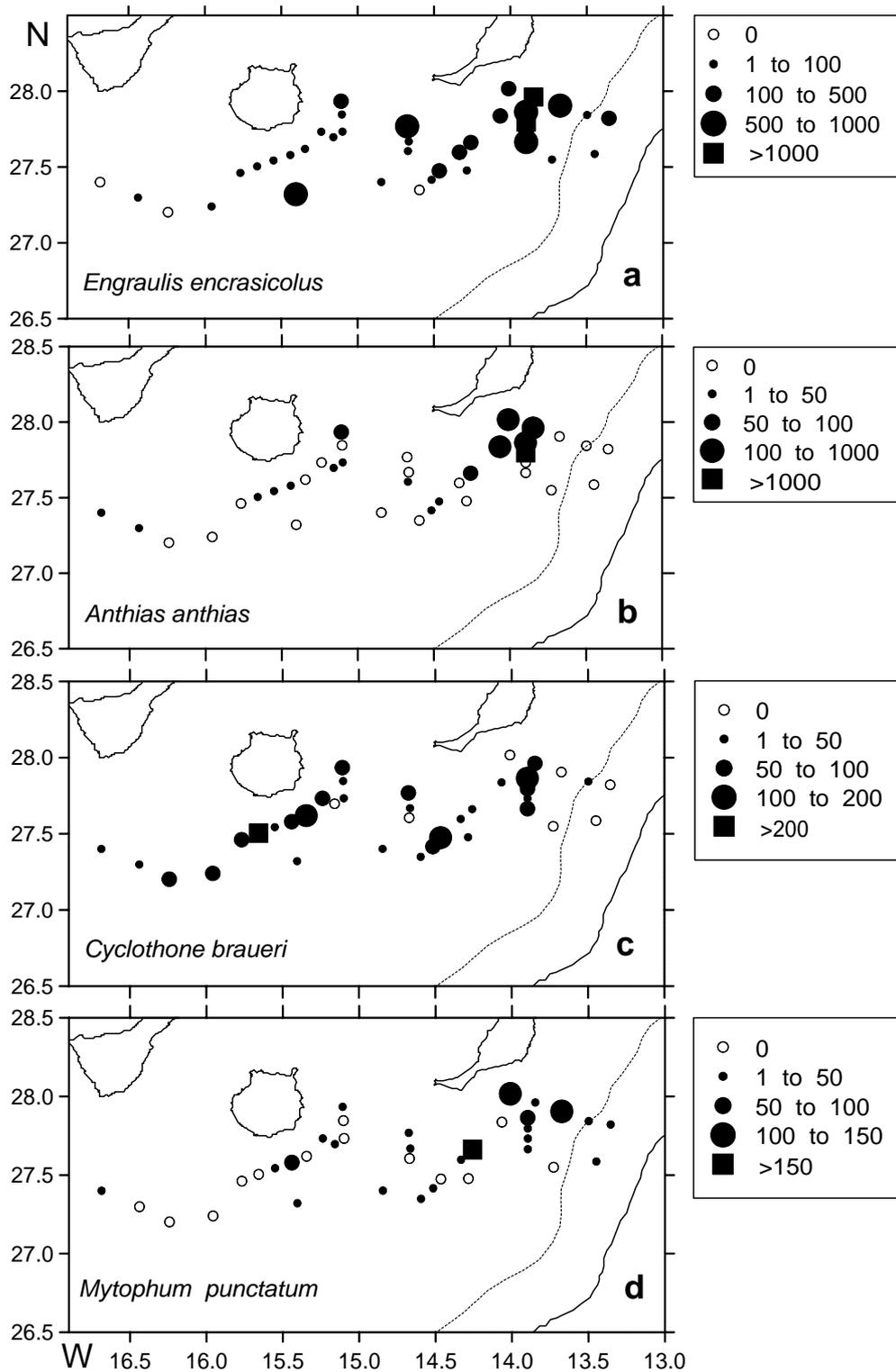


Fig. 4. Horizontal distribution of larval fish abundances (no. per 10 m²) of a) *Engraulis encrasicolus*; b) *Anthias anthias*; c) *Cyclothone braueri* and d) *Mytophum punctatum* - circle size is proportional to the abundance recorded at each sampling station.

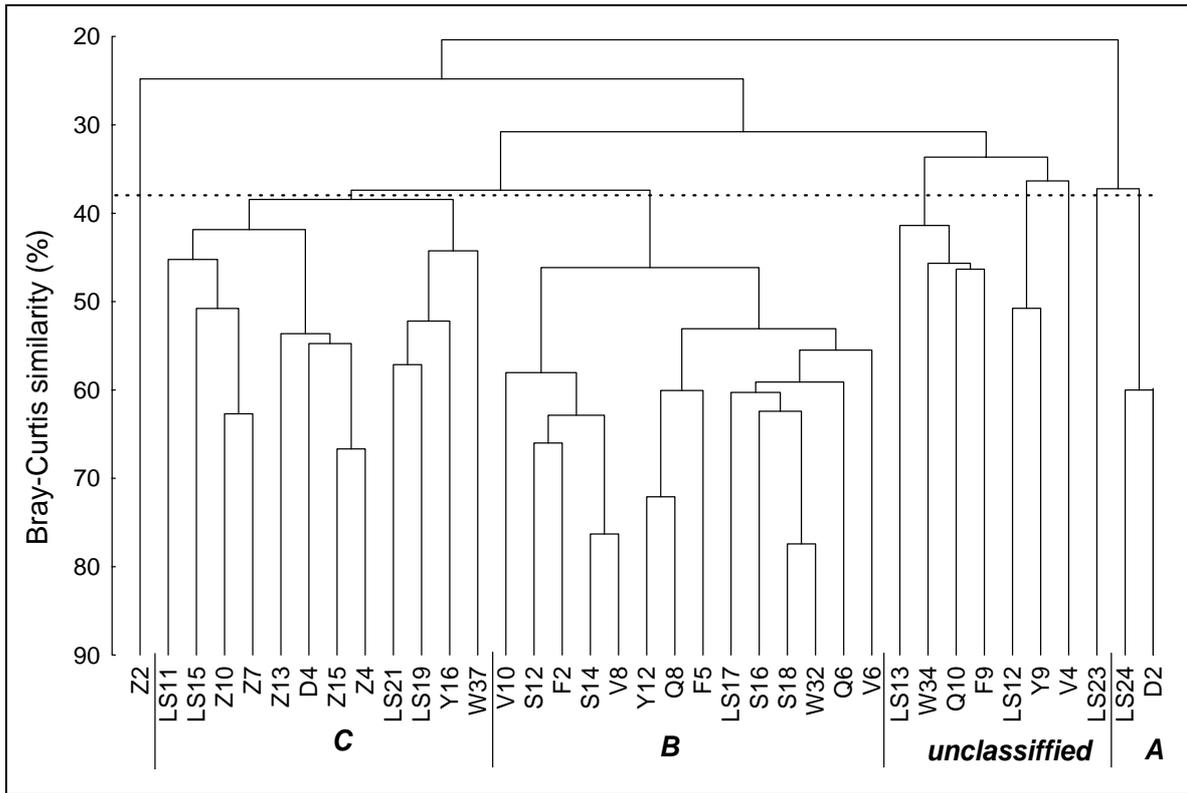


Fig. 5. Dendrogram showing classification of ichthyoplankton stations.