TESIS DOCTORAL

Temporal and spatial distribution of the ichthyoplankton in the Canary Islands

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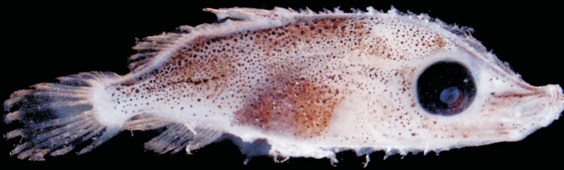

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Temporal and spatial distribution of the ichthyoplankton in the Canary Islands

(Distribución temporal y espacial del ictioplancton en aguas de las Islas Canarias)

Tesis Doctoral presentada por Dª Marta Moyano García de la Banda para obtener el grado de Doctor por la Universidad de Las Palmas de Gran Canaria.

Dirigida por Dr. D. Santiago Hernández León
Dr. D. Jose María Rodríguez López (co-director)

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A mis padres

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RESUMEN

A pesar del creciente interés en el estudio de las primeras fases de desarrollo de los peces, aún existen zonas donde esta comunidad es relativamente desconocida. Este es el caso de las Islas Canarias. En la presente tesis, gracias a una serie de muestreos semanales en la región costera de la isla de Gran Canaria durante más de dos años, se ha caracterizado de manera precisa la composición, estructura y variabilidad del ictioplancton presente en esta región subtropical. Clupeidos, Espáridos y Góbidos dominaron la comunidad neríticas, mientras que Mictófidos, Gonostomátidos y Photíctidos prevalecieron dentro de las familias oceánicas. La variabilidad temporal de la comunidad larvaria parece estar más relacionada con la temperatura y efectos a pequeña escala (hidrografía, productividad local, ciclo lunar), que con el aumento de productividad anual durante el bloom de finales de invierno. Se definieron dos asociaciones estacionales de larvas estrechamente ligadas a las características de la columna de agua: (1) invierno-primavera, en la que dominan *Sardinella aurita*, *Boops boops* y *Cyclothone braueri,* y son características especies como Pomacentridae sp1, *Trachurus picturatus* o *Scomber colias*; y (2) verano-otoño, donde Góbidos y *Cyclothone braueri* dominan, pero cuyas especies características son *Ceratoscopelus warmingii*, Pomacentridae sp2 y *Anthias anthias*, entre otras. Respecto a la variabilidad horizontal, se confirmó la presencia de dos zonas de retención para los huevos y larvas neríticas a barlovento y sotavento (estela cálida) de la isla. Sin embargo, no se encontraron diferencias significativas en la composición de la comunidad larvaria entre las diferentes zonas de la plataforma de la isla.

La Zona de Transición Costera Canario-Africana se caracteriza por una gran actividad de mesoscala, que afectará a la distribución de las larvas neríticas de las costas africanas. Esta interacción resulta especialmente evidente en el caso de las larvas, principalmente sardina y anchoa, transportadas en filamentos de afloramiento generados en la región de Cabo Juby-Cabo Bojador. Estos filamentos pueden ser atrapados por remolinos ciclónicos situados al sur de Gran Canaria. Este sistema remolino-filamento podrá, en función de su evolución, actuar como un mecanismo de retención o dispersión para las larvas de especies neríticas africanas. Parte de estas larvas pueden llegar a las costas de Gran Canaria, suponiendo un aporte para las poblaciones larvarias locales, al menos durante el verano. A pesar de la gran cantidad de información obtenida a partir de esta tesis, es necesario continuar con este tipo de estudios para evaluar la importancia de este transporte larvario y su aplicación a la gestión pesquera.

ABSTRACT

Despite the ongoing interest in the early life history of fishes, there still are a lot of regions in the world where this community is relatively unknown. This is the case of the Canary Islands. Thus, this thesis has precisely characterized the composition, structure and variability of the ichthyoplankton off Gran Canaria Islands, based on weekly surveys at the edge of the island shelf during more than two years. Clupeidae, Sparidae and Gobiidae were the most abundant neritic families, while Myctophidae, Gonostomatidae, and Photichthydae prevailed among the oceanic families. Temporal variability in the larval fish community seems to be more related to temperature and small-scale changes (hydrography, local productivity, and lunar cycle) than to enhanced annual productivity during the late winter bloom. Thus, two seasonal larval assemblages were identified: (1) a winter-spring assemblage, dominated by *Sardinella aurita*, *Boops boops* and *Cyclothone braueri*, and characterize by Pomacentridae sp1, *Trachurus picturatus* or *Scomber colias* species; and (2) summer-autumn assemblage when Gobids and *Cyclothone braueri* dominate and species such as *Ceratoscopelus warmingii*, Pomacentridae sp2 and *Anthias anthias* appeared. In relation to horizontal variability, two retention areas up- and downstream (warm lee) of the islands were confirmed for eggs and neritic larvae. Nevertheless, there were not significant differences in the composition of the larval assemblage between different sites on the island shelf during a relatively long-time scale.

The Canaries-African Coastal Transition Zone is characterized by a strong mesoscalar activity which influences the distribution of larvae of African neritic fish species. This interaction is particularly evident for those clupeoid larvae (sardine and anchovy) transported within upwelling filaments generated in the Cape Juby-Cape Bojador area. These filaments may be entrapped into cyclonic eddies normally formed south of Gran Canaria. This cyclonic eddy-filament system may act not only as a retention but also as a dispersal mechanism for larvae of African neritic species, depending on its evolution. During the summer some of these transported larvae may reach the eastern shores of Gran Canaria Island, contributing to the island's local larval fish community. Despite the information provided in this thesis, additional studies are necessary to assess the real importance of this larval transport and its applications to fisheries management.

PRESENTACIÓN DE LA TESIS

La presente tesis titulada *Distribución temporal y espacial del ictioplancton en aguas de las Islas Canarias*, resulta de la recopilación de una serie de trabajos encuadrados dentro de los proyectos de investigación Pelagic (EU-CICYT 1FD97-1084) y Conafrica (CTM2004-02319/MAR), dirigidos por el Dr. Santiago Hernández León, Catedrático de la Facultad de Ciencias del Mar de la Universidad de Las Palmas de Gran Canaria. El Dr. Hernández León ha dirigido esta tesis junto con el Dr. Jose María Rodríguez López, Investigador titular del Instituto Español de Oceanografía.

Esta tesis consta de una primera parte realizada íntegramente en inglés, estructurada en Introducción, Objetivos, Contribuciones originales, Síntesis de resultados y Discusión General, Conclusiones y Líneas futuras de investigación. De este modo, resumen y conclusiones de la tesis se encuentran en una lengua distinta a la lengua Española (Inglés), de acuerdo a la normativa para la obtención de la Mención europea del Título de Doctor (BOULPGC. Art.1 Cap.4, 5 de noviembre 2008).

La segunda parte de la tesis está escrita en castellano y, por lo tanto, consta de las 50 páginas en castellano requeridas por el Reglamento de Elaboración, Tribunal, Defensa y Evaluación de Tesis Doctorales de la Universidad de Las Palmas de Gran Canaria (BOULPGC. Art.2 Cap.1, 5 de noviembre 2008). Además, sigue la estructura exigida por este Reglamento: Introducción, Objetivos, Planteamiento y Metodología, Resultados, Discusión General, Conclusiones y Futuras Líneas de Investigación.

THESIS PREVIEW

This thesis entitled *Temporal and spatial distribution of the ichthyoplankton in the Canary Islands* compiles different studies carried out in the frame of the research projects Pelagic (EU-CICYT 1FD97-1084) and ConAfrica (CTM2004-02319/MAR). These projects were granted to Dr. Santiago Hernández León, Professor at the Marine Science Faculty of the Universidad de Las Palmas de Gran Canaria. Dr. Hernández León and Dr. Jose María Rodríguez López, researcher from the Instituto Español de Oceanografía, have supervised this thesis.

This thesis is structured into a general introduction that explains the unique contribution of the early life stages of fish to recruitment and summarizes previous studies carried out in the Canaries region. Then, the original contributions are compiled in manuscript format and are at different stages in the peer-review publication process (submitted or published). Afterwards, there is a synthesis of results and general discussion section, which precedes conclusions. Finally, further research studies on the ichthyoplankton of the region are suggested.

At the end, a summary in Spanish is included, containing more than 50 pages. This is a requirement from the PhD Thesis Regulations from the Universidad de Las Palmas de Gran Canaria (BOULPGC. Art.2 Chap.1, November 5th 2008). Besides, in order to obtain the *Doctor Europeus* Mention (BOULPGC. Art.1 Chap.4, November 5th 2008), Summary and Conclusions have been translated into English.

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INTRODUCTION

INTRODUCTION

The unique contribution of the early larval stages

The early life stages of fishes are referred to as ichthyoplankton. Although they are typically considered inert particles, fish larvae are interactive components of the ecosystem (Cowen, 2002; Fuiman, 2002). Most fishes have a pelagic stage, whose duration vary between weeks and months (Brothers *et al.*, 1983; Victor, 1986). During this pelagic stage, important changes occur in short time periods, For example, most fishes increase their weight 5 orders of magnitude throughout their life and three of them occur during this pelagic stage (Werner and Gilliam, 1984; Houde, 1987; Miller *et al.*, 1988). The sharp biomass increase during the short larval period evidences the importance of this stage as a recruitment modulator (Houde, 1987). Thus, growth and processes that favor larval survival are crucial for recruitment success (Cushing, 1975; Cowan and Shaw, 2002).

Mortality is critical during the larval stage of a fish, because larvae have to overcome survival rates below 1% (Houde, 1987; Chambers and Trippel, 1997). Variability in stock sizes has fascinated fishermen and scientists since the 19th century, but Hjort (1914, 1926) was the first one to propose that variable "year-class success" was determined during early life in marine fishes. He stated two clear hypotheses for these stock fluctuations: (1) scarcity of food during the early life stages (*Critical Period Hypothesis*), and (2) larval transport to unfavorable areas (*Aberrant Drift Hypothesis*). Hjort's first hypothesis proposes that the strength of a year class is determined shortly after yolk-sac absorption, when larvae must find suitable amounts and type of planktonic prey (Fig. 1). Failing to find adequate feeding conditions would lead to massive larval mortality in a short span of time.

Hjort´s hypotheses constituted the ground-work for later recruitment studies, mainly focused of the Critical Period hypothesis (Cowan and Shaw, 2002; Houde, 2008). Cushing (1975) combined Hjort´s two assumptions into the *Match-mismatch hypothesis*. Cushing suggested that a fixed time of spawning coupled with a variable time of plankton blooms generates variable larval fish survival, and so, variable

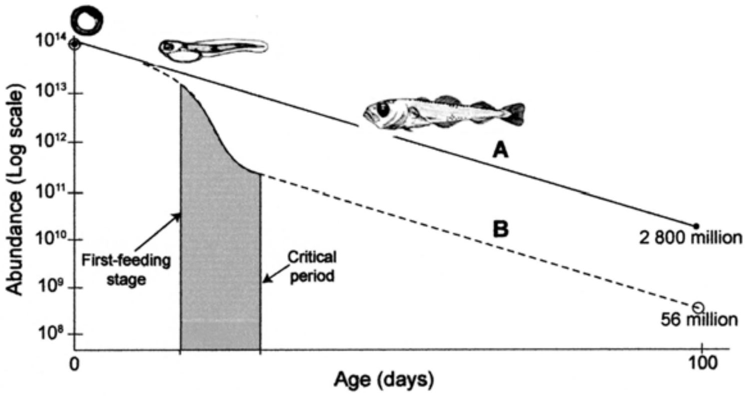


Figure 1. Illustration showing Hjort's Critical Period Hypothesis (1914, 1926). Larvae failing to find suitable food lead to mortalities >90%. From Houde (2008).

recruitment. In this hypothesis, food limitation at any point during the larval period could be a major contributor to recruitment variability, and abiotic factors that regulate the mixing of the water column and the timing and intensity of seasonal production cycles may be involved. Later, Lasker's (1981) *Stable Ocean Hypothesis* proposed that the presence of calm and stable oceanic conditions (i.e., Lasker events) in upwelling ecosystems promote stratification of the water column and, hence, the aggregation of fish larvae and their prey, supporting high feeding, survival and recruitment. Cury and Roy (1989) extended Lasker´s hypothesis in the *Optimal Environmental Window* model. They hypothesized that recruitment level in upwelling ecosystems is dome-shaped and most successful under moderate wind stress that controls both advective losses and turbulence-enhanced feeding success by larvae. Rothschild and Osborn´s (1988) *Plankton Contact Hypothesis* also acknowledged the importance of micro-turbulence for foraging success. These authors proposed that fish larvae can survive in low-prey scenarios, if encounter rates increase as a function of small-scale, wind-driven turbulence.

An extension of the Aberrant Drift hypothesis was proposed in the *Larval Retention* or *Member/Vagrant Hypothesis* (Illes and Sinclair, 1982). These authors stated that physical retention is critical in the recruitment process and depends on adult spawning in favorable areas for retention of early life stages, both eggs and larvae. This hypothesis has affinities with the *Migration Triangle Hypothesis* (Harden-Jones, 1969;

Cushing, 1975), since both of them are based on the fact that physical processes determine recruitment success, through defining larval drift and retention areas.

In the case of tropical environments, recruitment studies are more complicated than in temperate seas (Sale, 2004), but different works showed that reef fishes are not different from others in exhibiting variable recruitment success (Doherty and Williamson, 1988). Sale (1978) proposed the *Lottery Hypothesis*, supporting that priority of settler's arrival to the reef rather than adult requirements or abilities determine which species holds each site. Then, post-settlement processes could control recruitment levels. Nowadays, both pre- and post-settlements processes are acknowledged to influence recruitment (Jones, 1991; Doherty, 2002). Also, the open/close status of reef populations remains an open question (e.g., Cowen *et al*., 2000, 2006; Mora and Sale, 2002) until we are able to precisely quantify connectivity and self-recruitment mechanisms.

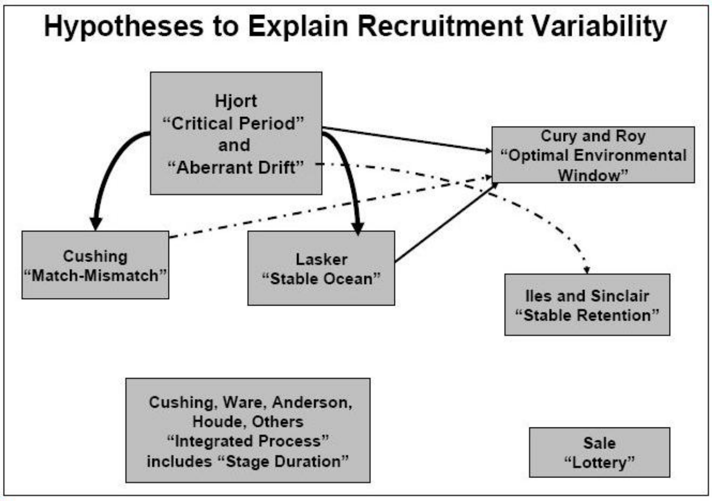


Figure 2. Hypotheses to explain recruitment variability in marine fish and their linkages to Hjort's (1914) Critical Period and Aberrant Drift hypotheses. Solid arrows indicate direct and broken arrows indirect derivations from Hjort's ideas. Thickness of the arrows stands for strength of the relationship. From Houde (2008).

All the above-mentioned hypotheses considered starvation and physical processes as the main drivers of recruitment variability, but nowadays, predation is considered as the main mortality factor influencing recruitment (Hunter, 1981; Bailey and Houde, 1989). Nevertheless, mortality is modulated by other factors: (1) *Temperature* that influences physiology, metabolism, behavior, and early life growth rates (Blaxter, 1992). It operates on all time and space scales (from cell level to large ocean basins); (2) *Physical processes* (diffusion, advection and dispersion), whose importance was already acknowledged in some recruitment hypotheses (Cushing, 1975, Heath, 1992); (3) *Prey*. Large amounts of prey are associated with increased survival rates and with faster larval growth (Zenitani, 2007). However, turbulence can increase encounter rates in environments with low prey densities (MacKenzie *et al.*, 1994); and (4) *Nutritional condition and growth rates* influence predation through larval size and growth rates (e.g., Meekan and Fortier, 1996; Vigliola and Meekan, 2002): *the faster you get bigger the better* (Houde, 1987). Many factors influencing larval behavior and physiology are size-dependent (Hunter, 1981). Thus, smaller larvae, with limited energy storage (yolk sac), are more susceptible to starvation and, consequently, to be predated.

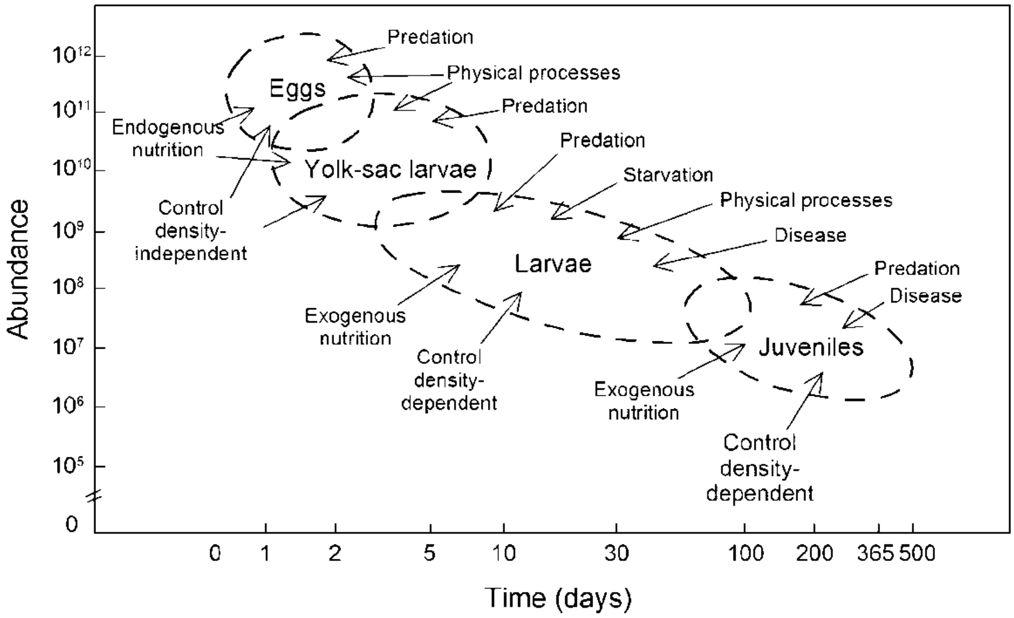


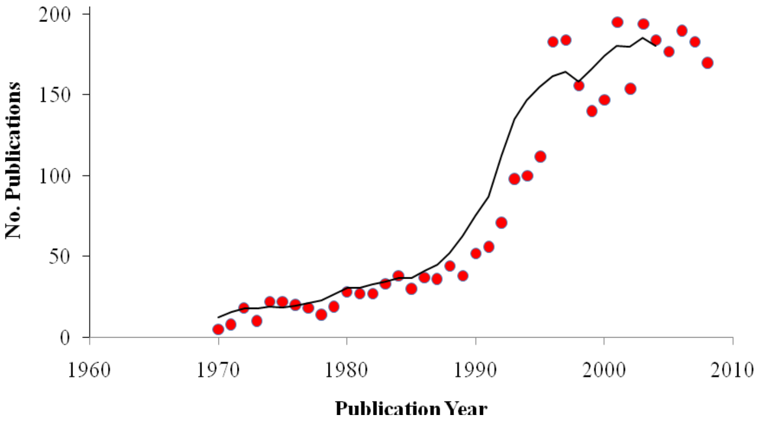
Figure 3. Schematic diagram of different processes acting on the early stages of a marine fish (eggs, yolk-sac larvae, larvae and juveniles). Note predation influences the four stages. Redrawn from Houde (1987).

Therefore, recruitment variability is now considered to be the result of an integration of processes operating on different time and space scales acting throughout the pre-recruit fish life-stage (Fig. 3). That is to say, recruitment success is not determined during a particular ontogenetic stage and it depends on the species, populations and environmental factors (Houde, 2008).

The use of new technologies like remote sensing (Platt *et al.*, 2007), hydrodynamic models coupled to Individual-Based Models (IBMs) (Werner *et al.*, 2001; Daewel *et al.*, 2008; North *et al.*, 2009) or *in situ* filming techniques (Leis, 2007) allowed testing old hypothesis on relevant scales (Platt *et al.*, 2003). For example, Hamilton *et al.* (2008) pointed out the importance of realized connectivity on ecological scales and the species-related life history traits. Thus, nowadays integrative processes combining data from different sources (field, lab and models) and different disciplines (climatology, oceanography, ecology, aquaculture) leads to data optimization. Then, hypothesis can be tested from the individual to the ecosystem level (Cury *et al.*, 2008).

Classical stock assessment models are influenced by natural variability at all scales (e.g., climatic, interannual) (Sharp, 2004). Thus, studies on recruitment and early life history stages of fish are becoming an important research line in the last decades (Fig. 4). Studies on these phases (eggs, larvae and juveniles) focus on a range of different topics: recruitment variability (Govoni, 2005; Houde, 2008), connectivity (Cowen *et al.*, 2006), biodiversity and global change (Boeing and Duffy-Anderson, 2008), toxic impact (Norcross *et al.*, 1996), taxonomy (Richards, 2006) or ecosystem structure and functioning (Mollmann *et al.*, 2008).

Figure 4. Papers or reviews published between 1970-2008 containing the words *ichthyoplankton* or *fish larva/fish larvae* within the title, abstract or keywords (Source: Scopus).



Larval fish assemblages

A larval fish assemblage can be defined as a suite of species whose larvae are collected in the same area at the same time (Miller, 2002). Therefore, a larval assemblage is by definition transient and does not necessarily imply or require evolutionary convergence or biological interactions (e.g., competition, predation). The species association within an assemblage only denotes that they have come to a similar solution for a precise stage of their lives (Miller, 2002).

Physical and biological processes interact in the formation, maintenance and disruption of larval fish assemblages over a range of temporal and spatial scales (Table 1). During the formation, larval fish assemblages reflect the synchrony and cohesion in the spawning pattern of adults (Frank and Legget, 1983) and larval behavior (e.g., Gray and Miskiewicz, 2000). In addition, these assemblages are usually associated with water masses (Grothues and Cowen, 1999; Hare *et al*, 2001), displaying a species distribution that reflects oceanographic processes cross- and alongshelf.

Table 1. Factors affecting formation, maintenance and disruption of larval fish assemblages, according to Boehlert and Mundy (1993).

Type of factor	**Influencing formation**	**Influencing maintenance**	**Influencing disruption**
Adult behavior	Spawning location Spawning time (tidal, diel, lunar, seasonal)	None	Predation (cannibalism) Influences on settlement
Egg development	Buoyancy (demersal Vs. Pelagic eggs, egg density) Incubation time Hatching location Hatching time	None	None
Larval behavior	Buoyancy at hatching Swimming ability at hatching	Habitat preference (temperature, salinity, light, depth) Vertical migration	Ontogenetic changes in vertical distribution Metamorphosis (settlement, schooling)
Biotic environment	Predation (absence will create “ecological safe sites”)	Prey presence	Predation Prey absence (starvation)
Abotic environment	Convergence Fronts	Eddies (Taylor columns) Upwelling Downwelling Internal waves Convergences Fronts	Diffusion Mixing Advection

The maintenance of these assemblages depends on a suite of conditions promoting larval growth and survival and the presence of physical processes to overcome the forces causing assemblage disruptions (e.g., cyclonic circulation, Werner *et al*., 1993; fronts, Galarza *et al*., 2009). Physical processes such as dispersal in warm-core eddies (Drinkwater *et al*., 2000) and upwelling filaments (Rodríguez *et al*., 2004), or diffusion within water masses (Fortier and Legget, 1985), are important disruptive factors for larval fish assemblages. Nevertheless, the main biological factors causing disruption are metamorphosis and predation. Predation is the most important mortality factor because differential mortality between species within the assemblage will lead to variation in the composition of the assemblage (Miller, 2002).

Numerous studies have dealt with the composition and the spatial and temporal variability of the structure of larval fish assemblages worldwide, such as in the Mediterranean Sea (Sabatés, 1990; Somarakis *et al*., 2002), Cantabric Sea (Rodríguez, 2008), California (Aceves-Medina *et al*., 2002), Benguela (Olivar and Shelton, 1993), Peru (Vélez *et al*., 2005) or Australia (Gray and Miskievicz, 2002; Muhling *et al*., 2008). However, larval fish assemblages are still not described around the Canary Islands. The absence of ichthyoplankton time series in the region hinders the assessment of species variability through time and, consequently, the influence of environmental variables on the larval community.

The unique environment off Gran Canaria Island

Gran Canaria is one of the major islands of the Canaries Archipelago (Fig. 5), located at 28-29 ºN. This archipelago is bathed by the Canary Current, considered as the natural extension of the Azores Current (Stramma, 1984). When the Azores Current approaches the eastern limb of the subtropical North Atlantic Gyre, it turns southwards forced by winds and by the presence of the African continent, constituting the Canary Current. At the latitude of Cape Blanc (20 ºN), the Canary Current separates from the African coast, becoming the North Equatorial Current (NEC) (Fedoseev, 1970; Mittelstaedt, 1991; Fiekas *et al*., 1992; Paillet and Mercier, 1997; Barton, 2001). Recirculation south of 20 ºN seems to occur in any season, but when the trade winds weaken (i.e., autumn and winter), the subsurface poleward flow (AAIW) surfaces, reaching the Canary archipelago (Knoll *et al.*, 2002; Hernández-Guerra *et al.*, 2003).

Seasonality in Gran Canaria waters is not as strong as in temperate seas, due to its subtropical regime. These waters are characterized by a strong stratification in the surface layers and by a deep chlorophyll maximum during most of the year (Hernández-León *et al.*, 2007). In winter, surface waters cool off and the seasonal thermocline is eroded, pumping nutrients into the euphotic zone. This process leads to the well-known

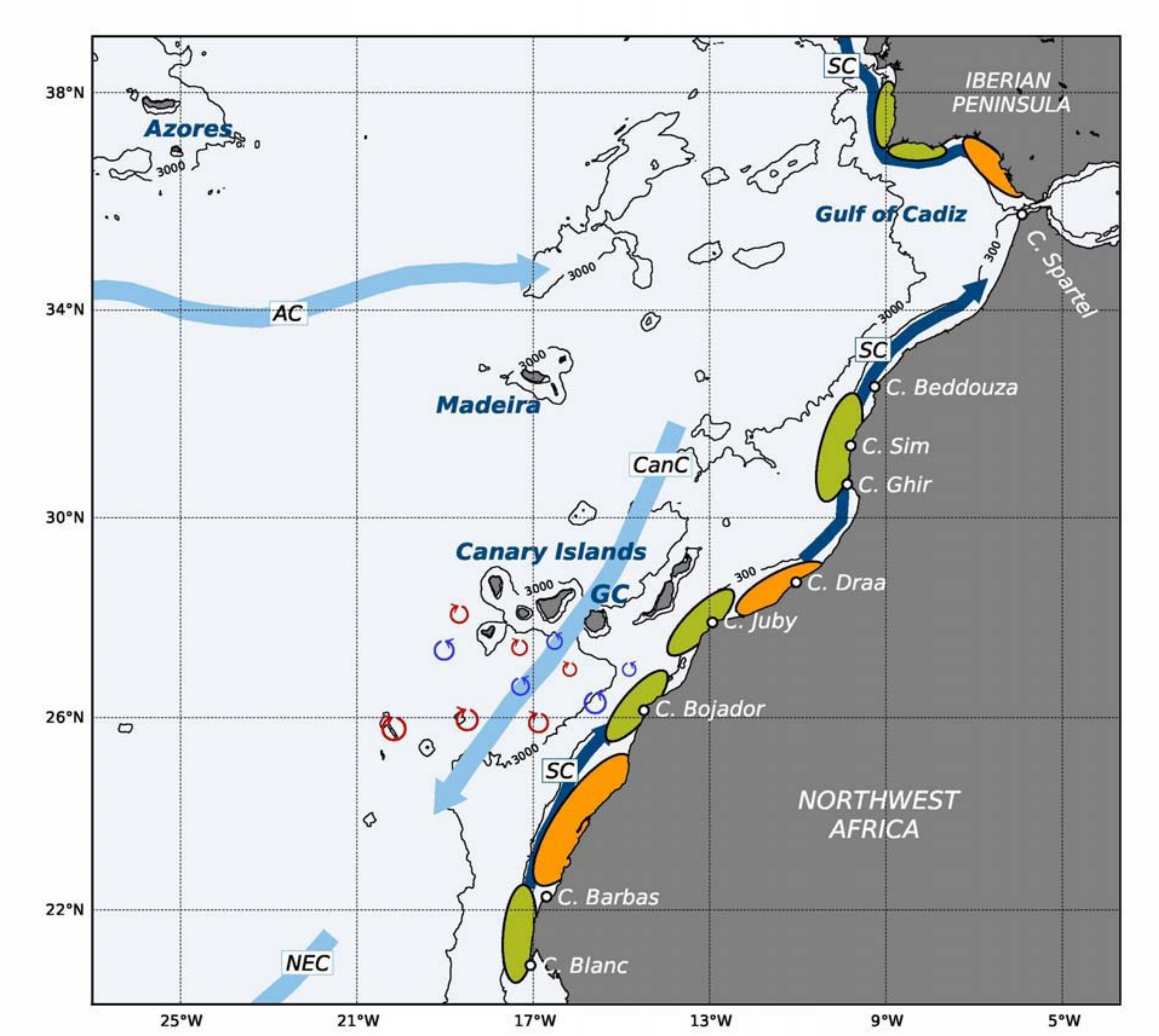


Figure 5. Schematic map of the Canary Basin showing the major capes, the different archipelagos (Azores, Madeira, Canary Islands) and the island of Gran Canaria (GC). Main currents (surface currents, lighter blue arrows,; slope current, darker blue arrows,) and mesoscale eddies (blue, cyclones; red, anticyclones) and the retention (orange) and dispersion (green) areas on the shelf are represented. AC: Azores Current, CanC: Canary Current, NEC: North Equatorial Current, SC: Slope Current. Redrawn from Arístegui *et al*. (in press) by E. Mason.

late winter bloom that promotes an increase in chlorophyll concentration and primary production (De León and Braun, 1973; Braun, 1980). This bloom, characteristic of subtropical waters (Menzel and Ryther, 1961), depends on the nutrient supply instead of light availability, as occurs in temperate regions. Off the the Canary Islands, chlorophyll *a* concentrations range between 0.05-0.2 $mg{\cdot}m^{-3}$ over an annual cycle in surface waters and between 0.2-0.3 $mg{\cdot}m^{-3}$ in the deep chlorophyll maximum, while during the bloom average values are 1.0-1.5 $mg{\cdot}m^{-3}$ in surface waters (Hernández-León *et al*., 2007). Arístegui *et al*. (2001) studied the late winter bloom off Gran Canaria and observed that chlophyll concentration displayed a “two peak structure”. They associated the first peak to large-sized cells (>2µm) and the second to small cells (<2µm). Similarly, these authors found a severe control on the phytoplankton biomass by microzooplankton grazing. Therefore, they concluded that the triggering of the phytoplankton bloom was produced by nutrients availability, while grazing was the main factor controlling the development of the bloom. This top-down control has recently been confirmed by Schmoker *et al.* (*in prep.*).

On the other hand, mesozooplankton biomass also shows annual maximum values during the late winter bloom (Hernández-León *et al*., 1984; Hernández-León, 1988), usually with 2-3 weeks-lag in relation to the first chlorophyll peak. Mesozooplankton biomass peaks two or three times during the bloom (Hernández-León *et al*., 2004). These authors attributed this variability to the predation pressure exerted by diel vertical migrant (DVMs) of the deep scattering layers during the lunar cycle. Lunar illumination influences the migration range of these DVMs and so, they are not able to reach upper layers (<100 m depth) during the full moon. The absence of predators will allow the epizooplankton to grow during the full moon. On the other hand, during the new moon, DVMs can reach upper layers and exert a higher predation pressure. Thus, zooplankton mortality rates will increase.

In the Canary region, the ichthyoplankton evolution during this bloom was unknown so far. Thus, assessing the coupling between primary production, zooplankton and fish larvae during the late winter bloom in this region will be very interesting. This may be a way of testing the match-mismatch hypothesis (Cushing, 1975), originally proposed for temperate waters, in a subtropical area.

Larval fish dynamics around Gran Canaria

In the particular environment of oceanic islands, early stages of local fish populations need to avoid currents that sweep them offshore. Self-recruitment is the main factor in maintaining these populations (Jones *et al*., 1999; Swearer *et al*., 1999; Paris and Cowen, 2004). The existence of island endemic species is a proof of self-recruitment success (Wing *et al*., 1998). Self-recruitment could be strengthened by the presence of barriers for dispersal, such as fronts that represent a barrier to faunal exchange (Galarza *et al*., 2009). Larval behaviour plays an important role to avoid dispersal and its magnitude is determined by the early onset of active larval swimming (Leis, 2007). However, Cowen *et al*. (2006) stated that larval inputs from outside the local area are required to sustain certain island fish populations. These authors also pointed out that typical larval dispersal distances of ecologically relevant magnitude are on the scale of only 10-100 km for a suite of species.

The influence of the local current regime around oceanic islands on the larval fish community has been explored in different studies. Hammer and Hauri (1981) registered higher zooplankton concentrations upstream of Pandora Reef, in the Great Barrier Reef. Similarly, Miller (1974) and Leis (1986) found higher larval fish densities upstream of Oahu (Hawaii) and Lizard Island (Great Barrier Reef), respectively. On the other hand, Boehlert *et al*. (1992) recorded higher abundances of fish eggs and larvae downstream of Johnston Atoll (Hawaii). In addition, Cowen and Castro (1994) collected higher densities of fish larvae very close to the shore off Barbados, in areas of reduced surface flow. Mesoscale oceanographic structures, such as eddies, contribute to this retention near shore (Sale, 1970; Leis, 1982).

In the particular case of the Canary Islands, the presence of the archipelago is an obstacle to the oceanic and atmospheric flows, generating high mesoscale oceanographic variability. Thus, cyclonic and anticyclonic eddies are shed from the islands, and warm wakes are formed south, leeward of the islands (Fig.5 and 6) (Arístegui *et al*., 1994; Barton *et al*., 1998). Eddies drift southward with the Canary Current (Fig. 5) forming a von Karman vortex street (Chopra and Hubert, 1962; La Violette, 1974). The life span of these island-generated eddies may be of several months, even more than one year (Sangrá *et al*., 2005, 2007).

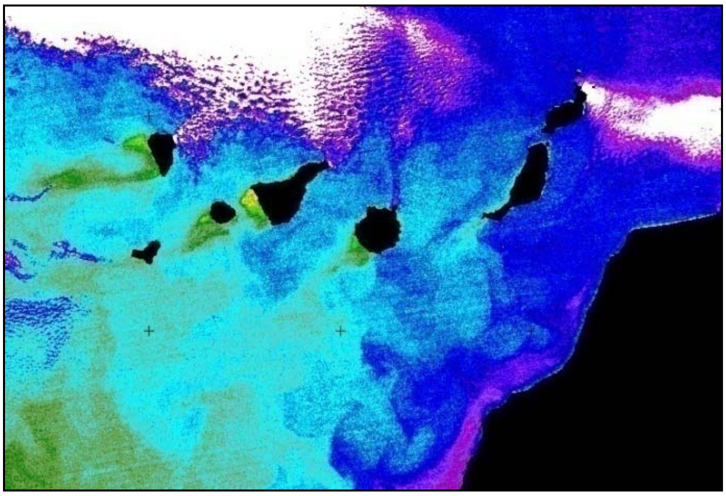


Figure 6. Sea Surface Temperature image showing the Canaries archipelago and the warm water leeward of the different islands

Early studies on zooplankton around Gran Canaria focused on the eastern and southern flanks of the island (Hernández-León and Miranda-Rodal; Hernández-León 1988; Arístegui *et al*., 1989). Hernández-León (1991) confirmed the *island mass effect* (Doty and Oguri, 1983) in Gran Canaria. This *island mass effect* is an increase in productivity up- or downstream of oceanic islands, surrounded by nutrient-poor (oceanic) waters. Hernández-León (1991) recorded an accumulation of zooplankton biomass in the warm wake up to 10 times higher than in surrounding waters. Zooplankton metabolic activity was lower than in areas characterized by strong winds, so the author concluded that the biomass increase was not due to increased productivity but to accumulation.

Afterwards, Rodríguez *et al*. (2001) studied the geostrophic flow around Gran Canaria Island and its influence on ichthyoplankton distribution (Fig. 7). These authors identified two retention areas for zooplankton and ichthyoplankton: (1) *N-NE upstream of the island*, a region of null flow is generated where the Canary current impinges on the island; (2) *S-SW downstream of the island*, within the warm wake.

On the other hand, water flow is enhanced in the eastern and western flanks of the island, particularly in the west, by the presence of Tenerife Island. In addition, south of Gran Canaria there are interactions with other mesoscale structures (Fig. 7), such as

(1) island-generated eddies in the SW, and (2) upwelling filaments arriving from the African coast, in the SE.

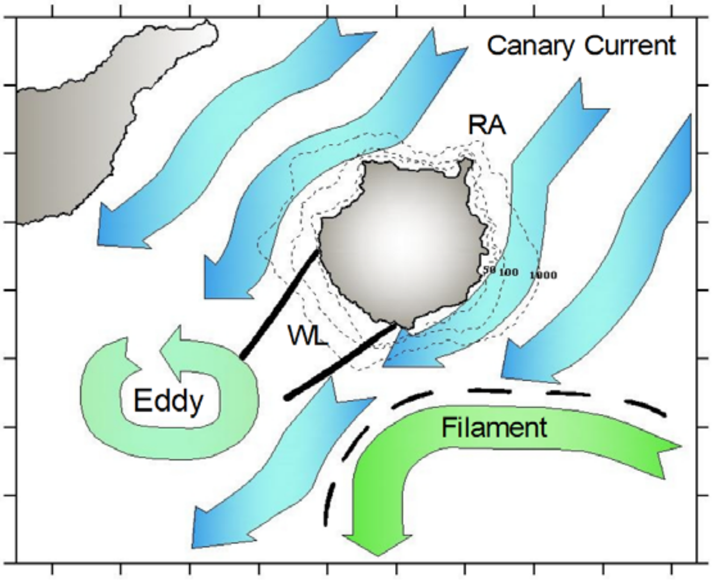


Figure 7. Schematic illustration showing the main hydrographic structures affecting Gran Canaria. Redrawn from Rodríguez *et al*. (2001). WL: warm lee; RA: Retention area.

Rodriguez *et al*. (2001) concluded that fish eggs and neritic larvae can benefit from those retention areas, even organisms with reduced swimming abilities (i.e., passive particles) would be retained in the island's warm wake.

Canaries-African Coastal Transition Zone: influence of mesoscale oceanographic activity on larval fish distribution

The Canaries Archipelago is close to the NW African coastal upwelling (~100 km). Accordingly, this archipelago lies in the transition zone between the cold and very productive waters of the coastal upwelling and the oligotrophic waters of the open ocean. Thus, this region is known as the Canaries-African Coastal Transition Zone (Canaries-African CTZ).

Upwelling filaments are common structures in eastern boundary upwelling systems (Flament *et al*., 1985). Filaments are cold features in surface waters, less than 100 km wide but hundreds of kilometers long which extend offshore from near the coast (Brink and Cowles, 1991). These structures were first studied in the California region (Traganza, 1980, 1981). These authors established that filaments have clear chemical and biological signatures in relation to surrounding waters. Afterwards, these plumes were documented in other eastern boundary currents: Benguela (Schillington *et al*., 1990; Nelson *et al*., 1998; Ducombe-Rae *et al*., 1992), Humbolt (Sobarzo and Figueroa, 2001) and NW Africa (Fig. 8) (e.g. Nykjaer *et al*., 1988; van Camp *et al*., 1991; Hernández-Guerra *et al*., 1993; Barton *et al*., 1998).

According to Strub *et al*. (1991), there are three conceptual models to explain the generation of filaments: (1) Convergences in the nearshore region that generate one-way jets (*squirts*), transporting coastally upwelled water to the deep ocean (Ikeda and Emery, 1984). (2) Eddies that draw recently upwelled water away from the coast (Mooers and Robinson, 1984). (3) A continuous southward jet meandering offshore and onshore, which during its onshore excursions, it may entrain coastally upwelled water generating filaments, which extend offshore on the next meander (Strub *et al*., 1991).

In the Canaries-African CTZ, the persistence of filaments near Cape Juby is related to the presence of a quasi-permanent cyclonic eddy located over the bathymetric trough downstream of the shallow part of the Fuerteventura-Africa channel (Barton *et al*., 2004). These authors argue that a filament would be generated when the upwelling is strong enough for the front and the associated jet to be entrained around the eddy, as shown in Barton *et al*. (1998). However, later studies found the presence of a dual filament structure (Barton *et al*., 2000, 2004). According to these authors, the origin of the northern filament was related to an anticyclonic eddy located south of Fuerteventura, while the generation of the filament closer to Cape Bojador was related to the quasi-permanent cyclonic eddy. Once they extend offshore, both filaments merged into a single weak structure.

The offshore transport of upwelled water has important biological effects. In California, higher concentrations of nutrients and phytoplankton (Chavez *et al*., 1991), and zooplankton (Mackas *et al*., 1991) were found within these structures in relation to surrounding waters. This transport has also been confirmed in the NW African upwelling for nutrients (García-Muñoz *et al.*, 2004), phytoplankton (Arístegui *et al.*, 1997), zooplankton (Hernández-León *et al.*, 2001, 2002), and fish larvae (Rodríguez *et al.*, 1999, 2004).

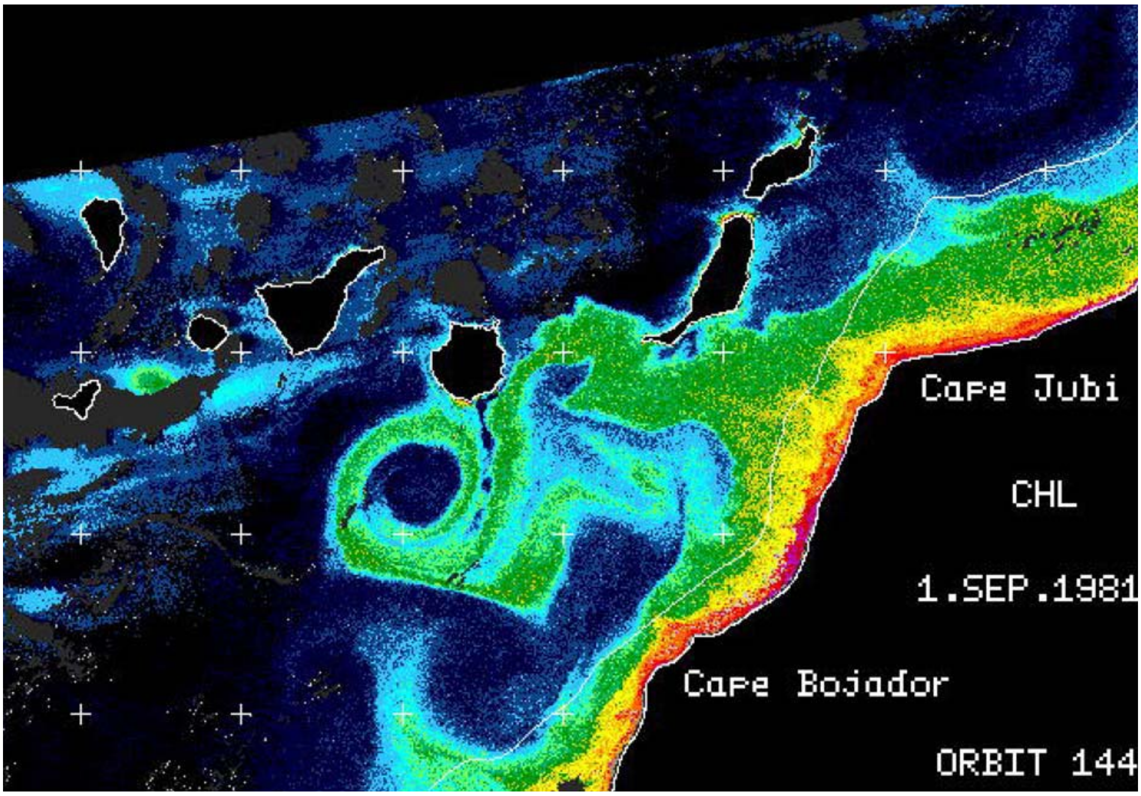


Figure 8. SeaWiFS image (September 1981) showing chlorophyll *a* distribution within a giant filament drifting from the Cape Juby región and entrained in an anti-cyclone south of Gran Canaria.

In the particular case of neritic fish larvae, their dispersal from the productive African waters to the open ocean may be detrimental for their survival. Different studies in the region have identified three main situations in relation to this larval transport (Rodríguez *et al.*, 1999, 2004; Bécognée *et al.*, 2006): (1) *Retention.* The filament is entrained in the quasi-permanent cyclonic eddy and most larvae may return to the African coast, to be recruited into the local fish populations; (2) *Dispersal I.* The filament extends to open ocean and so larvae would die from starvation or predation; (3) *Dispersal II.* The filament expands beyond the shelf and reaches the eastern shores of the Canaries Archipelago. Larvae may be recruited to the island fish populations, if they found suitable conditions.

Although the arrival of upwelling filaments to the easternmost islands has been described several times (La Violette, 1974; Pacheco and Hernández-Guerra, 1999), the impact of these filaments on local fish populations is unknown. Previous studies (Rodríguez *et al*., 1999, 2004; Bécognée *et al*., 2006) focused on the most characteristic species of the upwelling area, sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*). Still, the effect of these structures on the fisheries of sardine, anchovy and other less abundant species needs to be determined to improve fisheries management.

THESIS OUTLINE

The aim of this thesis was to address several questions:

1. What do we already know about ichthyoplankton of the Canaries-African Coastal Transition Zone?
2. What is the composition and structure of the larval fish assemblage of Gran Canaria Island waters?
3. Does this larval fish assemblage composition and abundance change along the year or along-shelf?
4. What is the fate of fish larvae transported in upwelling filaments from the African shelf? If they reach the Canary Islands, can they be detected?

We did a review of previous studies carried out in the Canaries-African CTZ to answer question 1 (**Chapter I**). Most of these studies dealt with sardine and anchovy larval dispersal within upwelling filaments or described the influence of hydrography on fish larvae distribution around islands.

An ichthyoplankton time series was performed to answer questions 2 and 3. This time series consisted on weekly samplings, during more than two years at the edge of the Gran Canaria's shelf (**Chapters II, III and IV**). This intense sampling resulted in a large amount of data that allowed us to accurately describe the composition and structure of the larval fish community off Gran Canaria and its temporal and horizontal distributions.

In relation to question 4, we assessed the role of upwelling filaments as dispersive structures for fish larvae using two approaches. First of all, a combination of (1) larval sampling at fixed stations located in the Gran Canaria shelf, and (2) remote sensing analysis carried out to determine the presence of larvae transported by upwelling filaments, off Gran Canaria (**Chapter II**). On the other hand, metabolic assessments of larvae transported within an upwelling filament were studied *in situ* during an intensive cruise performed in the Canaries-African CTZ (**Chapter V**).

METHODOLOGY

Ichthyoplankton studies in subtropical areas are challenging, as Leis (1991) explained for the tropics. Most of the larval fish research has been done in temperate regions, which are very different from our study area:

- The total number of fish species in the Canary región is high: 606 species (Brito *et al.*, 2002).
- Spawning periods for these species are longer than those of temperate regions, lasting several months or even the whole year.
- Larval and juvenile pelagic stages are difficult to identify or even undescribed for a lot of species.
- Larval densities are low. Indeed, it is frequent that larvae of common species are not present in most of the samples (Leis and Goldman, 1987; Leis and Trnski, 1989).

Sampling

The particular methodology used in each work within this thesis is described on the respective chapter. Nevertheless, on each study some general sampling was carried out:

- Physical variables were measured using with a CTD (Sea Bird SBE25 o Neil Brown Mark-III probe).
- Temperature (SST) and Chlorophyll *a* (SeaWiFS) remote images were compiled from the Physical Oceanography and Remote Sensing Group from the Universidad de Las Palmas de Gran Canaria (ULPGC) and the Earth Observation, Remote Sensing and Atmosferic Department (CREPAD) of the Spanish National Institute for Aerospace Technology (INTA).

- Chlorophyll *a* assessment through the fluorimetric method (Yentsch and Menzel, 1963) from water samples obtained with a Niskin bottle.
- Oblique Bongo hauls were performed to sample mesozooplankton and ichthyoplankton, with a 40 cm-diameter net fitted with a 200 µm mesh). During some research cruises, a Longhurst-Hardy Plankton Recorder (LHPR), with a 200 µm mesh, was also towed.

Mesozooplankton biomass was calculated as dry weight, using the method proposed by Lovegrove (1966), or as protein content, following the method by Lowry *et al.* (1951) modified by Rutter (1967).

Fish larvae were sorted under a stereoscopic microscope and were preserved in 4% buffered formaline. Since most of the larval sampling was done during daylight hours, late stages were not very well represented. But during research cruises, these late larval stages were collected together with mesopelagic juveniles at night with the LHPR net. Fish eggs were analyzed in some chapters, but only general trends were considered, due to their scarcity and difficulties involved in the identification process.

A suite of physiological parameters were analyzed in Chapter V. Electron Transfer System (ETS) was measured according to the method from Kenner and Ahmed (1975) modified by Gómez *et al.* (1996). AminoAcyl tRNA Synthetase (AARS) was assessed using the colorimetric method by Chang *et al.* (1984), modified by Yebra and Hernández-León (2004). Gut fluorescence (GF) was calculated from the crude homogenates, following Yebra *et al*. (2004).

Identification, Terminology and Systematics

A review of the spawning times and areas of fish species in the Canary region was done prior to start the identification process. In the case of the Canary Islands, the adults' species list found in Brito *et al.* (2002) was used together with those from the Check List of the Fishes of the Eastern Tropical Atlantic (CLOFETA, Queró *et al.*, 1990) and the Check List of the Fishes of the North eastern Atlantic and Mediterranean (CLOFNAM, Whitehead *et al.*, 1984). Spawning times described in Franquet and Brito

(1995) were also considered. In addition, specific literature was consulted for several species (ej., Lorenzo-Nespereira and Pajuelo, 1993; Méndez-Villamil *et al.*, 1997; Wienerroither, 2005). Due to the absence of a local ichthyoplankton guide, those from elsewhere were consulted: Mediterranean Sea (Ancona *et al.*, 1931-1956; Sabatés, 1988; Alemany, 1997), Northwest Atlantic (Fahay, 1983; Richards, 2006), Northeast Atlantic (Russell, 1976), Benguela (Olivar and Fortuño, 1991), California Current (Moser *et al.*, 1984), Indo-Pacific (Leis and Carson-Ewart, 2004).

During the identification process of fish larvae, several characters were used (Fig. 1): (1) morphological (e.g., body length, and the shape of the body, head, digestive tube and eyes; fin development and position; specialized larval characters), (2) meristics (e.g., myomere and radii count) and (3) pigmentation patterns (melanophores).

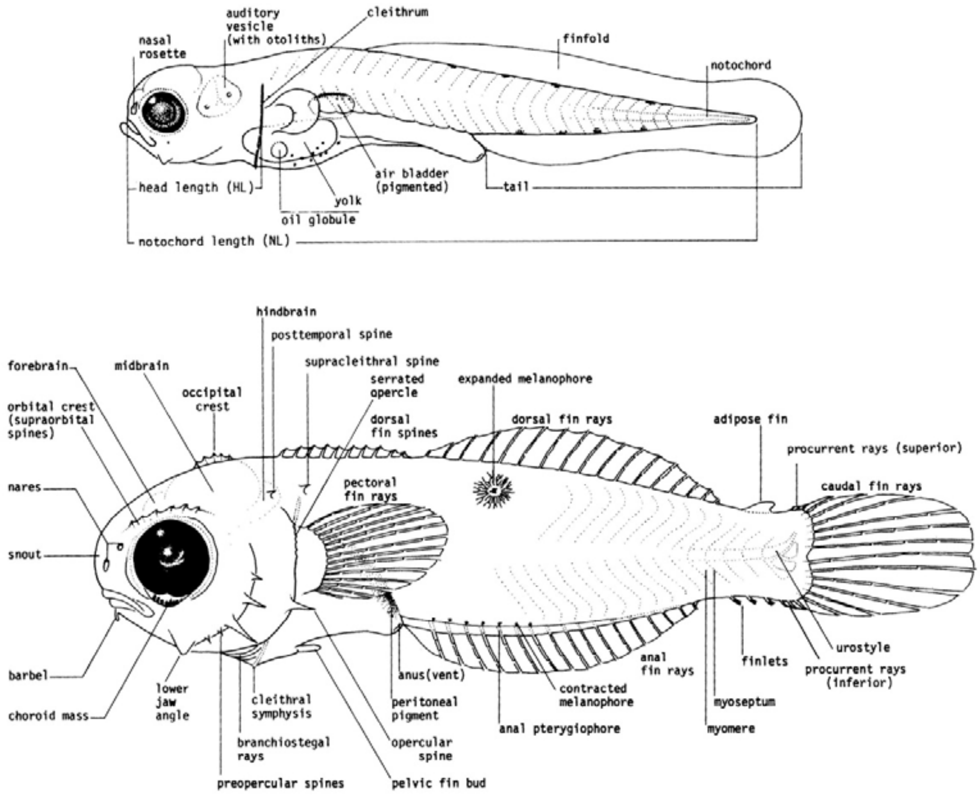


Figure 1. Scheme showing morphological characters of a larval fish in preflexion (above) and postflexion (below) stage. Extracted from Fahay (1983).

Larval identification was done to the lowest taxonomic level possible, although the small size or deterioration of some specimens complicated reaching species level.

The terminology used for larval development was that from Ahlstrom and colleagues (Kendall *et al.*, 1984). On the other hand, the systematic classification applied was that from Quer贸 *et al.* (1990), combined with Whitehead *et al.* (1984) and new accepted specific names (ej., *Scomber colias*).

An artificial classification is applied in most of the chapters within this thesis. This classification divides the species into three groups, according to adult ecology (Rodríguez *et al.*, 1999): (1) *Neritic*, species whose adults usually inhabit and reproduce on the shelf waters, over 200 m depth; (2) *Oceanic*, species whose adults inhabit and reproduce below 200 m depth; and (3) *Other*, this group includes all the unidentified larvae or those identified to the family level in those families that include neritic and oceanic species.

CHAPTER I

THE ICHTHYOPLANKTON ASSEMBLAGE OF THE CANARIES-AFRICA COASTAL TRANSITION ZONE: A SYNTHESIS

J.M. Rodríguez, M. Moyano and S. Hernández-León. The ichythyoplankton assemblage of the Canaries-Africa Coastal Transition Zone: a synthesis. *Progress in Oceanography (in press)*

Abstract

In this paper we synthesise relevant information on the ichthyoplankton assemblage of the Canaries-African Coastal Transition Zone (C-ACTZ). This CTZ shows the singularity that the Canary Archipelago interrupts the main flow of the Canary Current and Trade Winds, introducing large mesoscale variability, in the form of island warm wakes and cyclonic and anticyclonic eddies downstream of the islands. Besides, upwelling filaments stretch towards the archipelago from the African coastal upwelling, transporting phytoplankton, zooplankton and fish larvae. They also interact with eddies shed from the islands to exchange water properties and biogenic material. All these mesoscale features influence the composition, structure, abundance and distribution of the larval fish community (LFC) of the region. The Canary Current (CC) and eddies shed from the islands drag larvae of island neritic fish species into the oceanic region and contribute, along warm wakes, to the horizontal distribution of fish larvae. Upwelling and upwelling filaments transport larvae of African neritic species into the oceanic region. These larvae dominate the LFC and account for the relatively high average larval fish abundance found in the C-ACTZ during the summer upwelling season. Filaments originated in the region of Cape Juby-Cape Bojador are entrained around a quasi-permanent cyclonic eddy, trapped between Gran Canaria and the African coast, forming a system through which most of the African neritic larvae may return to the African shelf. However, some larvae reach the eastern islands of the Canary archipelago and they may be spread all over the neritic region of the archipelago by eddies shed from the islands. Also in summer, the distribution of the LFC of the C-ACTZ is vertically stratified and fish larvae seem to carry out little or not diel vertical migration. Overall, this study highlights the strong relationship between mesoscale oceanographic processes and the LFC in the C-ACTZ.

Keywords: Ichthyoplankton; larval fish community; spatial distribution; physical-biological interactions; Canaries-Africa transition zone; Canary Current System; NE Atlantic.

1.Introduction

The Canary Current (CC), fed by the Azores Current, flows equatorward from about 33 ºN to around 20 ºN, where it separates from the African coast to become the North Equatorial Current (Fedoseev, 1970; Mittelstaedt, 1991; Fiekas *et al.*, 1992; Paillet and Mercier, 1997; Barton, 2001). Recirculation south of 20 ºN seems to occur in any season, but in autumn and winter, when the Trade Winds weaken or turn northward, the subsurface poleward flow surfaces, reaching the Canary archipelago (Hernández-Guerra *et al.*, 1993; Knoll *et al.*, 2002).

The Canary Current System (CCS), like the other eastern boundary upwelling regions during the upwelling season, is characterised by an intense mesoscale oceanographic activity in the transition zone between the cool, nutrient-rich waters of the coastal upwelling regime and the warmer, oligotrophic waters of the open ocean (Barton *et al.*, 1998). The upwelling season off NW Africa, north of 25ºN, extends from July through September, although occasional small-scale and short-time upwelling events may arise at any time (Mittelstaedt, 1991; Van Camp *et al.*, 1991).

The CCS shows the singularity that the CC flows through the Canary archipelago, which spans the transition between coastal upwelling and oceanic waters. The abrupt topography of the Canary Islands presents an obstacle to the general southward flow of the CC and Trade winds. This produces strong variability in the atmospheric and oceanic flows giving rise to mesoscale oceanographic features. Warm wakes are formed leeward of the islands and cyclonic and anticyclonic eddies are generated downstream of these, drifting southward with the general flow of the CC (Mittelstaedt, 1991; Van Camp *et al.*, 1991; Hernández-Guerra *et al.*, 1993; Arístegui *et al.*, 1994; Arístegui *et al.*, 1997; Barton *et al.*, 1998; Barton *et al.*, 2000). All these structures are revealed in the Advanced Very High Resolution Radiometer (AVHRR) satellite images of sea surface temperature of the region (see Fig. 2 in Barton *et al.*, 2004). The CC, eddies and warm wakes participate in plankton transport and distribution in the region (Arístegui *et al.*, 1997; Basterretxea and Aristegui, 2000; Aristegui *et al.*, 2004).

On the other hand, upwelling filaments extend the influence of coastal upwelling into the ocean and towards the Canary archipelago (Hernández-Guerra *et al.*, 1993; Barton *et al.*, 1998; Barton *et al.*, 2004). The upwelling filaments generated between

Cape Juby and Cape Bojador are recurrent mesoscale oceanographic structures. They arise on the African shelf by the interaction between coastal upwelling and a cyclonic eddy, geographically trapped between Gran Canaria Island and the African coast (See Fig. 24 in Barton *et al.*, 1998). Filaments extend over 150 km offshore (Fig. 1a) and then they are entrained around the trapped cyclonic eddy (Figs. 1b and 2a), before returning shoreward (Barton *et al.*, 1998; Navarro-Perez and Barton, 1998; Barton *et al.*, 2004). These filaments transport colder and lower salinity coastal upwelled waters (Barton *et al.*, 1998; Navarro-Perez and Barton, 1998) and their load of chlorophyll (Hernández-Guerra *et al.*, 1993; Arístegui *et al.*, 1997; Basterretxea and Aristegui, 2000), mesozooplankton (Hernández-León *et al.*, 2002) and neritic fish larvae (Rodríguez *et al.*, 1999; Rodriguez *et al.*, 2004) to open ocean waters and towards the

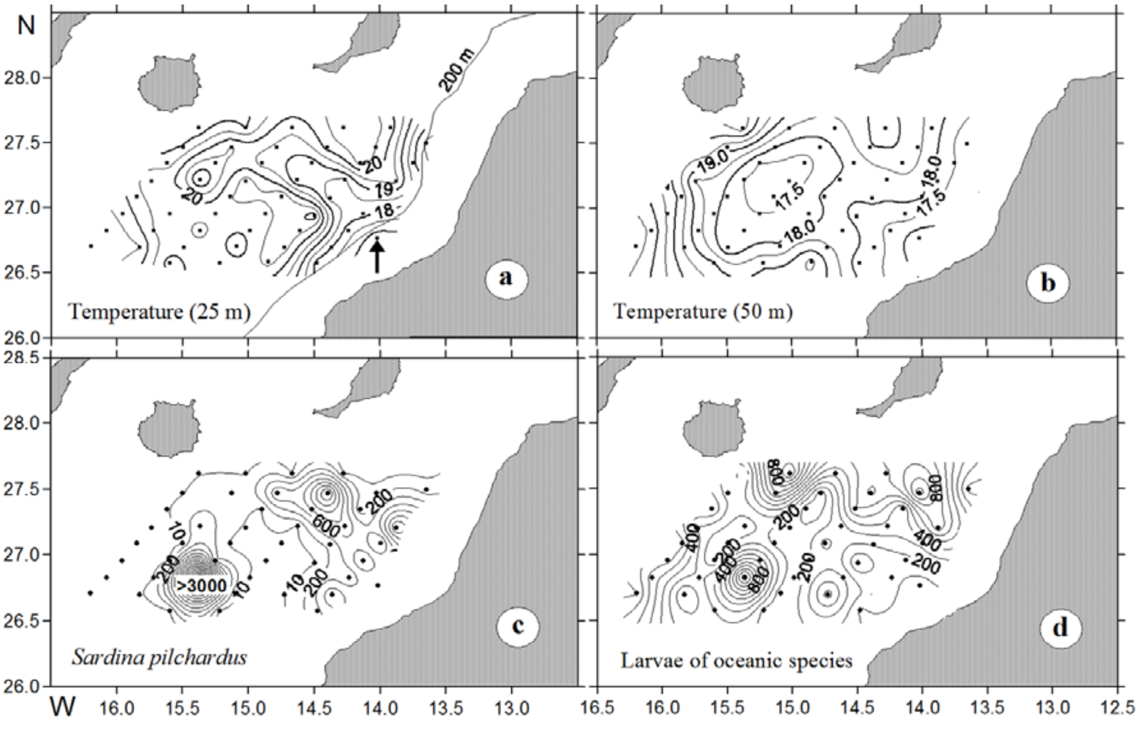


Figure 1. Horizontal distribution of (a) temperature at 25 m depth, showing the upwelling filament; (b) temperature at 50 m depth, showing the cyclonic eddy geographically trapped between Gran Canaria Island and the African shelf; (c) *Sardina pilchardus* larval abundance (no. of larvae 10 m^{-2}); (d) larval abundance of oceanic species (no. of larvae 10 m^{-2}) found during the Hespérides cruise carried out in the C-ACTZ between 9 and 16 August 1993. Dots represent sampling stations and the arrow (in a) indicates the only station sampled over the African shelf where relatively high *S. pilchardus* spawning was found. Notice the relatively high concentration of *S. pilchardus* larvae found at the periphery of the trapped cyclonic eddy

Canary Islands. The return flow of filament water into the coastal zone may reduce the impact of the offshore transport (Basterretxea and Aristegui, 2000). Nevertheless, eddies shed from the islands may also interact between them and with upwelling filaments to exchange water properties and organic matter, extending the zonal gradient for more that 300 km, the width of the archipelago's area of influence (Basterretxea and Aristegui, 2000; Aristegui *et al.*, 2004; Barton *et al.*, 2004; Sangrá *et al.*, 2005).

In coastal upwelling regions and adjacent areas with vertical shear, the interaction between vertical distributions, migrations and hydrodynamic processes is of special importance to the horizontal distribution of fish larvae (Parrish *et al.*, 1981; Norcross and Shaw, 1984; Olivar, 1990; Smith and Suthers, 1999). Neritic fish eggs and larvae with near-surface distributions are susceptible to the offshore transport in the Ekman layer associated with coastal upwelling (John, 1985; John and Re, 1995; Smith and Suthers, 1999). In contrast, fish larvae with deeper distributions render them liable to shoreward transport in the deep onshore flow, also associated with coastal upwelling (Hamann *et al.*, 1981; John, 1985; John and Re, 1995; Smith and Suthers, 1999). Moreover, fish larvae may carry out daily (Parrish *et al.*, 1981; Myers and Drinkwater, 1989) or ontogenically (Norcross and Shaw, 1984; John, 1985; Gorbunova *et al.*, 1986) vertical migrations between the two flow regimes to maintain their position in the sea.

In this paper, we synthesise relevant information on the ichthyoplankton community of the Canaries-African Coastal Transition Zone (C-ACTZ). The composition and structure of the Larval Fish Community (LFC) are described. The influence of mesoscale oceanographic processes on the composition and structure of the LFC and on the abundance and spatial distribution of fish larvae are also examined.

2. The larval fish community of the Canaries-African coastal transition zone

There are some characteristics that identify the LFC of the C-ACTZ: (i) it shows a high diversity, typical of subtropical systems (Longhurst and Pauly, 1987). The Shannon-Wiener's diversity, $H'(\log_e)$, and the Pielou's evenness index, J', values calculated from the Annex I, were respectively $H' = 4.03$ and $J = 0.72$. (ii) Most larvae belong to species of the oceanic-mesopelagic domain (Annex I) (iii) Myctophidae is the most diverse family (Annex I). This family contributes the greatest number of species to the mesopelagic fish assemblage (Parin, 1984; Nelson, 2006) and it has already been reported as the most diverse in the ichthyoplankton assemblage off NW Africa (Sabates and Rubies, 1985; Palomera, 1992). (iv) The LFC is dominated by the mesopelagic species *Cyclothone braueri* (Annex I). This species, either as larva or as adult, has been reported as the most abundant in a nearby oceanic area (Badcock, 1970; Badcock and Merret, 1976). (v) Larvae of tropical species (e.g. *Hygophum macrochir*, and *Vinciguerria nimbaria*) form part of the LFC. (vi) Larvae of African neritic species, transported by upwelling filaments, as we will see below, dominate the LFC during the summer upwelling season while during autumn the LFC is dominated by *C. braueri* and in winter and spring by two island neritic species, *Sardinella aurita* and *Boops boops* (Annex I). The island origin for these species is supported by two facts. First, all *B. boops* and most *S. aurita* larvae were caught in samples collected over the Gran Canaria Island shelf by Moyano and Hernandez-Leon (unpublished data) and Moyano *et al.* (2009) . Second, *S. aurita* reproduces all year round in the island waters (Bécognée *et al.*, 2006) while in winter and spring it is outside of its reproductive season in the African shelf (Ettahiri *et al.*, 2003), for which reason the African origin for this species should be rejected.

3. Horizontal distribution of fish larvae

3.1. Larval transport by currents and islands related mesoscale structures

The CC and eddies shed from the islands drag eggs and larvae of neritic fish species of the islands and carry them away, into the oceanic region (Rodríguez *et al.*, 2000; Rodríguez *et al.*, 2001). The most abundant of these species is *Anthias anthias*. Its island origin is supported by three observations: (1) this is a common species in the Canary archipelago waters (Brito *et al.*, 2002). (2) the absence of its larvae from the African shelf and from the area directly influenced by the African upwelling and upwelling filaments, both in summer 1993 (Rodríguez *et al.*, 1999; Rodriguez *et al.*, 2004) and in summer 1999 (Fig. 2b). (3) the presence of *A. anthias* larvae in very littoral waters of the Tenerife Island (Rodriguez and Lozano-Soldevilla, 1993), in samples collected around Gran Canaria Island (Rodríguez *et al.*, 2001) and in samples collected at the outer edge of a cyclonic eddy located directly south of Gran Canaria

Island (Rodriguez, 1998), when no influence of the African neritic larvae on the taxonomic composition of the LFC of the region was found (Rodríguez *et al.*, 2000).

Some neritic larvae of the archipelagos located upstream of the Canary Islands may also be contributed to the LFC of the C-ACTZ (Rodríguez *et al.*, 2000). Nevertheless, this contribution may be of little importance to the LFC of the region. These larvae would be transported by the Azores and the Canary currents but also eddies shed from islands of the archipelagos located upstream the Canaries, could participate in this transport. The participation of oceanic currents and eddies in larval fish transport has already been suggested (e.g., Wroblewski and Cheney, 1984; Leis, 1986; Lobel and Robinson, 1986; Hare and Cowen, 1991; Hutchings and Pearce, 1994; Logerwell and Smith, 2001).

On the other hand, island warm wakes and eddies shed from the islands may also play an important role in the retention and survival of larvae of local neritic fish populations. The reported accumulation of fish eggs and neritic fish larvae in the Gran Canaria's warm wake (Hernández-León, 1991) supports islands wakes as retention areas. A simulation model on dispersion of fish eggs and larvae, developed by Rodríguez *et al.* (2001), also shows the accumulation of both passive and swimming particles within the Gran Canaria lee. Likewise, this model shows that retention is possible within the cyclonic eddies found off this island (Rodríguez *et al.*, 2001). The concentration of larvae in the island wake and in eddies shed from the islands may account for the relatively high larval abundance (average of 904.2 larvae 10 m^{-2}) recorded off the Gran Canaria island during the Mast 1 cruise, carried out in the Canaries-ACTZ in October 1991 (Rodríguez *et al.*, 2001).

The larvae of tropical species (e.g. *Hygophum macrochir* and *Vinciguerria nimbaria*) that form part of the LFC (Annex I) could have been transported by the fall-winter surface poleward flow. Nevertheless, the presence in the region of these larvae also in summer and spring, when there is no surface poleward flow, and adults all year round (Brito *et al.*, 2002) indicate that these tropical species were established there and form stable populations in the region. That is to say, these species meet conditions to establish in a new area, i.e. they are able to reproduce successfully and their offspring can survive there (Sabatés *et al.*, 2006 and references herein). This may be related with the process of "tropicalisation" that, according to Brito *et al.* (2005), the ichthyofauna of the Canary Island waters is undergoing. The increase in tropical species in the Canary waters could be related with global warming, as fish species shift their distribution poleward to remain within suitable "climate envelopes" (Walther *et al.*, 2002). Nevertheless, an increase in knowledge with time of the ichthyofauna of the archipelago should be not forgotten either. From 1991 to 2002, 14 new species were recorded for the Canary archipelago waters (Brito *et al.*, 2002). But, according to these authors, many species of deep waters and even littoral species remain to be discovered.

3.2. Larval transport by upwelling filaments

The most abundant larval fish species transported by upwelling filaments are *S. pilchardus* and *E. encrasicolus*. These are species characteristic of the NW African coastal upwelling region (Jacques and Treger, 1986). In this region, *S. pilchardus* represents on average >70% of the total fish catches (FAO FISHSTAT) and it dominates the ichthyoplankton assemblage from Gibraltar to Cape Blanc. Percentages of 35.1% of the total egg catches and up to 94.0% of the total larval catches have been reported for this species in the region (Blackburn and Nellen, 1976; Palomera and Rubies, 1982). *S. pilchardus* reproduces all year round in the NW African shelf, within a thermal window of 15.5–20.0 ºC, with the spawning peak in winter (Furnestin and Furnestin, 1959; Ettahiri *et al.*, 2003). *E. encrasicolus* is less abundant in the NW African upwelling region. It represents around the 2.0% of the total fish catches (FAO FISHSTAT). Reported percentages of captures for the early life stages of this species in this region were 9.4% for eggs and 3.6% for larvae (Blackburn and Nellen, 1976; Sedletskaya, 1983). *E. encrasicolus* also reproduces during the whole year but with the spawning peak in summer (Furnestin and Furnestin, 1959; Ettahiri *et al.*, 2003).

For the Canary archipelago waters, there are no reported records of *S. pilchardus* egg collections and this species seems not to reproduce there. In regular sampling of landings of the Canary Islands' artisanal fleet, small (3-15 cm) *S. pilchardus* and only occasionally adults were found (Bécognée *et al.*, 2006; Santamaría *et al.*, 2008). In ichthyoplankton studies carried out along the eastern and southern Gran Canaria's shelf, (Bécognée *et al.*, 2006), after a year of study, sampling fortnightly, and Moyano *et al.* (2009) and Moyano and Hernandez-Leon (unpublished data) after a 21 month-study, sampling weekly, only found *S. pilchardus* larvae during short periods, always coinciding with the arrival of upwelling filaments at the Gran Canaria coast. All this, along with the presence of *S. pilchardus* larvae in the Canary waters in August (Rodriguez *et al.*, 2004; Moyano *et al.*, 2009), when the water temperature is > 22ºC, over the upper limit established for *S. pilchardus* spawning in the region (Furnestin and Furnestin, 1959), clearly indicates that these larvae had been transported from elsewhere. The African shelf origin is supported by the relatively important spawning of 5063 eggs 10 m^{-2} recorded in the only station sampled over the African shelf in August 1993, during the Hespérides cruise, and located at the root of the upwelling filament found during that cruise (Fig. 1a). Besides, the relatively shallow distribution of *S. pilchardus* larvae in the region, in summer (Fig. 3c) makes them susceptible to the transport by the upwelling filament flow, shallower than 100 m (Navarro-Perez and Barton, 1998). Also, the horizontal distribution of *S. pilchardus* larvae, all of them caught in the oceanic region, depicted the upwelling filament (Fig. 1c), indicating that these larvae were being transported by the filament (Rodríguez *et al.*, 1999). The relationship of *S. pilchardus* larvae with colder and less salty coastal upwelled water of the filament is supported by the relatively high negative correlation coefficients between *S. pilchardus* larval abundance and near surface (at 11 m depth) temperature and salinity (Spearman's rank correlation coefficient, $r = -0.65$ for temperature and $r = -0.56$ for near surface salinity, $p < 0.01$ in both cases).

In the Canary archipelago waters, *E. encrasicolus* is a rare species in the western and a common species in the eastern islands (Brito *et al.*, 2002). However, *E. encrasicolus* dominated the LFC in summer (Annex I). It is worth mentioning that 80.9% of the *E. encrasicolus* larvae were caught during the Fax cruise, carried out in the C-ACTZ in August 1999 (Fig. 2a). Also that during spring and summer of that year, the *E. encrasicolus* population of the westernmost islands of the Canary archipelago underwent a surprising outburst, after that, it decreased again to reaching the population level previous to the outburst (Brito *et al.*, 2002). Then, a question arises: was this outburst the result of a successful reproduction and recruitment of the island population or it was the result of larval transport by the upwelling filaments? The level or the size of the island's *E. encrasicolus* population previous to the outburst (Brito *et al.*, 2002) clearly indicates that these populations could not have produced it and underlies the necessity of larval advection from the African neritic region. The relatively high spawning density of *E. encrasicolus* (14877 eggs 10 m^{-2}) recorded during the Fax cruise

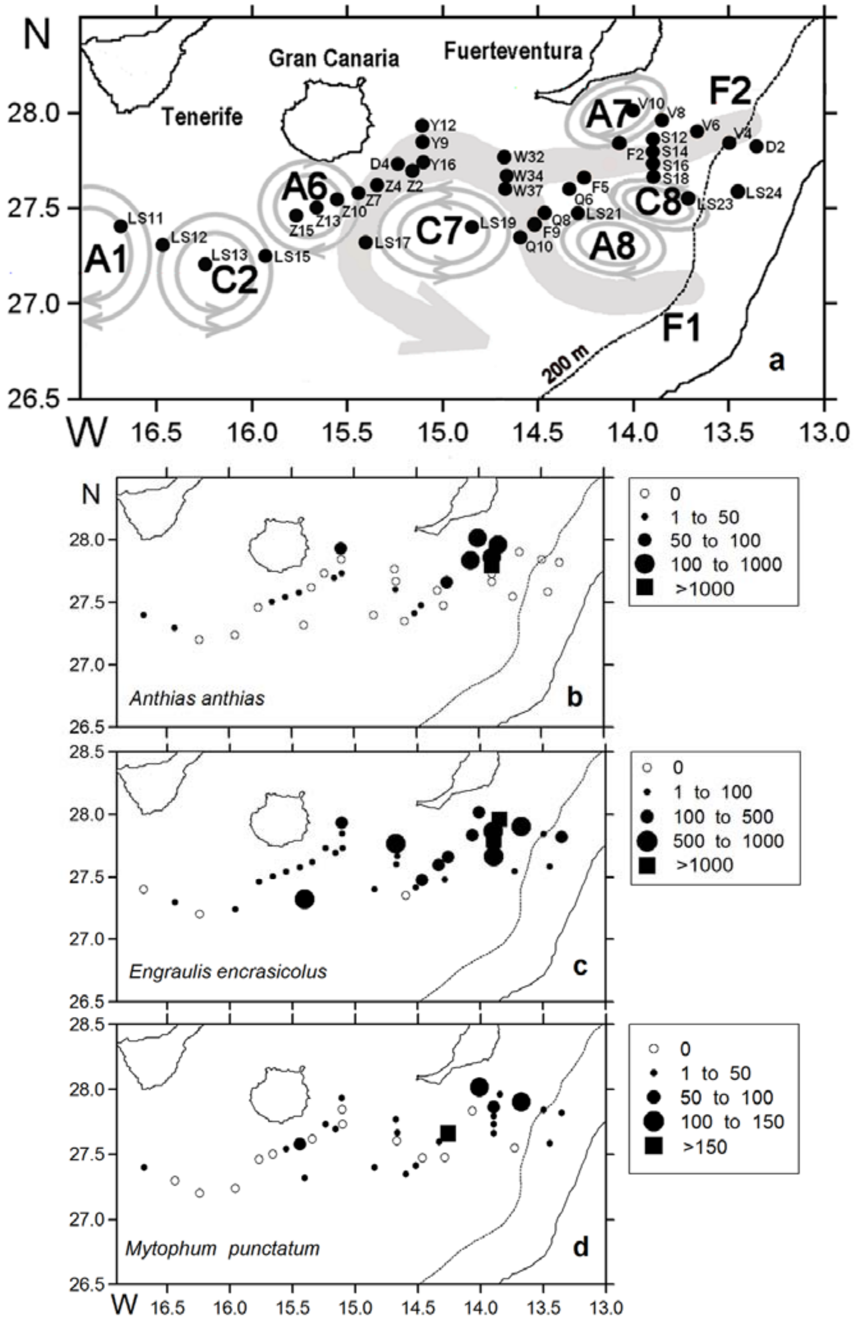


Figure 2. (a) location of ichthyoplankton stations of the Fax cruise, carried out in the C-ACTZ from 5 to 27 of August 1999, and schematic of the double filament-eddy structure found during that cruise. This structure was depicted from Sea surface AVHRR temperature images acquired at the time of the sampling and from CTD profiles. The location of cyclonic and anticyclonic eddies found during that cruise is also indicated; (b) Horizontal distribution of *Anthias anthias* larval abundance (no. of larvae 10 m^{-2}); (c) *Engraulis encrasicolus* larval abundance (no. of larvae 10 m^{-2}) and (d) *Myctophum puncatum* larval abundance (no. of larvae 10 m^{-2}) recorded during the Fax cruise.

at the station D2, located over the African shelf, at the root of the upwelling filament F2 (Fig. 2a) supports the African origin for *E. encrasicolus* larvae. Stn D2 along with Stn LS 24 (626 eggs 10 m^{-2}), also located over the African shelf, were the only positive stations for anchovy eggs found during that cruise. Besides, 83.9% of the *E. encrasicolus* eggs were collected in the 0-35 m layer of the station D2 (Rodríguez, 2006). This shallow location of *E. encrasicolus* eggs places them within the Ekman layer, of between 20 and 60 m depth in the region (Mittelstaedt, 1983), and makes them susceptible to the offshore transport. Also, the relatively shallow distribution of *E. encrasicolus* larvae (Fig. 3d) makes them susceptible to the transport in the upwelled waters of the filaments (Fig. 2c). Besides, as occurred with *S. pilchardus*, there was a significant relationship between the distribution of *E. encrasicolus* larvae and filament waters (Spearman's rank correlation coefficient, $r = -0.43$ for near surface temperature and $r = -0.59$ for near surface salinity, $p < 0.01$ in both cases).

Larvae of *S. pilchardus* in summer 1993 and *E. encrasicolus* in summer 1999 transported by upwelling filaments, were the main contributors to the relatively high larval abundance recorded in the oceanic region, far away from the African shelf, under the influence of these filaments (Rodríguez *et al.*, 1999; Rodriguez *et al.*, 2004). Maximum values of 4979 larvae 10 m^{-2} and of 3996 larvae 10 m^{-2} were recorded during the Hespérides (August 1993) and Fax (August 1999) cruises, respectively. While, during the Mast 1 cruise, carried out outside of the upwelling season and when no larvae of African neritic species were detected in the region (Rodríguez *et al.*, 2000), the maximum larval fish abundance found was of 1825 larvae 10 m^{-2}. On the other hand, the maximum abundances recorded for both species, 3447 larvae 10 m^{-2} for *S. pilchardus* and 1738 larvae 10 m^{-2} *E. encrasicolus*, in both cases well off the African shelf (Figs. 1c and 2c), were higher than those previously recorded for *E. encrasicolus* and *Sardinops ocellatus* in the Benguela upwelling region by Olivar and Shelton (1993) and those recorded for *Engraulis mordax* by Richardson and Pearcy (1977) in the upwelling region of the California Current. All the above may give us an idea of the amount of African neritic larvae transported by NW African upwelling filaments into the oceanic region of the A-CTZ. It should be added that upwelling filaments can also transport *S. pilchardus* and *E. encrasicolus* larvae into the oceanic region outside of the upwelling season (Bécognée *et al.*, 2009).

Most of *S. pilchardus* and *E. encrasicolus* larvae seem to return to the African shelf throughout the system formed by the Cape Juby-Cape Bojador filaments and the trapped cyclonic eddy. This is supported by the relatively important larval concentrations recorded in the periphery of the trapped cyclonic eddy, of *S. pilchardus* (3447 larvae 10 m^{-2}) in August 1993 (Fig. 1b and c) and of *E. encrasicolus* (1230 larvae 10 m^{-2}) in August 1999 (Fig. 2a and c). In both cases, these may represent a parcel of upwelled water with their load of larvae that was completing a circuit of the cyclonic eddy, estimated in 7 days (Barton *et al.*, 1998). In this way, these species would avoid the negative effect of the offshore transport of their offspring. However also, some larvae of *S. pilchardus* and probably of *E. encrasicolus* are transported by upwelling filaments to the Gran Canaria Island coast (Bécognée *et al.*, 2006; Moyano *et al.*, 2009). Besides, upwelling filaments on interacting with eddies shed from the islands, can transfer part of their load of larvae to them. As also these eddies interact between them, the African neritic larvae may be spread throughout the whole archipelago. This could have been the mechanism through which *E. encrasicolus* larvae reached the westernmost islands of the archipelago to produce the 1999's *E. encrasicolus* population outburst.

An interesting feature of the LFC in summer is that in August 1993 it was dominated by *S. pilchardus* (Rodríguez *et al.*, 1999) while in August 1999 it was dominated by *E. encrasicolus* (Rodriguez *et al.*, 2004). The dominance of the summer LFC either by *S. pilchardus* or *E. encrasicolus* seems to be related with the sea surface temperature in the African upwelling region. Lower temperatures would favour *S. pilchardus* spawning while higher temperatures would favour *E. encrasicolus* spawning. Thus, in August 1993, the average temperature of the surface layer (0-30 m) was of 17.1ºC at the shelf station where *S. pilchardus* spawning was recorded (Fig. 1a). While in August 1999 the average temperature of the surface layer at the station D2 (Fig. 2a) was 18.6ºC. According to Furnestin and Furnestin (1959), the 1993 temperature was in the optimum range (16-18ºC) for *S. pilchardus* spawning, while in August 1999 it was in the optimum range (18-23ºC) for *E. encrasicolus* spawning. Like *Engraulis mordax* in the northeast Pacific Ocean (Brodeur *et al.*, 2008), *E. encrasicolus* in the NW African upwelling region could be and indicator of warm phases while *S. pilchardus* could be an indicator of cold phases. Nevertheless, to relate environmental changes to changes in larval fish community, long ichthyoplankton time series are necessary.

4. Vertical distribution of fish larvae in summer

The distribution of mesozooplankton (Fig. 3a) and larval fish (Fig. 3b) communities of the C-ACTZ during summer were vertically stratified. This is consistent with vertical distributions reported for fish larvae in coastal upwelling and non upwelling regions (e.g., Ahlstrom, 1959; Brewer and Kleppel, 1986; Olivar, 1990; Leis, 1991) and in oceanic waters (e.g., Ahlstrom, 1959; Loeb, 1979; Boehlert *et al.*, 1985; Roepke, 1993). Species populations displayed two main patterns of vertical distribution. Larvae of *S pilchardus* (Fig. 3c), *E. encrasicolus* (Fig. 3d) and of some mesopelagic species, e.g. *C. braueri* (Fig. 5e) showed a relatively shallow distribution. While larvae of other mesopelagic species showed a deeper distribution, similar to that of *Myctophum punctatum* (Fig. 3f). The vertical location in the water column along with the birthplace of the larvae has implications for their horizontal distribution. The relatively shallow distribution of larvae of the African neritic species *S pilchardus* and *E. encrasicolus* places them, as mentioned above, within the Ekman layer and within the coastal upwelled waters of the filaments that transport them into the oceanic region. Besides, larvae of oceanic species with shallow distribution could be washed away by the Ekman layer and upwelling filaments, resulting in horizontal distributions of these larvae as that found during the Hespérides cruise (Fig. 1d). On the other hand, the presence of larvae of *M. punctatum* over the African shelf (Fig. 2d), the only oceanic species caught there, would be related with its spawning behaviour and with the vertical distribution of its larvae. This is an oceanic to slope spawning-species (John, 1986) and the relatively deep distribution of their larvae would place them within the onshore compensation flow associated with coastal upwelling, which would transport them into the shelf. According to Hamann *et al.* (1981), the presence of these larvae in the region of the NW African coastal upwelling is evidence of an onshore transport.

The vertical distribution of *S. pilchardus* and *E. encrasicolus* larvae, although apparently shallow for the region, was deeper and wider than those found for these species in the NE Atlantic (Southward and Barret, 1983; John, 1985; John and Re, 1995), in the NW Mediterranean (Palomera, 1991; Olivar and Sabates, 1997; Olivar *et al.*, 2001) or for *E. encrasicolus* in the Northern Benguela region (Olivar, 1990). Also, related species around the world, e.g

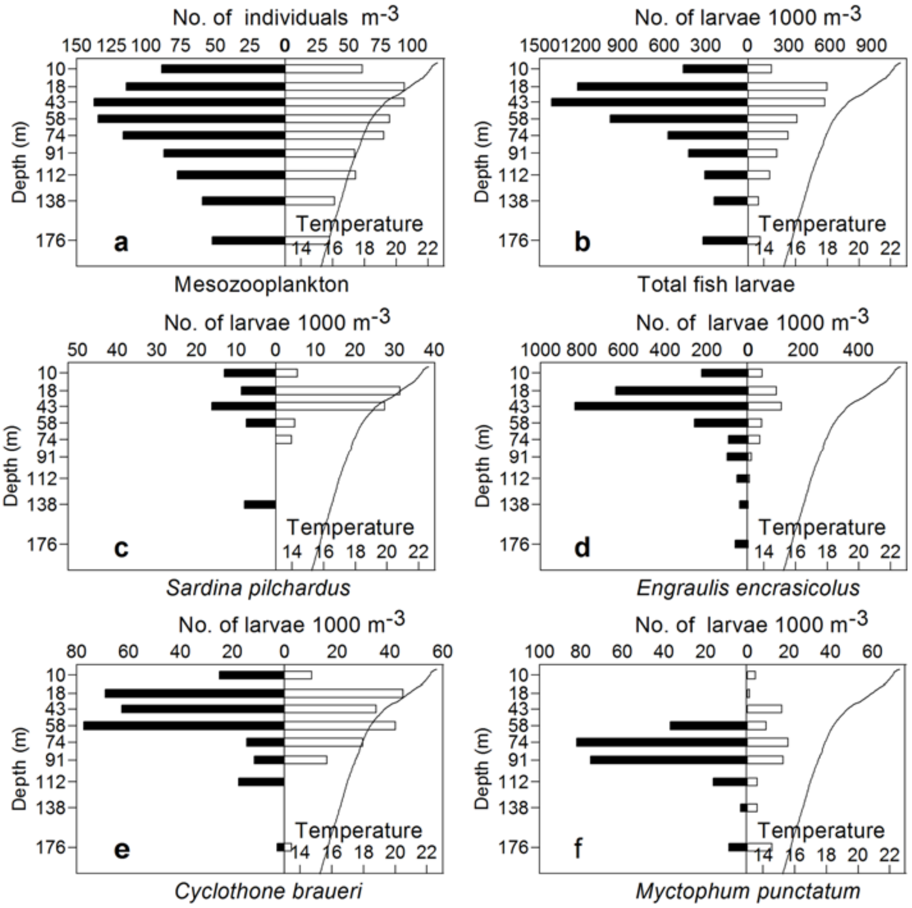


Figure 3. Mean day (open bars)/night (filled bars) vertical concentrations of: (a) mesozooplankton; (b) total fish larvae; (c) *Engraulis encrasicolus*; (d) *Sardina pilchardus*; (e) *Cyclothone braueri*; (f) *Myctophum punctatum* found during the Fax cruise. The mean vertical profile of temperatures recorded at ichthyoplankton stations is overlapped to the vertical distributions of mesozooplankton and fish larvae. Notice different scales of upper X axis. Y axis values indicate the average depth of each sampling stratum.

Sardinops coerulea and *Engraulis mordax* in the California Current (Ahlstrom, 1959; Boehlert *et al.*, 1985; Moser and Pommeranz, 1999), *Sardinops ocellatus* in the Northern Benguela Region (Olivar, 1990) or *Sardinops sagax* and *Engraulis rigens* in the Peru Current (Sameoto, 1982) showed a shallower and a narrower vertical distribution. It must be emphasized that in the cruises included in this study, only a few anchovy larvae were caught over the African shelf, all in the surface layer. The rest of *E. encrasicolus* and all *S. pilchardus* were caught in the oceanic region, far away from the coastal upwelling area. There, the thermocline slope is weak (Fig. 3) compared with the thermocline slope in temperate neritic regions in summer or in subtropical upwelling regions where the above studies were carried out (Rodríguez, 2006). This is in accordance with the vertical distribution reported for *E. ringens* and *S. sagax* larvae in the region of the Peruvian upwelling region, shallow in coastal area and deeper in open waters (Gorbunova *et al.*, 1986). Larvae of Myctophydae species showed similar vertical distributions to those found for these larvae in subtropical or tropical oceanic regions (e.g., Gorbunova, 1973; Loeb, 1979; Boehlert *et al.*, 1992; Roepke, 1993). Nevertheless, these larvae also showed deeper distribution than those reported for larvae of Myctophidae species in the northern Benguela region (Olivar, 1990) or in the upwelling region of the California Current (Ahlstrom, 1959; Auth and Brodeur, 2006). That is to say, different environmental conditions of the water column in the C-ACTZ would account for different vertical distributions of fish larvae found in this region in summer, in relationship with the other main coastal upwelling regions.

Rodriguez *et al.* (2006) made an attempt to investigate the diel vertical migration (DVM) of fish larvae in the C-ACTZ, in summer. Nevertheless, as these authors acknowledge, their study show several limitations. The most outstanding were that it was not specifically designated to study diel vertical migrations and that, apart from the larval fish community and *E. encrasicolus*, the other taxa were in relatively low abundance. The accuracy of the estimation of migration amplitude is related to the abundance of organisms (Irigoien *et al.*, 2004). Thus, estimations for organisms present in low abundance must be treated with caution. Despite of these limitations, we consider it important to give some information about the DVM of fish larvae because it may have important implications for the horizontal distribution of fish larvae in this region of vertical shear.

In the C-ACTZ, in summer, the epipelagic mesozooplankton (Fig. 3a) and the LFC (Fig. 3b) seem to carry out little or no daily vertical migration. Fish larvae generally seem to maintain positions at intermediate depths coinciding with depths of maximum mesozooplankton densities (Fig. 3a and b). Perhaps, feeding conditions there are optimal, and light levels reduce the predation risk. This would account for the significant correlation found between the spatial distributions of fish larvae and mesozooplankton (Rodríguez, 2006). *E. encrasicolus* larvae showed a size-related DVM with the migration of large larvae towards the surface at night. This behaviour has already been reported for this (Palomera, 1991; Olivar *et al.*, 2001) and other anchovy species (Hunter and Sanchez, 1976; Brewer and Kleppel, 1986). Larger anchovy larvae would move to the surface to swallow air and fill their swim bladder in order to save the energy required to maintain a position in the water column during the night (Hunter and Sanchez, 1976). In the absence of a strong physical barrier, as it happens in the C-ACTZ in summer, even these larvae could passively sink during the resting period (Munk *et al.*, 1989; Brodeur and Rugen, 1994; Olivar *et al.*, 2001). This would result in the broader night-time distribution observed for *E. encrasicolus* against the more stratified, light gradient dependent daytime pattern actively maintained by larvae (Heath *et al.*, 1988; Leis, 1991; Ponton and Fortier, 1992).

5. Conclusions

This paper reviews current knowledge on the LFC of the C-ACTZ. While the oceanography has been widely studied during the last two decades, there is little information on the ichthyoplankton biology and ecology of the region. Nevertheless, we show that there is a strong relationship between mesoscale oceanographic processes and the LFC. Several mesoscale processes, such as upwelling filaments, influence the composition, structure, abundance and the spatial distribution of the LFC in the region. They are responsible for the relatively high larval fish abundance found in summer, in the oceanic region and also for the contribution of African neritic larvae to the neritic fish populations of the Canary Islands. Recent observations (S. Hernández-León, unpub.) suggest that this contribution is especially important for populations of small pelagic coastal fishes (e.g. *S. pilchardus* and *E. encrasicolus*). So, in the context of global change, more effort should be devoted to studying the ichthyoplankton of the region, to understand the potential influence of global warming on the recruitment success of neritic fish populations of the NW Africa and of the Canary Islands.

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CHAPTER II

LARVAL FISH ABUNDANCE AND DISTRIBUTION DURING THE LATE WINTER BLOOM OFF GRAN CANARIA ISLAND, CANARY ISLANDS

M. Moyano, J.M. Rodríguez and S. Hernández-León (2009) Larval fish abundance and distribution during the late winter bloom off Gran Canaria Island, Canary Islands. *Fisheries Oceanography* 18(1): 51-61.

Abstract

The species composition, distribution and abundance of fish larvae off Gran Canaria (Canary Islands), an oceanic island in the NE Atlantic, were studied from January to August 2005. Weekly samplings were carried out at six stations in the eastern and southern flanks of the island, at the edge of the island shelf, in order to analyze the fluctuations of the planktonic community. The highest chlorophyll a values were recorded in March, coinciding with the lowest values of temperature in the mixed layer, which gave rise to the 'late winter bloom'. Mesozooplankton biomass peaked with only a week-lag to phytoplankton, and its average value (13.5 ± 10.9 SD mg dry weight m^{-3}) was typical for the area. A clear windward-leeward distribution pattern was found for small mesozooplankton and neritic larvae, showing higher values in two stagnation points, upstream and downstream of the island. A total of 128 taxa of fish larvae were identified. Neritic and oceanic larvae appeared in quite similar proportions. Only three families accounted for half of the total larval fish collected: Myctophidae (24.9%), Sparidae (12.7%) and Clupeidae (11.9%). *Sardinella aurita* (8% of total larvae collected) was the most abundant species, appearing during the whole period of study and at each of the six sampled stations. *Sardina pilchardus* larvae were rarely captured but were always encountered with the arrival of NW African upwelling filaments to the island coast, suggesting that these larvae were transported in those mesoscale structures.

Keywords: Canary Islands, clupeoids, fish larvae, mesozooplankton, temporal distribution, upwelling filaments

Introduction

Processes acting during the early life history of fish often determine the success of recruitment, as only a tiny portion of the eggs are able to reach the adult stage. Thus, the study of fish larvae dynamics should be an ordinary tool in fisheries management. Also, these studies are necessary for a broader understanding of fish biology and ecology (Fuiman, 2002). Nevertheless, they are not routinely performed in some areas. This is the case in the waters surrounding the Canary Islands, where the phenological changes in the abundance of eggs and larvae of most fish species are still unknown.

The Canary Islands are located in the NE Atlantic between 27º and 29ºN, very close to the NW African upwelling. They span the transition between the cold and highly productive waters of the coastal upwelling and the oceanic waters of the subtropical gyre (Barton *et al.*, 1998). During most of the year, the water column is characterized by a sharp thermocline that restrains the pumping of nutrients to upper layers. In February–March, this thermocline is eroded by cooling of surface waters, promoting an increase in the primary production and chlorophyll concentration. This period is known as the ‘late winter bloom’, and is considered the most productive season in these waters (De León and Braun, 1973; Braun, 1980; Arístegui *et al.*, 2001). The thermocline starts to be restored in April–May, leading to the normal situation of a surface euphotic zone with reduced inorganic nutrients (Arístegui *et al.*, 2001). Mesozooplankton biomass evolves with a short lag with respect to phytoplankton (Hernández-León *et al.*, 2004).

An abrupt bathymetry characterizes these islands, with a profile that sharply rises from depths of over 2000 m to narrow island shelves and deep inter-island channels, acting as an obstacle to the south-western flow of the Canary Current and the Trade Winds. This introduces a strong variability in the atmospheric and oceanic flows, giving rise to the formation of warm wakes, cyclonic and anti-cyclonic eddies in the lee of the islands, structures which appear to be recurrent all year round (Arístegui *et al.*, 1994; Barton *et al.*, 1998, 2000). This hydrographical circulation pattern around the island has relevant consequences for enrichment, retention and transport of fish eggs and larvae in the region (Rodríguez *et al.*, 2001). These authors proposed a theoretical distribution model that identified two stagnation regions, where neritic ichthyoplankton accumulates: one located upstream of the island and the second one in the warm lee, downstream of the island. Also, higher mesozooplankton biomass values were found in those regions (Hernández-León, 1991; Hernández-León *et al*., 2001). Those findings support the suggestion that local spawning populations might be successfully retained in the vicinity of the nearshore island waters, as previously observed in different oceanic islands (Swearer *et al*., 1999; Cowen *et al*., 2000). However, these retention processes around the island are also influenced by mesoscale activity. Mesoscale eddies might concentrate and retain fish larvae near islands (Sale, 1970), representing a suitable area for their development in the oceanic domain (Lobel and Robinson, 1986, 1988).

The Canaries-African Coastal Transition zone is considered an area of high mesoscale activity due to the interactions among the upwelling system and the Canary Current (Barton *et al*., 1998). Upwelling filaments, cyclonic and anticyclonic eddies are typical mesoscale structures of this region (Hernández-Guerra *et al*., 1993; Rodríguez *et al*., 1999). Filaments produced in the NW African upwelling between Cape Juby and Cape Bojador (Fig. 1) are known to periodically reach the eastern shores of the Canary Islands (La Violette, 1974; Hernández-Guerra *et al*., 1993; Barton *et al*., 1998; Pacheco and Hernández-Guerra, 1999). Their importance lies in their capacity to transport nutrients (Jones *et al*., 1991), phytoplankton (García-Muñoz *et al*., 2004) and zooplankton (Mackas *et al*., 1991; Hernández-León *et al*., 2002). In the case of fish larvae in the Canaries area, Rodríguez *et al*. (1999) identified these recurrent mesoscale features as favourable for retention for the African coastal species, but they may also play an important role in the colonization and refreshment of the Canary Island fish populations (Bécognée *et al*., 2006). These works also indicated that *Sardina pilchardus* and *Engraulis encrasicolus* larvae were good tracers for these mesoscale features. Both species showed maximum abundances in the upper 60 m (Rodríguez *et al*., 2006), the range in depths that encompasses the Ekman layer (John, 1982; Mittelstaedt, 1983) and the bulk of surface waters transported by filaments.

The main goal of this work was to describe for the first time the whole near-shore larval fish assemblage off Gran Canaria Island and its spatial and temporal distribution during an intensive 8-month study. A special effort was made to study the role of clupeoid larvae as tracers of upwelling filaments, also because of the importance of clupeoid populations as a commercial resource in the Canaries Archipielago, mainly for their use as live bait for tuna fishing (Ramos *et al*., 1995).

Materials and Methods

Sampling was carried out from January to August 2005 on board the RV Solana II during daylight hours. Six sampling stations, 10 nautical miles apart and located over the 100 m isobath, were sampled weekly (Fig. 1). Vertical profiles of temperature, salinity and fluorescence were obtained with a CTD SBE25 (Sea-Bird Electronics Inc., Bellevue, WA, USA). Phytoplankton chlorophyll was derived from depth profiles of in situ fluorescence, calibrated with samples collected at 15 m with a Niskin bottle. This chlorophyll *a* was measured fluorometrically in a Turner Design bench fluorometer, previously calibrated with pure chlorophyll a (Sigma-Aldrich Inc., St. Louis, MO, USA; Yentsch and Menzel, 1963). Samples of 500 mL of sea water were filtered through Whatman GFF filters and preserved in liquid nitrogen until their analysis. Pigments were extracted in cold acetone (90%) for 24 h. For the final determination of

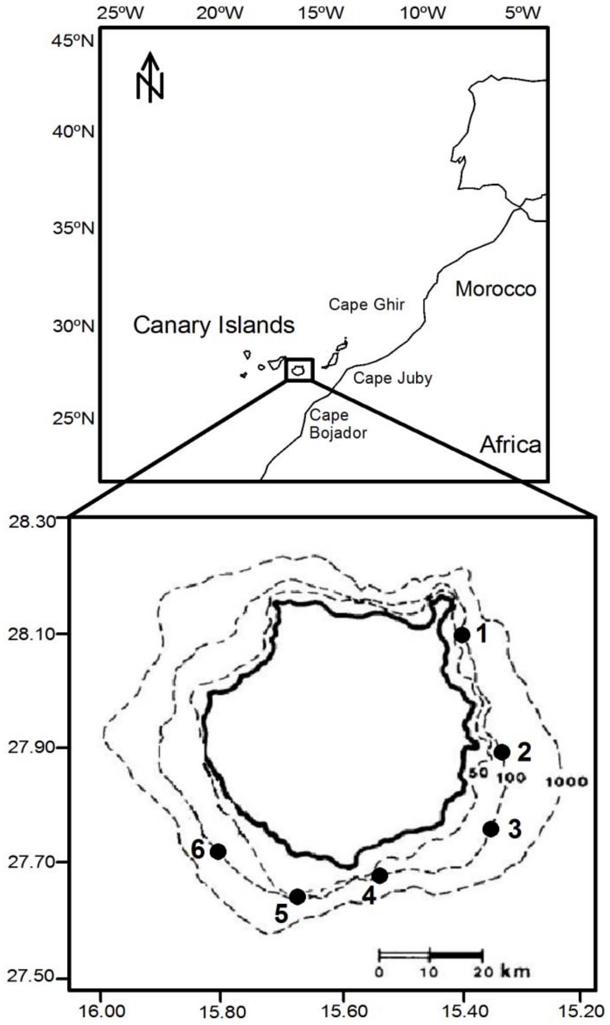

Figure 1. Map of the study area, showing the location of the six sampling stations around Gran Canaria Island, Canary Islands (northeast subtropical Atlantic).

chlorophyll *a*, the acetone extracts were acidified, allowing chlorophyll and phaeopigments to be estimated independently. Satellite Sea Surface Temperature (SST) and chlorophyll Sea-viewing Wide Field-of-view Sensor (SeaWiFS) images were obtained for the whole study period in order to detect filaments shed from the African coastal upwelling. Oblique zooplankton hauls were performed with a Bongo net of 40 cm in diameter, equipped with 200-µm mesh size nets and with a flowmeter (General Oceanics Inc., Miami, FL, USA), to measure the volume of filtered water. The net was towed at two to three knots (2 knots = ~1 m s^{-1}) from a maximum of 90 m up to the surface. One of the samples was fractionated with a 1-mm mesh and both size fractions were used to quantify mesozooplankton biomass as dry weight, following the method of Lovegrove (1966). The other sample was quickly preserved in a 4% solution of sea water and buffered formaline for further taxonomical analyses. Once in the laboratory, all fish larvae were sorted, counted, measured and identified to the lowest taxonomic level possible, using a stereoscopic microscope.

For taxonomical organization, the Greenwood classification was used (CLOFETA, Check-List Of the Fishes of the Eastern Atlantic, Queró *et al*., 1990). However, the high fish diversity (more than 600 described species of adult fishes in the Canaries, according to Brito *et al*., 2002), the high number of undescribed larvae and the absence of knowledge about the spawning period of most fish species in the region complicated this task. After identification, larvae were classified into three categories (Neritic, Oceanic and Other) in relation to the adult behaviour, according to Rodríguez *et al*. (1999). Those species whose adults normally inhabit and reproduce up to 200 m depth over the shelf were considered Neritic. Those inhabiting and reproducing in deeper waters (>200 m depth) were considered Oceanic. The Other group included all the unidentified larvae and those identified to the family level, which included neritic and oceanic species. Differences in larval abundances and mesozooplankton biomass between stations were assessed with the non-parametric Kruskal–Wallis test, using the statistical package STATISTICA 7.0 (Statsoft Inc., Tulsa, OK, USA, 2006).

Results

Temperature and salinity of the mixed layer exhibited the typical seasonal variation around the Canary Islands (17.7–22.9 ºC and 36.5–36.87, respectively).

Temperatures below 19 ºC were recorded in early February, promoting mixing of the water column, and establishing conditions supporting the beginning of the late winter bloom (Fig. 2a). The chlorophyll *a* maximum appeared in mid-March, followed by mesozooplankton biomass (Fig. 2b) and larval fish abundance peaks (Fig. 2c). Mesozooplankton and neritic fish larvae followed a similar trend during the whole period of the bloom, with approximately one peak per month. Average values of mesozooplankton biomass (±SD) were 13.5 (±10.9) mg dry weight·m^{-3}, whereas larval fish mean abundance was 0.59 (±0.46) ind·m^{-3}.

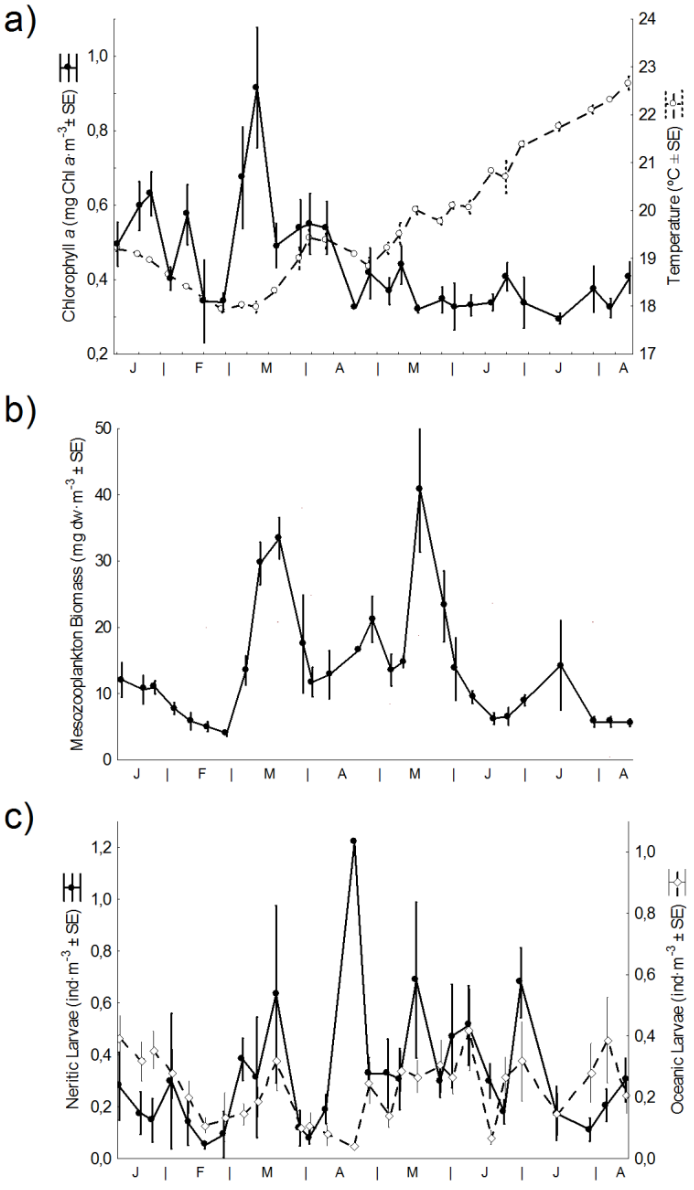

Figure 2. Average values (±SE) of stations 1–6 for each sampling day of **(a)** temperature in the mixed layer (ºC), dotted line, and chlorophyll a (mg Chl a·m^{-3}), solid line; **(b)** mesozooplankton biomass (mg dry weight·m^{-3}); **(c)** neritic (solid line) and oceanic (dotted line) larval fish abundance (no. of individuals·m^{-3}).

Fish eggs were too scarce to determine spawning times or grounds, so this study focused on fish larvae. A total of 1911 larvae belonging to 46 different families was caught during the study (Table 1). The identification was carried out to the species level in two categories: (i) those whose genus and species were distinguished, and (ii) those whose genus was recognized and followed by sp. or sp. 'plus a number' in order to differentiate species. Fish larvae classified to the family level are shown as 'Unidentified spp' included in their respective family.

Neritic and Oceanic larvae were caught in almost the same percentages (44.9% and 42.7%, respectively), whereas the Other group contributed 12.4% to the total catch. Oceanic larvae were dominated by myctophids and gonostomatids (26.6% and 7.3% of the total larval catches, respectively), the former being by far the most diverse family. They showed relatively high abundances during the whole study period (Fig. 3a). Those families, along with photichthids, accounted for almost 90% of the Oceanic larvae. Neritic larvae were dominated by sparid, clupeoid and gobid larvae (12.7%, 11.9% and 8.7%, respectively). Sparids displayed a similar temporal pattern as Myctophids, whereas Gobids exhibited a clear maximum in mid-April (Fig. 3b).

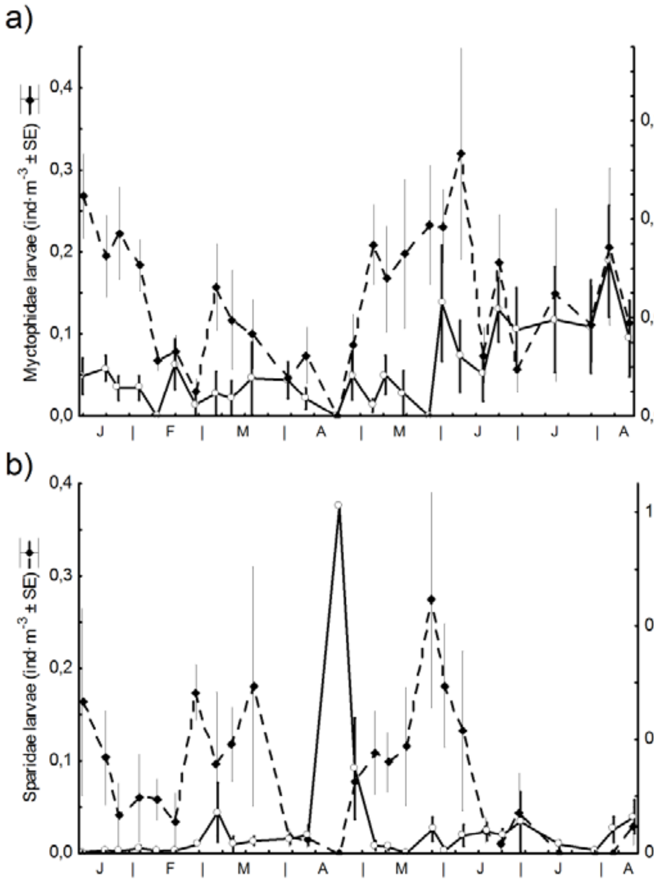

Figure 3. Time-course evolution of average larval abundance (no. of individuals m^{-3}) of **(a)** Myctophidae (dotted line) and Gonostomatidae larvae (solid line); **(b)** Sparidae (dotted line) and Gobiidae larvae (solid line) average larval abundance.

In relation to species, *Sardinella aurita* was the most abundant (8.1% of total larval catches), followed by *Boops boops* (6.6%), *Cyclothone braueri* (6.2%) and Pomacentridae sp. 2 (3.3%). Most of the larvae from the genus Lampanyctus were not identified to species level, but were also relatively abundant, accounting for 6.5% of the total larval catches. Identification of sparids and gobids was not detailed because these families have a large number of species, with long and overlapping spawning periods, and only quite small larvae were captured. Despite this, larvae of a few sparid species of commercial interest were identified, such as *Pagrus pagrus* and *Pagellus bogaraveo*. Some larvae of the genus *Diplodus* were also caught, but their identification to species level was not possible.

The temporal evolution of clupeoid species (Fig. 4) resembled that of sparids and myctophids, with three marked peaks of abundance. Four different species of this taxon were identified: *S. aurita* (88.0% of total clupeoid larvae), *S. pilchardus* (2.1%), *E. encrasicolus* (1.7%) and *Sardinella maderensis* (0.4%). Unidentified clupeoids represented 7.6% of total clupeoid catches. S. aurita appeared during the whole period of study, with maximum values in March and May–June. *S. aurita* larval sizes ranged

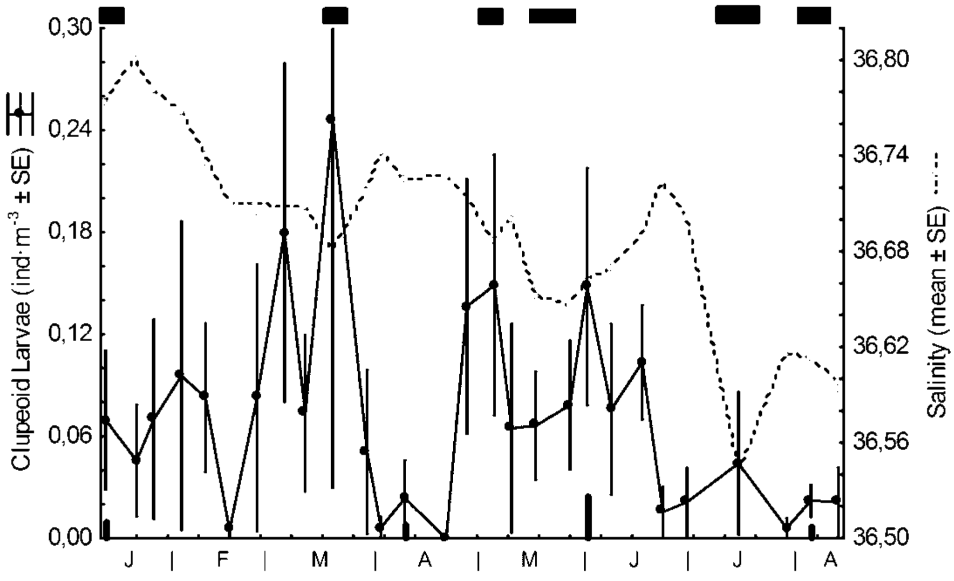

Figure 4. Time-course distribution of salinity in the mixed layer (dotted line) and average abundance (no. of individuals·m^{-3}) of total clupeoid abundance (solid line) and *Sardina pilchardus* larval catches (solid bars). Horizontal bars indicate the periods when an upwelling filament reached Gran Canaria coast. Note the relationship of low salinity values, filament influence and pilchard larvae appearance.

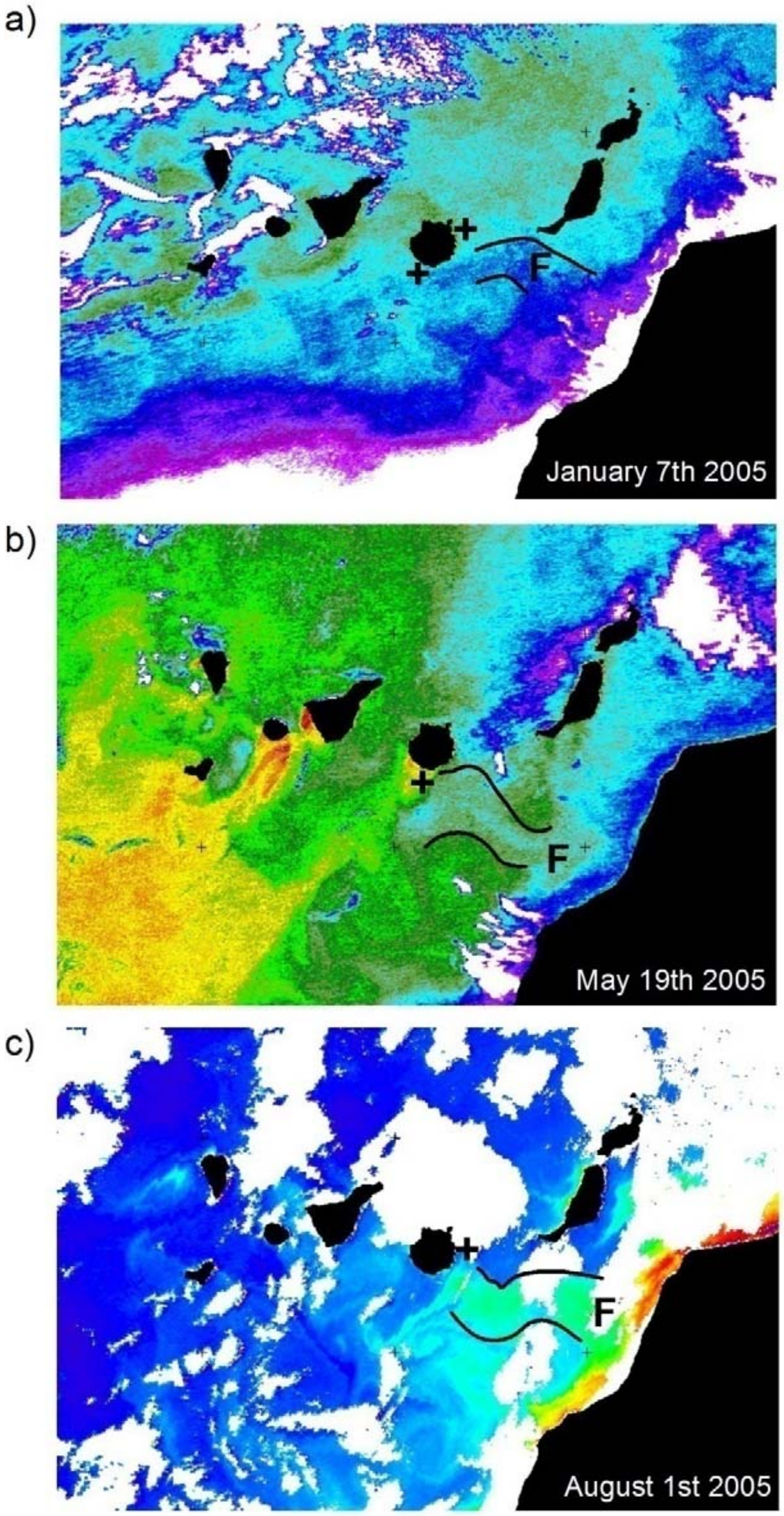

Figure 5. Sea surface temperature distribution from remote sensing from (a) January 7, 2005, (b) May 19, 2005. (c) Chlorophyll distribution from SeaWiFS sensor from August 1, 2005. Filaments are limited with lines and labeled (F) and the stations in which sardine larvae were found are marked with a cross (+). Notice how the filaments shed from the northwest African upwelling reach the eastern coast of Gran Canaria island, coinciding with the *Sardina pilchardus* larvae.

Table 1. Taxonomic list of larval fish species captured. Their origin, based on the adult spawning habitat (N, neritic; Oc, oceanic; O, other) and their percentage in relation to the total catch of larvae are also shown.

Species	Origin	%
Family NETTASTOMATIDAE		
Nettastoma melanurum (Rafinesque, 1810)	N	0.16
Anguiliforme sp1	O	0.21
Unidentified spp	O	0.31
Family CLUPEIDAE		
Sardina pilchardus (Walbaum, 1972)	N	0.26
Sardinella aurita (Valenciennes, 1847)	N	8.10
Sardinella maderensis (Lowe, 1838)	N	0.05
Unidentified spp	N	3.50
Family ENGRAULIDAE		
Engraulis encrasicolus (Linnaeus, 1758)	N	0.21
Family BATHYLAGIDAE		
Bathylagidae sp1	Oc	0.47
Family GONOSTOMATIDAE		
Cyclothone acclinidens (Garman, 1899)	Oc	0.16
Cyclothone alba? (Brauer, 1906)	Oc	0.10
Cyclothone braueri (Jespersen & Tåning, 1926)	Oc	6.22
Cyclothone pseudopalida (Mukhacheva, 1964)	Oc	0.10
Gonostoma atlanticus (Norman, 1930)	Oc	0.10
Gonostoma sp	Oc	0.52
Gonostomatidae sp1	Oc	0.05
Unidentified spp	Oc	0.05
Family STERNOPTYCHIDAE		
Argyropelecus hemigymnus (Cocco,1829)	Oc	0.31
Family PHOTICHTHYIDAE		
Ichthyococcus ovatus (Cocco, 1938)	Oc	0.16
Vinciguerria attenuata (Cocco, 1938)	Oc	0.16
Vinciguerria nimbaria (Jordan & Williams, 1896)	Oc	0.21
Vinciguerria poweriae (Cocco, 1938)	Oc	0.94
Vinciguerria spp	Oc	1.78
Family CHAULODONTIDAE		
Chauliodus sp	Oc	0.16
Unidentified spp	Oc	0.05
Family STOMIIDAE		
Photonectes sp	Oc	0.10
Stomias boa (Risso, 1810)	Oc	0.05
Stomias sp1	Oc	0.26
Unidentified spp	Oc	0.10
Family SYNODONTIDAE		
Synodontidae sp1	N	0.21
Unidentified spp	N	0.31
Family MYCTOPHIDAE		
Benthosema suborbitale (Gilbert, 1913)	Oc	0.84
Ceratoscopelus maderensis (Lowe, 1839)	Oc	1.93
Ceratoscopelus warmingi (Lütken, 1892)	Oc	1.78
Diaphus holti (Tåning, 1918)	Oc	0.05
Diaphus rafinesquii (Cocco, 1838)	Oc	0.05
Diogenichthys atlanticus (Tåning, 1918)	Oc	1.62
Hygophum benoiti (Cocco, 1838)	Oc	0.63
Hygophum hygomii (Lütken, 1892)	Oc	0.16
Hygophum macrochir (Günther, 1864)	Oc	0.73
Hygophum reinhardtii (Lütken, 1892)	Oc	0.47
Hygophum taaningi (Bekker, 1965)	Oc	0.05
Hygophum sp	Oc	0.10
Lampadena sp	Oc	0.05
Lampanyctus pusillus (Johnson, 1890)	Oc	0.05
Lampanyctus sp1	Oc	0.10
Lampanyctus sp2	Oc	0.16
Lampanyctus spp	Oc	6.58
Lobianchia dofleini (Zugmayer, 1911)	Oc	1.10
Lobianchia gemellarii (Cocco, 1938)	Oc	0.94
Lobianchia sp	Oc	0.42
Myctophidae sp2	Oc	1.99
Myctophidae sp3	Oc	0.10
Myctophidae sp4	Oc	0.42
Myctophum nitidulum (Garman, 1899)	Oc	0.47
Myctophum selenops (Tåning, 1928)	Oc	0.10
Notolychnus valdiviae (Brauer, 1904)	Oc	0.47
Notoscopelus resplendens (Richardson, 1845)	Oc	0.31
Notoscopelus sp	Oc	1.62
Symbolophorus sp	Oc	0.31
Unidentified spp	Oc	2.98
Family SCOPELARCHIDAE		
Benthalbella infans (Zugmayer, 1911)	Oc	0.16
Family EVERMANELLIDAE		
Unidentified spp.	Oc	0.16
Family PARALEPIDAE		
Lestidiops jayakari pseudosphyraenoides (Ege, 1918)	Oc	0.05
Paralepis coregonoides (Risso, 1920)	Oc	0.05
Sudis hyalina (Rafinesque, 1810)	Oc	0.10
Unidentified spp	Oc	0.10
Family SCOMBERESOCIDAE		
Unidentified spp	Oc	0.05

Table 1 (cont.)

Species	Origin	%	Species	Origin	%
Family MACRORHAMPHOSIDAE			Family TRACHINIDAE		
Macroramphosus scolopax	Oc	0.78	Trachinus draco (Linné, 1758)	N	0.16
(Linnaeus, 1758)			Trachinus sp	N	0.31
Family GADIDAE			Family GEMPYLIDAE		
Phycis sp	Oc	0.05	Diplospinus multistriatus (Maul,	Oc	0.63
Unidentified spp	Oc	0.05	1948)		
Family MELAMPHAIDAE			Gempylus serpens (Cuvier, 1829)	Oc	0.10
Melamphaes simus (Ebeling, 1962)	Oc	0.05	Unidentified spp	Oc	0.21
Family CAPROIDAE			Family TRICHIURIDAE		
Capros aper (Linnaeus, 1758)	Oc	0.10	Benthodesmus elongatus(Clarke,	Oc	0.05
Family SERRANIDAE			1879)		
Anthias anthias (Linnaeus, 1758)	N	1.83	Lepidopus caudatus (Euphrasen,	Oc	0.10
Epinephelinae	N	0.05	1788)		
Serranidae sp1	N	0.05	Family SCOMBRIDAE		
Serranus cabrilla (Linnaeus, 1758)	N	0.16	Sarda sarda (Bloch, 1793)	Oc	0.05
Unidentified spp	N	0.63	Scomber colias (Houttuyn, 1792)	Oc	0.05
Family CARANGIDAE			Family GOBIIDAE		
Trachurus picturatus (Bowdich,	Oc	0.05	Lebetus guilletii (Le Danois,	N	0.26
1825)			1913)		
Family CORYPHAENIDAE			Lebetus scorpiodes (Collet, 1874)	N	0.21
Coryphaena hippurus (Linnaeus,	Oc	0.05	Unidentified spp	N	8.20
1758)			Family BLENNIDAE		
Family MULLIDAE			Ophioblennius atlanticus	N	0.37
Mullus barbatus (Linnaeus, 1758)	N	0.10	(Valenciennes, 1836)		
Mullus surmuletus (Linnaeus,	N	0.21	Blennidae sp1	N	0.05
1758)			Family OPHIDIIDAE		
Family BRAMIDAE			Unidentified spp	N	0.05
Unidentified spp	Oc	0.47	Family NOMEIDAE		
Family SPARIDAE			Nomeidae sp1	Oc	0.31
Boops boops (Linnaeus, 1758)	N	6.58	Family TETRAGONURIDAE		
Diplodus spp	N	2.46	Tetragonurus atlanticus (Lowe,	Oc	0.05
Oblada melanura (Linnaeus, 1758)	N	1.52	1839)		
Diplodus spp	N	2.46	Family SPHYRAENIDAE		
Oblada melanura (Linnaeus, 1758)	N	1.52	Sphyraena sp	N	0.05
Pagellus acarne? (Risso, 1826)	N	0.26	Family SCORPAENIDAE		
Pagellus bogaraveo (Brünnich,	N	0.94	Scorpaena sp	O	0.05
1768)			Unidentified spp	O	0.42
Pagrus pagrus (Linnaeus, 1758)	N	0.37	Family TRIGLIDAE		
Unidentified spp	N	0.63	Unidentified spp	O	0.16
Family CENTRACANTHIDAE			Family BOTHIDAE		
Unidentified spp	Oc	0.05	Arnoglossus imperialis	N	0.05
Family LABRIDAE			(Rafinesque, 1819)		
Coris julis (Linnaeus, 1758)	N	0.52	Arnoglossus thori (Kyle, 1913)	N	0.05
Sparisoma cretense (Linnaeus,	N	0.05	Arnoglossus sp	N	0.21
1758)			Bothus podas (Delaroche, 1809)	N	0.21
Symphodus sp	N	0.10	Unidentified spp	N	0.05
Thalassoma pavo (Linnaeus, 1758)	N	0.05	Family SCOPHTHALMIDAE		
Unidentified spp	N	0.31	Lepidorhombus boscii? (Risso,	N	0.05
Family POMACENTRIDAE			1810)		
Pomacentridae sp1	N	1.04	Family TETRAODONTIDAE		
Pomacentridae sp2	N	3.29	Unidentified spp	N	0.4
Unidentified spp	N	0.0			
Family CHIASMODONTIDAE					
Chiasmodontidae niger (Johnson,	Oc	0.05			
1890)					

from 2.6 to 18.2 mm. However, *S. pilchardus* larvae were caught only at four events: January 11, April 8, May 31 and August 8 (Fig. 4), with sizes ranging between 5.5 and 13.4 mm. As revealed from remote sensing (Fig. 5), upwelling filaments might be interacting with the eastern shores of Gran Canaria during three of those events. In the case of April 8, the high cloud density precluded the usefulness of the satellite information. The presence of those filaments in the island waters was also reflected in the low salinities encountered in the mixed surface layer (Fig. 4), especially for the May and August events. On the other hand, *E. encrasicolus* appeared in the samples only three times, on May 26, August 4 and 12. Their sizes varied from 6.4 to 12.2 mm and their presence seemed to coincide with that of upwelling filaments. However, anchovy eggs appeared frequently during May and June (not shown).

Horizontal distributions of neritic fish larvae around the island exhibited a clear north–south pattern, with higher abundances windward (station 1) and leeward (stations 4, 5) (Fig. 6a). The abundance of larvae was standardized (the maximum value of abundance at the six stations on each sampling event was converted to 100%) in order

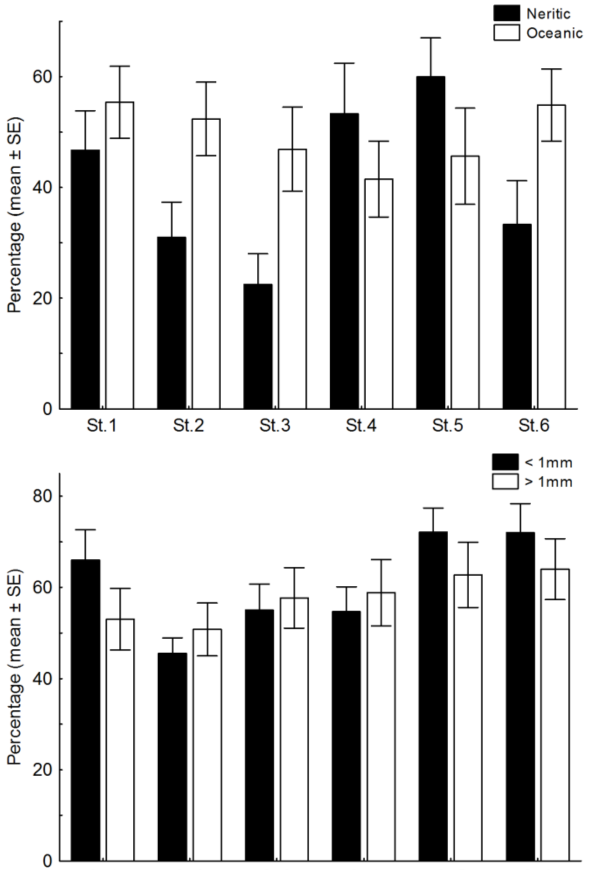

Figure 6. Average percentage of the abundance (no. of individuals m)3) and standard error (SE) of (a) total fish larvae in the six stations sampled: neritic (black bars) and oceanic larvae (white bars); (b) mesozooplankton biomass (mg dry weight m)3): lower (black bars) and higher (white bars) of 1000-lm size fraction. Note the north⁄south distribution of neritic larvae and smaller size fractions of mesozooplankton.

to compare the spatial distribution of catches among the different seasons. Average values showed significant differences for neritic larvae (K–W ANOVA, $P < 0.05$) but not for oceanic larvae (K–W ANOVA, $P > 0.05$). Mesozooplankton biomass also followed this north–south distribution pattern, with higher values at stations 1, 5 and 6 (Fig. 6b). Only the abundance of the size fraction <1 mm significantly differed among stations (K–W ANOVA, $P < 0.05$). Myctophids were the most abundant family at every station, displaying slight differences in abundance between the collection sites (K–W ANOVA, $P > 0.05$) (Fig. 7), as did photichids and gonostomatids. However, the three families tended to exhibit higher values in stations 2 and 3. On the other hand, average values of abundance for other representative neritic families (e.g., sparids, clupeids) fluctuated among stations, being less abundant in those two stations. Only for gobids was this trend was significant (K–W ANOVA, $P < 0.05$). At these eastern stations, the Canary Current flow is intensified and the conditions for these unspecialized larvae are unsuitable.

Discussion

The temporal evolution of phytoplankton and zooplankton followed the pattern of the typical late winter bloom in subtropical waters (Fig. 2). The thermocline was eroded due to the sea surface temperature cooling in winter, promoting an increase in primary production and chlorophyll *a* concentration in February–March. Zooplankton exhibited a lag of only 1 week with phytoplankton, and its biomass split its maximum values into three peaks, showing the characteristic pattern in coastal and oceanic waters of this region (Arístegui *et al*., 2001; Hernández-León *et al*., 2004). This trend led the former authors to propose that phytoplankton biomass was controlled by grazing during part of the productive cycle. However, Hernández-León *et al*. (2004) went a bit further and suggested that this pattern could be the result of the interplay of resource and consumer controls. The increase in primary production due to mixing and nutrient enrichment is followed by the consumer control exerted by diel vertical migrants and their lunar linked behaviour. Fish larval abundance seemed to follow a similar pattern as zooplankton during the late winter bloom. Neritic species were mainly responsible for the abundance peaks, whereas abundance of oceanic larvae was more constant over time. The larval distribution pattern around the island agrees with previous works in oceanic islands (Miller, 1979; Leis, 1986) and with the retention model described in Rodríguez *et al*. (2001). Two retention areas up- and downstream of the island will allow neritic larvae to avoid the flow that would sweep them offshore. Both areas showed a community dominated by sparids, clupeids and gobies. On the other hand, these families were less abundant in the eastern flank of the island, leading to a larval assemblage in which mesopelagic species, such as myctophids and gonostomatids, prevailed. Also in this flank, typically oceanic species of photichthids and gempylids constituted an important percentage of total collected larvae (Fig. 7).

Taxonomic analyses revealed a high diversity of fish larvae, reflected in the high number of taxa recorded and in their relative low abundance (35 of the 46 families individually contributed <1% of the total larvae). This is characteristic of subtropical waters (Longhurst and Pauly, 1987). The fact that sampling was done during daylight

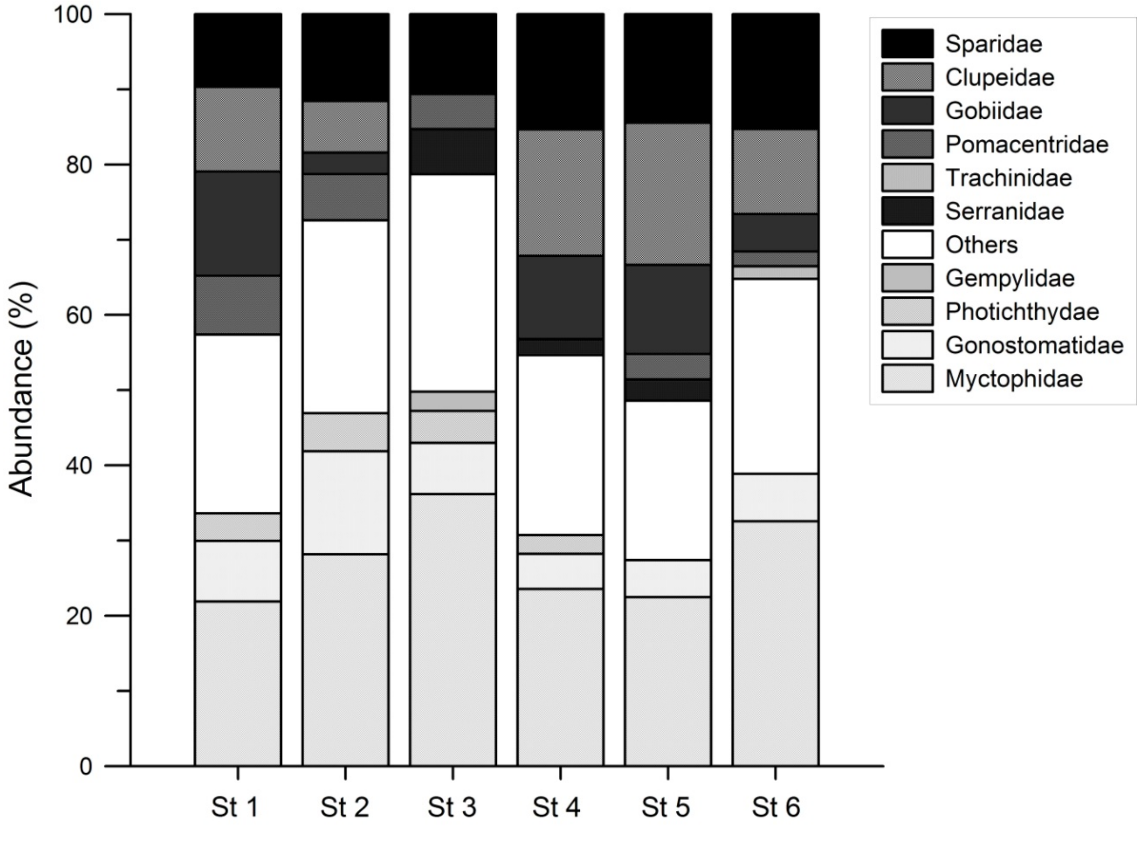

Figure 7. Percent contribution to each sampling station´s total abundance of the top 10 families of collected larvae.

may have influenced larval densities, as Rodríguez *et al*. (2006) found lower abundances during day tows compared to night tows in these waters. However, in that study there were no significant diel vertical migrations (DVM) by epipelagic mesozooplankton or total fish larvae. Only a few species displayed significant DVM (e.g., *S. pilchardus* was more abundant in surface waters during daylight), but its opposing pattern resulted in no net DVM for the larval population. Therefore, the present study could be considered a good representation of the larval fish community in the region.

The high contribution of oceanic species to larval catches is easily explained by the bathymetric and hydrographic conditions around oceanic islands. Myctophids, gonostomatids and photichthids represented the bulk of oceanic species and more than one third of total captured larvae. This contribution is lower than that reported in other studies conducted in the area (Rodríguez *et al*., 1999, 2000; Rodríguez, 2000), probably due to a better representation of oceanic stations in those studies that focused on a broader study area. The most frequent myctophid was the *Lampanyctus* species, and the most frequently captured gonostomatid was *Cyclothone braueri*. Adults of the latter species were observed to be quite abundant around the eastern islands of the Archipielago (Bordes *et al*., 1999). In fact, the genus *Cyclothone* is considered to be one of the most abundant vertebrates on Earth (Richards, 2006) and generally one species in the genus dominates larval assemblages in tropical and subtropical regions (Loeb, 1980).

Neritic larvae were dominated by sparid, clupeoid and gobid species. The first two are both ecologically and economically important to the region. The abundance of clupeoids, sparids and myctophids shared a similar temporal pattern and suggested an inverse relationship with salinity (Figs 3 and 4). As this is the first study to analyse the nearshore larval community, higher abundances of neritic families were recorded compared to previous works in the area (Rodríguez *et al*., 1999; Rodríguez, 2000).

Clupeoids were target species in the present work, due to their commercial importance around the islands and the suggested transport within NW African upwelling filaments. *S. aurita* was the most abundant clupeoid, appearing throughout the study period. Therefore, this species spawns throughout the year in Gran Canaria, as already proposed by Bécognée *et al*. (2006). In Senegalese and Mauritanian waters, *S.*

aurita also spawns throughout the year, with higher activity from June to September (Boely *et al*., 1982). On the other hand, on the Moroccan coast, reproduction occurs only from June to August (Ettahiri *et al*., 2003). The latter authors established the thermal window for *S. aurita* spawning from 18 to 21ºC off the NW African coast.

However, *S. pilchardus* larvae were caught only four times during the study period. Previous studies (Santana, 1979; Méndez-Villamil *et al*., 1997) reported that this species reproduces from December to April off Gran Canaria, whereas on the Moroccan coast it reproduces all year round (Furnestin and Furnestin, 1959; Ettahiri *et al*., 2003). The latter authors established a spawning thermal range for pilchard of 16.0–19.5_C in the upwelling area. Consequently, the presence of pilchard larvae in Gran Canaria during August, when surface temperature was above 22ºC, clearly indicates that these larvae were advected from elsewhere. In addition, biometric studies of *S. pilchardus* adults carried out in Gran Canaria during 2005 and 2006 only found immature individuals (I. Herrera, *pers. comm*.), on the basis of which these authors suggested that this species might not be reproducing around the islands. Considering this hypothesis and the coincidence of the arrival of upwelling filaments towards the island with the presence of *S. pilchardus* during this study, we wonder whether this larval drift from the African coasts might be the only source of sardine to Gran Canaria Island or just a recurrent contribution. Further research on this topic is needed in order to assess the real status of the sardine population of Gran Canaria.

E. encrasicolus appeared only three times during May and August, also coinciding with filament events. Their spawning period in the Canary Islands is not well documented, but eggs were found in late spring and early summer during this study. However, in the NW African coast, they are known to spawn throughout the year (Furnestin and Furnestin, 1959; Ettahiri, 1996). The latter authors found a spawning thermal window for this species from 16.6 to 21ºC off the Moroccan coast, which would be consistent with the temperatures recorded off Gran Canaria during May, June and July.

In summary, we have evaluated the time-course of composition and abundance of the larval fish assemblage around Gran Canaria Island during the late winter bloom. Neritic families mainly represented by sparids, clupeids and gobies dominate the larval community of two retention areas located up- and downstream of the island. These regions also recorded higher values of small mesozooplankton. The match between the abundance of clupeoid larval and the decrease in salinity suggest that transport of larval fish within upwelling filaments from NW Africa to the islands may be a recurrent feature. The importance of those contributions to the Canaries local clupeoid population, especially in the case of the sardine, needs further evaluation.

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CHAPTER III

TEMPORAL AND ALONG-SHELF DISTRIBUTION OF THE LARVAL FISH ASSEMBLAGE OFF GRAN CANARIA, CANARY ISLANDS

M. Moyano and S. Hernández-León. Temporal and along-shelf distribution of the larval fish assemblage off Gran Canaria, Canary Islands. *Submitted to Scientia Marina (Larval Fish Conference 2008 Proceedings)*

Abstract

Temporal and spatial variations of the larval fish community off the island of Gran Canaria (Canary Islands) were studied in weekly surveys from October 2005 to June 2006. A total of 156 taxa, belonging to 51 families and 15 orders, were identified. Myctophidae was by far the most abundant family (30%), followed by Sparidae (11%), Clupeidae (9%) and Gonostomatidae (7%). As expected for an oceanic island, neritic and oceanic taxa contributed in similar proportions. Leeward and windward retention areas were found for total egg and neritic larval abundance. However, seasonality showed a stronger influence on the annual larval assemblage than sampling site, the latter non-significant on a long time scale. Results suggest the presence of two seasonal larval assemblages corresponding to the two main characteristic periods of the water column in these waters: mixing (winter) and stratification (summer). In addition, a significant relationship was recorded between lunar illumination and small mesozooplankton biomass, suggesting that it may be extended to certain neritic families. The most abundant neritic larvae (Sparidae) showed this lunar pattern, partially supporting a recent hypothesis about the effect of lunar illumination on larval fish survival and development in subtropical waters.

Keywords: ichthyoplankton, larval assemblages, mesozooplankton, seasonal variation, lunar illumination, Canary Islands.

Introduction

In an attempt to understand population dynamics of marine fishes, studies have historically focused on the growth and survivorship of their early life stages (Hjort, 1914; Houde, 1987; 2008), as it is during these pre-recruitment stages that the success of a year class is determined. In the particular environment of oceanic islands, fish larvae from local populations need to avoid advection. Physical retention (Boehlert *et al*, 1992; Cowen and Castro, 1994) and larval behaviour (Paris and Cowen, 2004; Leis, 2007) are involved in the maintenance of larval fish populations close to shore, a phenomenon known as "conservation" (Leis, 1982). Moreover, self-recruitment, dependent upon larval retention, is considered to be the main factor sustaining local fish populations (Jones *et al.*, 1999; Swearer *et al.*, 2002). Nevertheless, in certain areas larval inputs from the outside may also be necessary to maintain those populations (Cowen *et al.*, 2006).

Gran Canaria is one of the major islands of the Canary Archipelago, located in the NE Atlantic at latitude 28ºN. The proximity of this archipelago to the NW African coastal upwelling determines its unique environmental conditions. The interaction between the Canary Current flowing through the islands, the coastal upwelling and Trade Winds creates an area of high mesoscale activity (Barton *et al.*, 1998). Thus, warm wakes and eddies are generated south of the Islands (Arístegui *et al.*, 1994; Sangrá *et al.*, 2007), and upwelling filaments frequently reach the shores of the easternmost islands of the archipelago (La Violette, 1974; Pacheco and Hernández-Guerra, 1999). The influence of these mesoscale oceanographic structures on the ichthyoplankton off Gran Canaria Island was first described by Rodríguez *et al*. (2001). These authors identified two retention areas for eggs and neritic larvae: 1) upstream (north-northeast) where the weak inflowing Canary Current separates as it impinges on the island; 2) downstream (south-southwest) where a warm lee is generated. High values of mesozooplankton biomass have also been recorded in this warm lee (Rodríguez *et al.*, 2001; Hernández-León *et al.*, 2004).

Despite the higher productivity found in the warm lee and the frequent influence of upwelling filaments, the Canary waters are typically oligotrophic (De León and Braun, 1973; Braun, 1980). During most of the year, the presence of a seasonal thermocline restrains the vertical flux of nutrients up to the surface, limiting phytoplankton growth (Arístegui *et al*., 2001). This thermocline is eroded during winter, due to surface cooling, causing the mixed layer to reach its maximum depth (Barton *et al*., 1998). During this short mixing period, phytoplankton can grow faster and bloom, the *late winter bloom* of subtropical regions (De León and Braun, 1973; Braun, 1980). Mesozooplankton doubles its biomass during this late winter bloom (Hernández-León 1988; Hernández-León *et al*., 2004). However, the influence of these seasonal variations on the larval fish assemblage off the Canary Islands is still unknown.

Few studies have dealt with the taxonomic composition of the whole larval fish community in the area (Rodríguez, 2000; Rodríguez *et al*., 1999, 2001). Besides, most of these studies consisted of short-time surveys and their sampling stations were either located in the oceanic region or near the coastal upwelling. Only Bécognée *et al.* (2006) carried out an annual study in shallow waters off Gran Canaria, but their study only focused on clupeoid and scombrid larvae. Therefore, the main goal of this work was to analyze the temporal and horizontal variations of the ichthyoplankton distribution and composition off Gran Canaria. In addition, the interactions between the ichthyoplankton and the bio-physical environment were studied. The use of these data to determining species spawning periods and grounds were examined.

Material and methods

Weekly sampling was carried out from October 2005 to June 2006 during daylight hours, on board the R.V Solana II, at the eastern and southern flanks of Gran Canaria (Fig. 1). Five sampling stations, 10 nautical miles apart, were located over the 100 m isobath. CTD casts were performed to obtain vertical profiles of temperature, salinity and fluorescence using a SBE25 (Sea-Bird Electronics Inc., Bellevue, WA, USA). For data analysis, the depth of the mixed layer (ML) was considered to be 20-30 m. Phytoplankton chlorophyll *a* (Chl *a*) was derived from vertical profiles of in-situ fluorescence, calibrated with samples collected at 15 m with a Niskin bottle. These samples of 500 ml of seawater were filtered through Whatman GFF filters and preserved in liquid nitrogen. Then, chlorophyll *a* concentrations were measured by the flourimetric method (Yentsch and Menzel, 1963).

Plankton samples were taken with oblique Bongo net tows down to 90 m depth and at a speed of about 2-3 knots. Nets were fitted with 200 μm mesh and with a flowmeter (General Oceanics), to measure the volume of filtered water. The first sample was fractionated with a 1000 μm mesh to quantify small (200-1000 μm) and large mesozooplankton (>1000 μm) biomass as dry weight, following the method of Lovegrove (1966). The second sample was quickly preserved in 4% buffered formaline for further taxonomical analyses. Once in the laboratory, all fish larvae were sorted. Larvae were identified to the lowest taxonomic level possible, using a dissecting microscope (Leica MZ 9.5). Fish eggs were sorted from November 2005 to June 2006 but only Clupeidae eggs were identified. Greenwood classification (CLOFETA, Queró *et al.*, 1990) was used for taxonomical organization of fish larvae. And, following Rodriguez *et al.* (1999), these larvae were divided into three categories (Neritic, Oceanic and Other) in relation to adult behaviour.

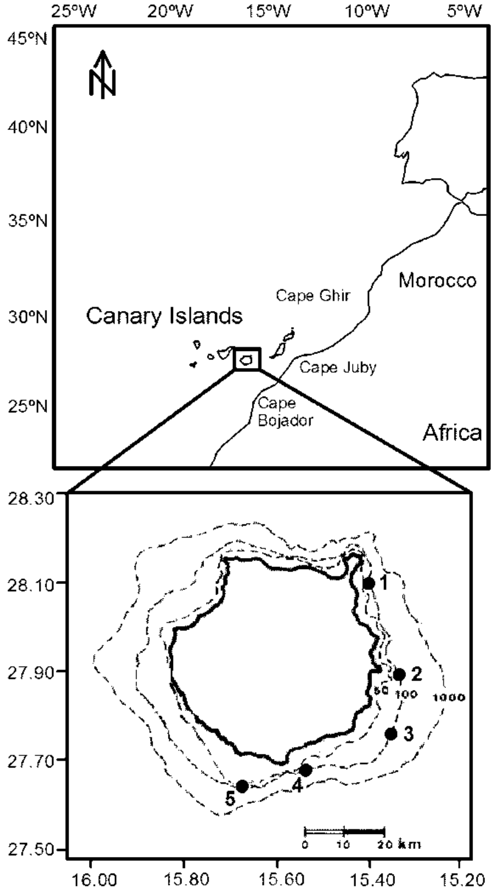

Figure 1. Map of the study area showing the location of the five sampling stations over the Gran Canaria shelf, Canary Islands (Northeast Subtropical Atlantic).

In order to analyze the relationships of environmental variables and larval abundance, Spearman´s rank correlation was carried out. Differences in ichthyoplankton abundance and mesozooplankton biomass among stations and months were analyzed using the non parametric analysis of variance for repeated measures (Friedman test). To assess the variability of the mesozooplankton and larval fish abundance through the lunar cycle, standardization was performed, considering the maximum value in abundance for each complete lunar cycle as 100%. Then, Kruskal Wallis ANOVA (K-W ANOVA) was carried out on those standardized variables to analyze differences among the four lunar phases centred in new, crescent, full and waning moon. Parametric tests were not used because most of the variables did not meet the underlying conditions of normality (Kolmogorov-Smirnov) and homogeneity of variances (Levene´s test). All statistical procedures were performed using the Statistica 7.0 software package (StatSoft Inc. 2006).

In addition, a two-way analysis of similarities (ANOSIM, Primer software, Clarke and Warwick, 2005) was conducted to test for significant differences in the structure of the species composition among months, averaged across sites, and sites, averaged across months. Only species contributing at least 5% to total abundance were considered. Prior to generating the Bray Curtis resemblance matrix to perform the ANOSIM procedure, data were square-root transformed to reduce the weighting of dominant species. Temporal variability was analyzed on a monthly basis to reduce biasing due to the effect of plankton patchiness.

Results

Oceanographic conditions and ichthyoplankton and zooplankton distribution

Environmental variables followed the typical annual cycle in the Canary Island waters (Fig. 2). During October and November, the water column was well stratified with surface temperatures around 23 ºC (Fig. 2a). In December, surface waters cooled, and the mixing period started. In January, when the mixed layer temperatures dropped below 19 ºC (Fig. 3a), nutrients were pumped to the surface, promoting a progressive increase in chlorophyll *a* (Fig. 2, Fig. 3a). After the bloom, in April-May, the thermocline started to reform, leading to a surface euphotic zone depleted of inorganic

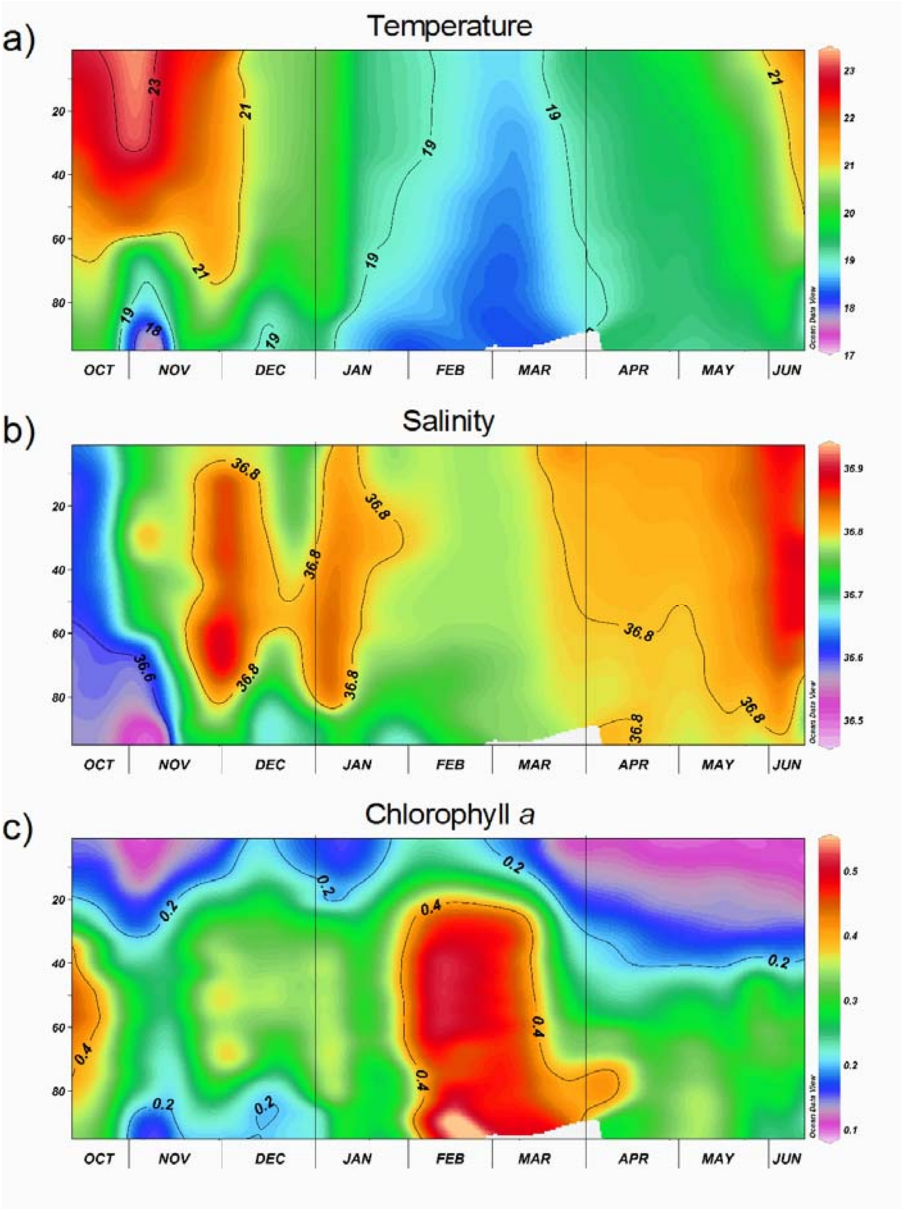

Figure 2. Temporal variation of **a)** temperature (ºC), **b)** salinity and **c)** chlorophyll *a* (mg Chl *a*·m^{-3}) during the sampling period in the warm lee area (station 5).

nutrients. Environmental parameters on the eastern flank (st 2 and 3) were significantly different from those in the island wake (st 4 and 5). Stations located to the east of the island showed lower temperature and salinity values than those to the south (Friedman ANOVA, $p<0.01$, in both cases). Maximum chlorophyll *a* concentrations were measured at the southern stations located in the warm wake.

During the late winter bloom, chlorophyll *a* concentrations peaked twice (Fig. 3a). The highest mesozooplankton biomass was recorded 24 days after the second peak (Fig. 3b). Mean mesozooplankton biomass was 12.3 ± 8.9 SD mg dry weight·m^{-3}. Ichthyoplankton distribution was highly variable during the whole period of study (Fig. 3c). Average concentrations were 1.05 ± 1.4 SD eggs·m^{-3} and 1.2 ± 0.8 SD larvae·m^{-3}. Neritic larval abundances did not show significant differences across months (Friedman ANOVA, $p>0.05$), whereas oceanic larvae did (Friedman ANOVA, $p<0.01$). Oceanic larvae were more abundant in January, February and October.

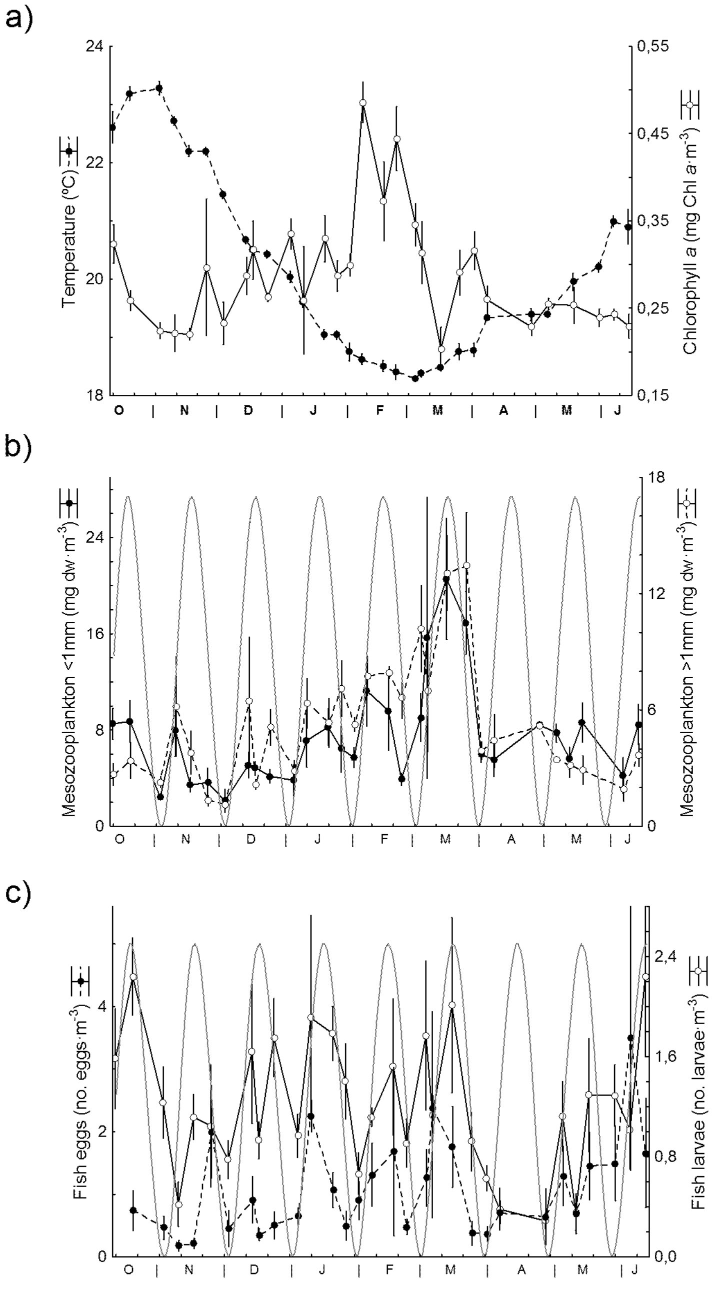

Figure 3. Temporal distribution of **a)** average temperature in the mixed layer (ºC) and average chlorophyll *a* (mg chl a·m^{-3}), **b)** Size fractionated mesozooplankton biomass (mg dry weight·m^{-3}), **c)** concentration of fish eggs (no.eggs·m^{-3}) and fish larvae (no.larvae·m^{-3}). Average values for the five sampling stations are shown. Note that lunar illumination is plotted as a fine grey line in the background for 3b and 3c.

Ichthyoplankton abundance and mesozooplankton biomass suggested a monthly periodicity (Fig. 3b,c) and so the lunar cycle was considered as an influencing factor (Figs. 3, 4). Lunar illumination explained the mesozooplankton biomass trend, of the two size fractions, as significant lower values were found during new moon and higher during crescent and full moon (KW-ANOVA, $p<0.005$). On the other hand, lower abundance of neritic larvae also appeared during the new moon, although this pattern was not significant (KW-ANOVA, $p>0.05$). Oceanic larvae did not show any significant trend (KW-ANOVA, $p>0.5$).

The planktonic community was not homogeneously distributed along the island's shelf. Small and large-sized mesozooplankton biomass appeared in higher values south of the island (Friedman ANOVA, $p<0.05$). Similarly, fish eggs and neritic larvae were found in significantly lower concentrations at the eastern stations (Fig. 4; Friedman ANOVA, $p<0.001$). On the other hand, oceanic larval abundance did not exhibit significant differences among stations ($p>0.05$).

Environmental factors (average temperature and salinity in the mixed layer, and chlorophyll *a* concentration) were correlated with mesozooplankton biomass (Table 1). In addition, the biomass of both size-fractions was positively correlated with fish eggs and neritic larval abundance. Oceanic larval abundance showed a different temporal

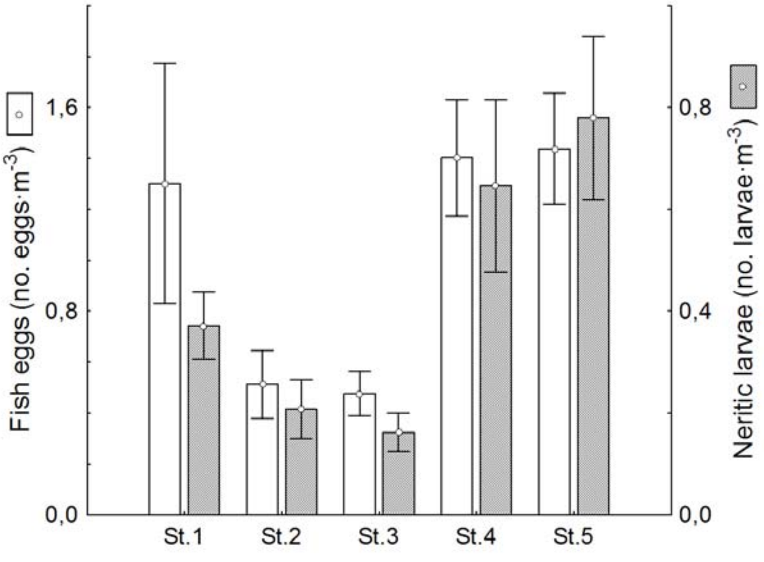

Figure 4. Average abundance (no·m^{-3}) and standard error (SE) along the five sampling stations of total fish eggs (white bars) and neritic larvae (grey bars).

trend than fish eggs and neritic larvae and so they were only correlated with salinity in the mixed layer ($p<0.001$).

Table 1. Matrix showing the Spearman correlation coefficients for environmental and biotic variables. Abbreviations: Temp. (Average temperature in the mixed layer, ºC), Salinity (Average salinity in the mixed layer), Chl *a* (Chlorophyll *a*, mg Chla·m^{-3}), Sm. Zoop, Lg. Zoop. (Small and Large Zooplankton size fraction Biomass, mg dry weight·m^{-3}), F Eggs (Fish Eggs, no·m^{-3}), F Larvae (Fish Larvae, no·m^{-3}), Neritic L, Oceanic L (Neritic and Oceanic Larvae, no·m^{-3}).

	Temp.	**Salinity**	**Chl *a***	**Sm. Zoop.**	**Lg. Zoop.**	**F Eggs**	**F Larvae**	**Neritic L**
Salinity	**0.37***							
Chl *a*	**-0.49***	**-0.38***						
Sm. Zoop.	**-0.34***	**-0.36***	**0.18***					
Lg. Zoop.	**-0.63***	**-0.49***	**0.29***	**0.56***				
F Eggs	-0.11	-0.002	0.09	**0.34***	**0.22****			
F Larvae	0.03	-0.12	**0.18****	**0.34***	**0.22***	0.38		
Neritic L	0.01	0.09	0.08	**0.37***	**0.21****	**0.41***	**0.68***	
Oceanic L	0.04	**-0.32***	0.24	0.09	0.10	0.13	**0.66***	0.10

* ($p<0.05$), ** ($p<0.001$)

Ichthyoplankton taxonomic composition

A total of 3897 fish larvae, comprising 121 taxa from 41 families, were caught (Table 2). Myctophidae was by far the most abundant family (31.5% of total larvae collected), mainly represented by *Ceratoscopelus warmingii*, *Hygophym hygomii*, and the species of the genera *Notoscopelus* and *Lampanyctus*. The high contribution of mesopelagic species was also evidenced by the relatively high abundance of Gonostomatidae (7.8% of total larvae), *Cyclothone braueri* being the most frequent. Sparidae, Clupeidae and Gobiidae were the greatest contributing families to neritic larvae collected (10.4%, 8.7 and 6.6% of total larvae, respectively). *Sardinella aurita* and *Boops boops* were the most abundant species within this neritic group. Gobiidae were not identified at species level due to the high number of species that inhabit the region and the complexity of the identification process.

Since this study did not cover the complete annual cycle of the ichthyoplankton assemblage, seasonal analysis may lead to biased conclusions. However, some strong trends were observed in the spawning patterns of some species. During winter, *Boops*

boops, *Sardinella aurita* and *Cyclothone braueri* dominated the larval assemblage (Table 2). Other less abundant species, such as *Trachurus picturatus* and *Scomber colias*, considered winter-spawners in the region, were only found during this period. On the other hand, warm water species such as *Ceratoscopelus warmingii* and *Hygophum hygomii* appeared in higher densities during fall and late spring. Pomacentridae sp2 and *Trachinus draco* are probably summer spawners in the region, as they were only found during the stratified period.

Table 2. Taxonomic list of larvae collected and percentage contribution of each taxa to the total larvae collected each month and during the complete study period.

	O	N	D	J	F	M	A	M	J	%
ANGUILIFORMES	0.73	0.5	0.14							**0.16**
FAMILY CLUPEIDAE										
Sardina pilchardus (Walbaum, 1972)			0.28	0.16		0.17				**0.10**
Sardinella aurita (Valenciennes, 1847)	1.21	0.76	4.50	6.57	4.46	17.08	6.85	6.13	14.01	**6.93**
Sardinella maderensis (Lowe, 1838)	2.42		0.14	0.16				0.99	1.17	**0.51**
Unidentified spp				1.28		0.66	1.37	6.52	0.39	**1.21**
FAMILY BATHYLAGIDAE										
Bathylagidae sp.1			1.83	1.44		0.17				**0.59**
FAMILY GONOSTOMATIDAE										
Cyclothone acclinidens (Garman, 1899)	0.48		0.14							**0.08**
Cyclothone braueri (Jespersen & Tåning, 1926)	9.93	5.81	5.63	8.17	7.64	4.98	2.74	6.13	8.17	**6.75**
Cyclothone pallida (Brauer, 1902)			0.14							**0.03**
Cyclothone pseudopalida (Mukhacheva, 1964)	0.73	0.25								**0.10**
Cyclothone sp.	2.18	1.26	0.28	0.32						**0.46**
Gonostoma atlanticus (Norman, 1930)						0.17				**0.03**
Gonostoma spp	0.24									**0.03**
Unidentified spp		1.01	0.14	0.16	0.32		5.48	0.20		**0.31**
FAMILY STERNOPTYCHIDAE										
Argyropelecus hemigymnus (Cocco,1829)	0.24	0.25		0.16	0.96	0.33				**0.21**
FAMILY STOMIIDAE										
Idiacanthus fasciola (Peters, 1877)			0.14							**0.03**
Stomias boa (Risso, 1810)			1.97	0.80	0.32	0.66		0.20		**0.64**
Unidentified spp			0.28	0.48	0.96	0.17				**0.23**
FAMILY PHOTICHTHYiDAE										
Ichthyococcus ovatus (Cocco, 1938)					0.64	0.17				**0.08**
Vinciguerria attenuata (Cocco, 1938)	0.24									**0.03**
Vinciguerria nimbaria (Jordan & Williams, 1896)	0.97	0.51		0.32	0.32	0.17		0.59		**0.33**
Vinciguerria poweriae (Cocco, 1938)	0.48	0.25	0.70	0.80	0.96	0.17	1.37	0.59	0.39	**0.56**
Vinciguerria spp	0.97	0.25	0.28	0.64	6.37	1.82		0.40	1.56	**1.23**

FAMILY MALACOSTEIDAE								0.20		**0.03**
FAMILY CHLOROPHTHALMIDAE										
Chlorophthalmus sp.1								0.20		**0.03**
FAMILY NOTOSUDIDAE										
Scopelosaurus lepidus (Krefft & Maul, 1955)					0.32	0.17				**0.05**
FAMILY SYNODONTIDAE										
Synodontidae sp.1		0.76	0.28	0.32	0.32		1.37		0.39	**0.26**
FAMILY MYCTOPHIDAE										
Ceratoscopelus maderensis (Lowe, 1839)	0.24	1.01	0.84			0.17	2.74	0.40	0.39	**0.44**
Ceratoscopelus warmingii (Lütken, 1892)	7.75	4.29	4.36	1.76		0.17	5.48	10.67	5.45	**4.21**
Diaphus brachycephalus (Taning, 1928)									0.39	**0.03**
Diaphus holti (Taning, 1918)	0.73									**0.08**
Diaphus metopoclampum (Cocco, 1829)	0.24							0.20		**0.05**
Diaphus mollis (Taning, 1928)		0.25		0.16				0.40	0.78	**0.15**
Diaphus rafinesquii (Cocco, 1838)	0.48	0.51	0.56	0.32		0.17		0.20		**0.31**
Diaphus spp	2.18	0.76	0.98	0.96	0.32			1.58	0.78	**0.92**
Diogenichthys atlanticus (Tåning, 1918)	0.97	0.76	0.42	0.16	1.91	1.16		0.20		**0.64**
Hygophum benoiti (Cocco, 1838)	1.21	0.25		0.48	1.27	0.17				**0.36**
Hygophum hygomii (Lütken, 1892)	3.87	7.07	8.72	3.04	0.32	0.50		0.20		**3.34**
Hygophum macrochir (Günther, 1864)	1.45	0.76	1.55	0.80	0.32			0.20	0.39	**0.72**
Hygophum reinhardtii (Lütken, 1892)	1.45	4.04	1.13	0.32		0.17		0.20	0.39	**0.90**
Hygophum taaningi (Becker, *1965*)	0.97	0.76	0.98	1.12	0.32	0.33		0.20	0.78	**0.69**
Hygophum spp	1.94	0.76	0.84	1.28	0.64	0.50		0.40		**0.82**
Lampadena sp.1				0.48					0.39	**0.10**
Lampadena spp	2.66	1.26	0.28	0.16	0.32		1.37	1.38		**0.72**
Lampanyctus sp.1	0.97	0.25								**0.13**
Lampanyctus spp	4.84	4.04	2.53	2.88	4.14	2.49	8.22	1.58	2.33	**3.08**
Lepidophanes guentheri (Goode & Bean, 1896)		0.25	0.14		0.64					**0.10**
Lobianchia dofleini (Zugmayer, 1911)			2.11	4.65	1.27	1.82	1.37		0.39	**1.57**
Lobianchia gemellarii (Cocco, 1938)			1.69	1.44	0.32	0.50				**0.64**
Lobianchia spp	0.48	2.27	3.09	2.72	1.59	1.66		0.40		**1.72**
Myctophidae pte.1	0.24							0.20		**0.05**
Myctophidae pte.2	2.91	1.77	0.70						0.39	**0.64**
Myctophidae pte.3	1.94	0.25		0.48						**0.31**
Myctophidae sp.C				0.32	0.32	1.00	4.11	0.20	0.39	**0.36**
Myctophum nitidulum (Garman, 1899)	2.18	0.51	0.70	0.32	0.64	0.17				**0.54**
*Myctophum selenops (*Tåning, 1928)			0.28		0.64					**0.10**
*Nannobrachium lineatum (*Tåning, 1928)									0.78	**0.05**
Notolychnus valdiviae (Brauer, 1904)		0.76								**0.08**
Notoscopelus resplendens (Richardson, 1845)	0.24		0.28	0.80	0.64	0.50		0.40		**0.38**
Notoscopelus spp	0.97	0.51	2.39	5.77	6.37	3.98	2.74	1.19	3.89	**3.10**
Symbolophorus spp			0.28	0.48	0.32	0.50				**0.23**
Unidentified spp	4.60	5.05	4.50	5.13	6.05	2.99	5.48	0.59	2.72	**3.95**
FAMILY EVERMANELLIDAE			0.28	0.16						**0.08**
FAMILY PARALEPIDAE										
Lestidiops jakari pseudospyraenoides (Ege, 1918)		0.25		0.32						**0.08**
Sudis hyalina (Rafinesque, 1810)				0.16						**0.03**

Unidentified spp			0.14					0.20	0.39	**0.08**
FAMIILY MACRORHAMPHOSIDAE										
Macroramphosus scolopax (Linnaeus, 1758)	0.48	0.51	0.14		1.27	0.50				**0.31**
FAMILY SYGNATHIDAE										
Hippocampus hippocampus (Linnaeus, 1758)									0.39	**0.03**
FAMILY MELAMPHAIDAE										
Melamphaes simus (Ebeling, 1962)		0.25	0.42	0.16						**0.13**
FAMILY GADIDAE										
Phycis spp					0.32					**0.03**
FAMILY HEMIRHAMPHIDAE										
Hemirhamphus balao (Le Sueur, 1823)	579					0.17				**0.03**
FAMILY CAPROIDAE										
Capros aper (Linnaeus, 1758)			0.14	1.28	0.64					**0.28**
FAMILY SERRANIDAE										
Anthias anthias (Linnaeus, 1758)	0.48	0.25	1.13	0.16	0.64	0.17	1.37	1.38	3.50	**0.82**
Serranidae sp.1				0.16	0.32	0.33				**0.10**
Serranus cabrilla (Linnaeus, 1758)			0.14					0.59	0.39	**0.13**
Serranus spp				0.32				0.20		**0.08**
Unidentified spp	0.24		0.14	0.48		0.17		0.79	0.39	**0.28**
FAMILY CARANGIDAE										
Trachurus picturatus (Bowdich, 1825)				0.32	0.64	0.33		0.20		**0.18**
Unidentified spp						0.17				**0.03**
FAMILY CORYPHAENIDAE										
Coryphaena hippurus (Linnaeus, 1758)			0.28		0.32	0.83	1.37		0.39	**0.26**
FAMILY MULLIDAE										
Mullus barbatus (Linnaeus, 1758)								0.59		**0.08**
FAMILY BRAMIDAE	0.48		0.14			0.66				**0.18**
FAMILY SPARIDAE										
Boops boops (Linnaeus, 1758)	0.24		5.91	6.89	3.18	12.94	2.74	9.49	1.56	**5.85**
Diplodus spp	1.94	0.51	0.14	0.80	8.92	4.31	1.37	1.78	0.39	**2.08**
Oblada melanura (Linnaeus, 1758)		0.25			3.82	1.49		2.17		**0.85**
Pagellus acarne? (Risso, 1826)		0.76	1.27	0.32		0.50				**0.44**
Pagellus bogaraveo (Brünnich, 1768)			0.98		0.32					**0.21**
Pagellus spp					0.32					**0.03**
Pagrus pagrus (Linnaeus, 1758)	0.24			0.32				0.40	1.17	**0.21**
Unidentified spp		0.76	1.27	1.76		0.17		0.99	0.78	**0.80**
FAMILY CENTRACANTHIDAE										
Centracanthus cirrus (Rafinesque, 1810)	0.24		0.28	0.32	0.64					**0.18**
Unidentified spp			0.14	0.16						**0.05**
FAMILY LABRIDAE										
Coris julis (Linnaeus, 1758)	0.48					0.17			0.39	**0.10**
Symphodus spp					0.32	0.50		0.20		**0.13**
Thalassoma pavo (Linnaeus, 1758)				0.16				0.20		**0.05**
Unidentified spp		0.51	0.14	0.16	0.32	0.33		0.40	0.39	**0.26**
FAMILY POMACENTRIDAE										
Pomacentridae sp.1	0.24		2.81	1.76	1.59	0.50	2.74	0.40		**1.13**
Pomacentridae sp.2	0.24							0.99	8.56	**0.72**
Unidentified spp				0.32						**0.05**
FAMILY CHIASMODONTIDAE										

Chiasmodon níger			0.14	0.16						**0.05**
FAMILY TRACHINIDAE										
Trachinus draco (Linnaeus, 1758)	0.97	0.25								**0.13**
FAMILY GEMPYLIDAE										
Diplospinus multistriatus (Maul, 1948)			0.70	0.96		0.33				**0.33**
Nealotus tripes (Jonhson, 1865)			0.14							**0.03**
Unidentified spp		0.51	0.14						0.78	**0.13**
FAMILY TRICHIURIDAE										
Benthodesmus elongatus (Clarke, 1879)		0.25	0.98	0.32	0.64					**0.31**
FAMILY SCOMBRIDAE										
Sarda sarda (Bloch, 1793)					0.32					**0.03**
Scomber colias (Houttuyn, 1792)				2.72	0.96	0.66				**0.69**
Unidentified spp									1.17	
FAMILY GOBIIDAE										
Lebetus guilletii (Le Danois, 1913)					0.64			0.20		**0.08**
Unidentified spp	5.57	30.81	2.53	1.28	2.23	5.64	9.59	2.77	8.17	**6.52**
FAMILY BLENNIIDAE										
Ophioblennius atlanticus (Valenciennes, 1836)	0.73			0.16	0.32	0.17		1.38	1.17	**0.41**
FAMILY OPHIDIIDAE										
Unidentified spp								0.40	0.78	**0.10**
FAMILY TETRAGONURIDAE										
Tetragonurus atlanticus (Lowe, 1839)			0.42	0.80		0.17				**0.23**
FAMILY SCORPAENIDAE										
Scorpaena porcus (Linnaeus, 1758)			0.14	0.16		0.33				**0.10**
Scorpaenidae Pte.1				0.32						**0.05**
Unidentified spp			1.13	1.12	0.96	1.00			0.39	**0.64**
FAMILY TRIGLIDAE			0.14	0.32		0.17				**0.10**
FAMILY BOTHIDAE										
Arnoglossus imperialis (Rafinesque, 1819)				0.16						**0.03**
Arnoglossus thori (Kyle, 1913)	0.48	0.51	0.14	0.16						**0.15**
Arnoglossus spp		0.25	0.28							**0.08**
Bothus podas (Delaroche, 1809)	0.48									**0.05**
Unidentified spp			0.42	0.48					0.39	**0.18**
FAMILY TETRAODONTIDAE	0.48		0.14						1.17	**0.15**

The temporal distributions of the families Clupeidae and Sparidae were analyzed in detail due to their relatively high abundances and their important ecological and commercial roles (Fig. 5). Both families displayed a monthly trend similar to that shown by mesozooplankton biomass (Fig. 5a,b). Sparidae larvae exhibited significant lower abundances during the new moon (KW-ANOVA, $p<0.05$) and *Boops boops* showed higher density peaks during the illuminated phase of the lunar cycle (i.e., crescent and full moon) (KW-ANOVA, $p<0.05$) (Fig. 5c). Larvae of the genus *Diplodus* also showed lower values during the new moon, although these differences were not significant (KW-ANOVA, p>0.005).

ANOSIM results indicated that there was a significant diference between months (seasonality), whereas sampling sites only seemed to have a marginal effect on the community composition during the sampling period (ANOSIM, R= 0.275, p<0.01 and

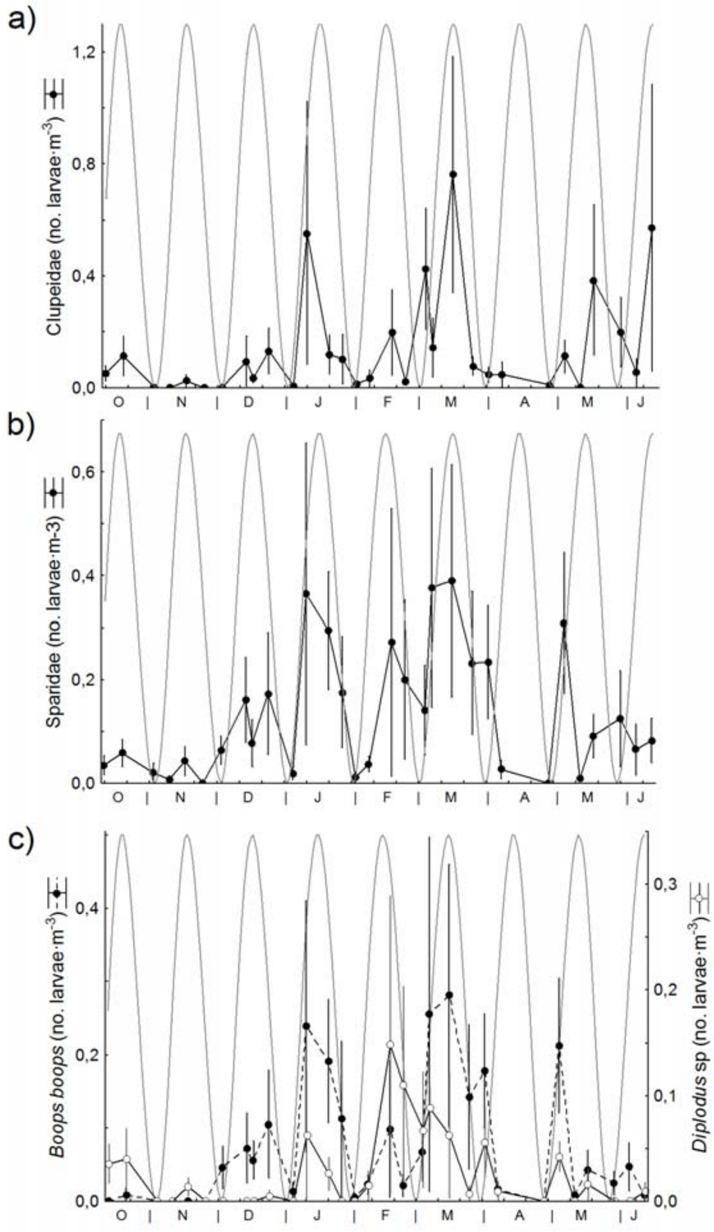

Figure 5. Temporal variation of average abundance (no. larvae·m^{-3}) of **a)** Clupeidae larvae, **b)** Sparidae larvae and **c)** *Boops boops* and *Diplodus* sp larvae. Note that lunar illumination is plotted in all graphs as a fine dotted line.

R = 0.055, $p<0.05$, respectively). Although sampling site did not significantly affect the composition and structure of the complete larval fish assemblage, two neritic families, Clupeidae and Gobiidae, were found in significantly higher abundances in the retention spots upstream (station 1) and downstream (stations 4 and 5) of the island (Fig. 6, Friedman ANOVA $p<0.01$). On the other hand, mesopelagic families (e.g. Myctophidae, Gonostomatidae, Photichthydae) had slightly higher abundances on the eastern flank of the island where the flow is locally enhanced, although this pattern was not significant (Friedman ANOVA $p>0.05$).

Discussion

A typical feature of subtropical waters is that seasonal patterns are weak (Barton *et al.*, 1998). The water column is strongly stratified almost all year round, showing a seasonal thermocline and a deep chlorophyll maximum (Hernández-León *et al.*, 2007). Trade Winds reach maximum strength in summer and, even so, maximum temperatures are recorded during this stratified period (Barton *et al.*, 1998). Surface cooling during winter combined, with wind stirring, weakens the almost permanent stratification. This short mixing stage promotes the most productive season in these waters, although its magnitude and extension are much smaller than in temperate waters (Arístegui *et al.*, 2001). These authors attributed the first chlorophyll peak to an abrupt increase in phytoplankton cells <2 µm (mostly diatoms), whereas in the second peak, cells >2 µm were at higher densities. In our study, maximum abundances of mesozooplankton biomass were registered with a lag of three weeks after the second chlorophyll peak. This mesozooplankton bloom was split into two peaks, which has been related to the result of the interplay between resource and consumer controls (Hernández-León *et al.*, 2004). These authors considered that although resources were a limiting factor after the first zooplankton bloom, mesozooplankton biomass variability was a consequence of the predatory pressure exerted by diel vertical migrants.

Average values of mesozooplankton biomass and larval fish abundance were found in the expected range of previous studies (Rodríguez *et al.*, 2000; Hernández-León *et al.*, 2004; Becognée *et al.*, 2006; Moyano *et al.*, 2009). Larval fish diversity was high, typical of subtropical waters (Longhurst and Pauly, 1987). The high contribution of mesopelagic species (i.e., Myctophids and Gonostomatids) is characteristic of oceanic islands due to the narrow island shelf. Therefore, the composition of the larval fish community, at the family-level, is similar to that of other oceanic islands (Leis, 1991; Boehlert *et al.*, 1992). Larval abundances were also similar to those found in similar studies off the Balearic Islands in the Mediterranean Sea (Alemany *et al*., 2006), off Australia (Smith and Suthers, 1999; Muhling *et al*., 2008) and in the Agulhas Current (Beckley and van Ballegooyen, 1992).

Unlike mesozooplankton, larval abundance did not show any temporal peak during the late winter bloom period. This temporal pattern abundance may be a consequence of the low seasonality in the water properties found in the Canary Islands compared to temperate seas. This mild seasonality results in an extension of the spawning periods of fish species (Lowe-McConnell, 1987). This is the case for Gran Canaria where larvae of the most abundant species are present for several months (i.e., *Boops boops*) or all year round (i.e., *Sardinella aurita, Cyclothone braueri*).

Nevertheless, some species' larval concentrations exhibited some sort of seasonality, suggesting the presence of winter and summer assemblages. During winter, the larval assemblage was dominated by *Boops boops* and *Sardinella aurita* and also characterized by the presence of *Scomber colias* and *Trachurus picturatus*. This is in agreement with the spawning periods of these species in the Canary waters. *Boops boops* spawns from November to July, with a maximum peak during March and April (Franquet and Brito, 1995) and, in our study, larvae of this species appeared in higher densities in March, and also in January. *Sardinella aurita* spawns throughout the year around Gran Canaria, peaking in summer (June to September) and winter (December to February) (Bécognée *et al*., 2006). Moyano *et al.* (2009) also found high densities in spring. On the other hand, *Scomber colias* and *Trachurus picturatus* larvae appeared during the mixing period of the water column (i.e, January to March) coinciding with their spawning time described for the area (Franquet and Brito, 1995; Lorenzo and Pajuelo, 1996). Our study is the first to record early stages of both species near Gran Canaria, although *Scomber colias* is the most abundant pelagic species in the archipelago (Lorenzo and Pajuelo, 1996). The presence of small sized *Scomber colias* larvae confirms that this species reproduces successfully in the island waters, and that the larval transport within upwelling filaments from the African coast, if real, might act as a complementary source of individuals to the existing stock. Therefore, the extension of the spawning periods (Lowe-McConnell, 1987) in the area is evident when comparing to temperate Mediterranean Sea waters. Both ecosystems share neritic and oceanic species in their larval community structure (Sabatés *et al.*, 1990; Somarakis *et al.*, 2002; Isari *et al.*, 2008), but their presence during the year is completely different. *Sardinella aurita* and *Hygophum hygomii* are summer spawners in the Mediterranean Sea (Goodyear *et al.*, 1972; Olivar and Palomera, 1994; Sabatés *et al.*, 2006), while their larvae are present during the whole year off Gran Canaria (Bécognée *et al.*, 2006). Similarly, *Scomber colias* is a summer spawner in the Mediterranean (Sabatés, 1990), but it only reproduces during winter in the Canaries (Lorenzo and Pajuelo, 1996).

During late summer, the larval community is dominated by the myctophids *Ceratoscopelus warmingii* and *Hygophum hygomii*. The former has a broad tropical distribution occurring worldwide (Bekker, 1983). Little is known about their reproduction in the region. *Ceratoscopelus warmingii* spawning peaks in spring near Hawaii (Clarke, 1973) and its larvae provide a substantial year-round contribution to the larval fish assemblage of the North Pacific Central gyre (Loeb, 1980). Both temporal patterns in the Pacific are consistent with our results that suggest that they reproduce the whole year round, showing lower densities during the colder months. *Hygophum hygomii* seemed to be present in Gran Canaria waters year-round, peaking in the warmer months, as in the Mediterranean (Goodyear *et al*., 1972). Therefore, it might be reasonable to consider that they extend this period to early winter due to the warmer conditions of the Canary Island waters. In addition, *Trachinus draco*, Pomacentridae sp2 and Tetraodontidae species seem to be summer-spawners, but little is known about their ecology in the area. Hence, these species may be characteristic of the summer assemblage, but a better representation of the summer months during this study precludes any conclusion.

In relation to local hydrography, mesozooplankton biomass and fish eggs and neritic larval abundance benefit from local retention, showing lower values at the eastern flank of the island, where enhanced flow advects them away, and accumulating in the windward and leeward zones. This variability in the plankton community around islands has been observed in several studies (Hammer and Hauri, 1981; Boehlert and Mundy, 1993), and it was already proposed for Gran Canaria by Rodríguez *et al.* (2001). Here, we confirm this pattern on a finer scale, particularly for members of the families Clupeidae and Gobiidae. However, the complete larval community

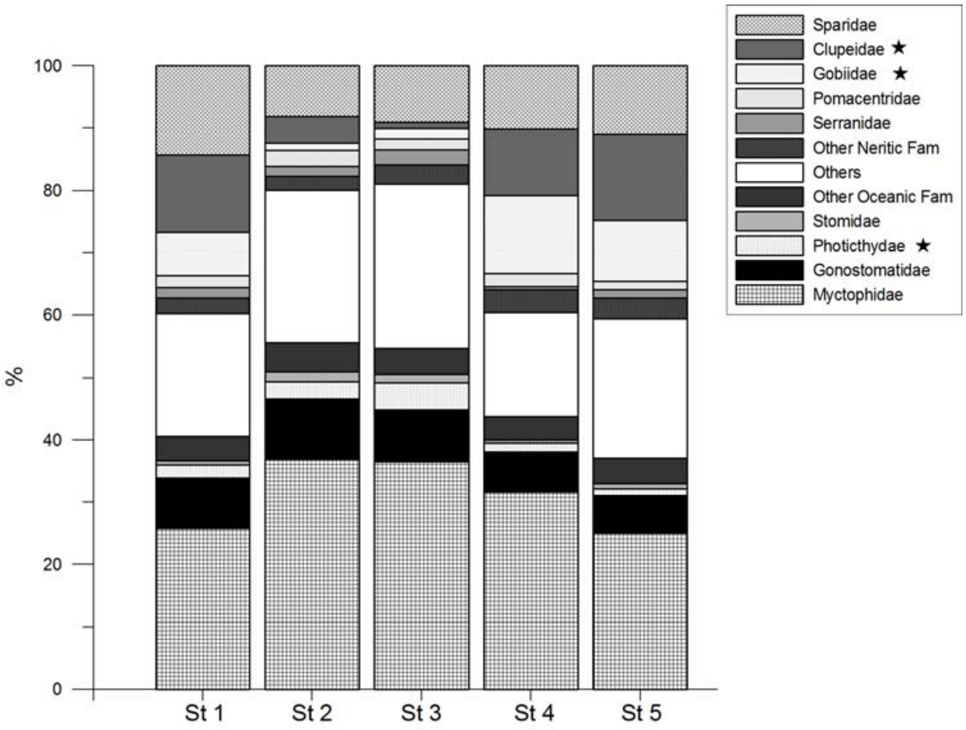

Figure 6. Percentage contribution of the most abundant families to the total larval fish catches at each sampling.

composition and structure did not vary between retention and exposed sites on a long-term basis.

Lunar illumination

Probably the most striking results in this work are those related to the lunar illumination. We showed clear evidence of the mesozooplankton biomass increasing during the illuminated phase of the lunar cycle: low values during the new moon that increase through crescent and full moon, and then going down again during the waning moon. This pattern was explained by Hernández-León (1998), for zooplankton, to be a result of predator pressure. During full moon, diel vertical migrants (DVMs) do not reach the upper layers of the ocean (<100 m depth), reducing the predatory pressure on epipelagic zooplankton. On the other hand, during the dark phase of the lunar cycle, DVMs reach the upper layers feeding on the increased zooplankton biomass. Hernández-León *et al*. (2001) found strong differences between full and new moon and emphasized the importance of this process on the flux of energy and organic matter from the euphotic to the mesopelagic zone. Recently, Hernández-León (2008) formulated a hypothesis about the influence of lunar illumination on fish spawning and larval fish abundance. This author found evidence of a coupling of fish reproduction and the epipelagic zooplankton bloom during the illuminated period of the lunar cycle, arguing that this pattern may constitute a short-term version of the match–mismatch hypothesis (Cushing, 1990). This coupling would be explained as a result of (1) the lower predatory pressure on fish larvae, (2) the enhanced feeding of adult fish promoted by the increase in zooplankton during the lunar cycle, insofar as this energy intake would be converted into reproduction products and, (3) the enhanced feeding by fish larvae on zooplankton during the lunar cycle. Therefore, our results partially confirm this hypothesis for neritic larvae. Clupeids and Sparids were the clearest cases, probably because their abundances were high enough to notice the trend. Maximum abundances for both groups recorded during the illuminated phase supports the idea that spawning is coupled to promote larval survival in a low-predation, high-feeding scenario. Further research on this lunar influence would provide insights into the short-term variations of the ichtyoplankton community and the natural variability of fisheries.

In conclusion, the variability of the larval fish community off Gran Canaria suggests the presence of two seasonal assemblages corresponding to the mixing and stratification periods. Despite the presence of some species year-round, winter and summer spawners seem to define the annual larval fish assemblage. In this sense, temporal variations seemed to play a more important role on the community structure than location around the island over time. The periodicity in the temporal distribution of neritic larval fish abundance and small mesozooplankton biomass questions the ultimate factors governing the larval dynamics. Finally, the influence of the DVM lunar-linked predator pressure cycle on mesozooplankton and larval fish abundances seems to govern their temporal variability. Therefore, a better understanding of larval dynamics would profoundly improve the scope of fisheries management and, especially, of marine reserves in the Archipelago.

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CHAPTER IV

INTRA- AND INTERANNUAL VARIABILITY IN THE LARVAL FISH ASSEMBLAGE OFF GRAN CANARIA, AN OCEANIC ISLAND IN THE NE ATLANTIC

M. Moyano and S. Hernández-León. Interannual and seasonal variations on the larval fish assemblage off Gran Canaria, an oceanic island in the NE Atlantic. *Submitted to Marine Biology*.

Abstract

Larval fish assemblages were studied weekly at Gran Canaria Island, Canary Islands, from January 2005 to June 2007. Two contrasting hydrological and biological periods were studied. The former year was characterized by lower temperature and salinity increasing through 2006 and 2007. In constrast, chlorophyll and mesozooplankton decreased during winter through the same period. Ichthyoplankton abundance, however, did not exhibit the same pattern as larger values were observed during 2006. The larval fish community of this oceanic island located near the NW African upwelling was composed of both neritic and oceanic taxa. Two families accounted for almost half of the collected larvae: Clupeidae (21.9%) and Myctophidae (20.5%). Although larval concentration did not exhibit any seasonal peak linked to changes in zooplankton production, the ichthyoplankton composition gradually changed during the year due to the high diversity and extended spawning periods of the fish species represented in samples. Nevertheless, “winter” and “summer” assemblages were identified, corresponding to the mixing and stratification periods of the water column. These assemblages were characterized by changes in the most abundant annual taxa (*Sardinella aurita, Cyclothone braueri*, *Ceratoscopelus* spp and Gobids) and by the presence of typical winter (*Pagellus bogaraveo*, Pomacentridae sp1) or summer spawners (Pomacentridae sp2, *Trachinus draco*, *Arnoglossus thori*, Tetraodontidae sp1). Upwelling filaments shed from the NW African coast reached the sampling area three times during this study, but changes in the local larval community were only detected in August 2005. Although hydrological and biological variables in the water column showed rather different characteristics among years due to climatic conditions, the ichthyoplanktonic community appeared to follow a different pattern, perhaps related to the previous year’s conditions. The results obtained from this work provide the first long-term plankton and larval fish analysis in the area and form a basis for understanding the life cycle scheduling and interactions among species as well the potential magnitude in variability in transport processes of early life stages.

Key words: ichthyoplankton, larval assemblages, mesozooplankton, seasonal variation.

Introduction

Larval fish assemblages are temporary associations and their study has sought to understand why they occur in the places and at the times they do, and how these spatial and temporal distributions relate to patterns in recruitment (Miller, 2002). Physical and biological processes interact in the formation and maintenance of larval assemblages (Boehlert and Mundy, 1993). Then, these assemblages are often delineated by water masses on a regional scale (Grothues and Cowen, 1999; Hare *et al.*, 2001; Muhling *et al.*, 2008) and reflect the reproductive seasonality of the fish species (Frank and Leggett, 1983) and larval behaviour (Boehlert and Mundy, 1993). The duration of these larval assemblages depends on the presence of a suite of conditions promoting larval growth and survival and the presence of physical processes (e.g., fronts, (Galarza *et al.*, 2009)) that overcome the forces causing the disruption of the assemblage (e.g., dispersal, (Drinkwater *et al.*, 2000). The composition, structure and variability of larval fish assemblages have been thoroughly examined in many temperate coastal systems (e.g. (Sabatés, 1990; Olivar and Shelton, 1993; Gray and Miskiewicz, 2000; Hare *et al.*, 2001; Doyle *et al.*, 2002), displaying a species distribution that reflects oceanographic processes cross- and alongshore. However, tropical and subtropical oceanic islands are unique environments where larval fish assemblages (and the processes impacting them) have been much less studied (Leis, 1991; Boehlert and Mundy, 1993).

Retention mechanisms are critically important for larval fish in oceanic islands. Although physical processes (Lobel and Robinson, 1986, 1988; Boehlert *et al.*, 1992; Cowen and Castro, 1994) and larval behaviour (Leis, 2007) have a profound influence on the recruitment potential of oceanic island fish populations, self-recruitment is considered the main factor maintaining these populations (Jones *et al.*, 1999; Cowen *et al.*, 2000). In the particular environment of Gran Canaria Island, the *island mass effect* (Doty and Oguri, 1956; Hamner and Hauri, 1981) has been confirmed to influence zooplankton (Hernández-León, 1991) and ichthyoplankton distribution (Rodríguez *et al.*, 2001). Based on simple Lagrangian trayectories, the latter authors confirmed the potential for retention of two stagnation areas for fish eggs and neritic larvae around the island: N-NE, upstream; and S-SW, downstream in the wake area. However, Moyano *et al*. (submitted) did not find significant changes in the larval fish community composition among those sites during an intensive 8-month study. Therefore, those weak-flow regions only cause the accumulation of total egg and neritic larvae, but the larval fish community at those spots is not significantly different from other sites on the island shelf on longer time scales.

The Canaries Archipielago is located in the NE Atlantic close to the NW African upwelling. The interactions between the Canary Current flow though the islands, the coastal upwelling and the trade winds result in an area of high mesoscale oceanographic activity (Barton *et al.*, 1998). Therefore, wakes and eddies are typical south of the islands (Arístegui *et al.*, 1994; Sangrá *et al.*, 2007) and also upwelling filaments might reach periodically the eastern shores of the westernmost islands (La Violette, 1974; Pacheco and Hernández-Guerra, 1999). The influence of all these structures is particularly dramatic in oligotrophic waters such as those surrounding the Canary Islands (Hernández-León, 1991; Arístegui *et al.*, 1997) where the annual average chlorophyll concentration is only ~25% higher than in the surrounding oceanic domain (Braun and Real, 1984). The most productive period in Canary waters is the late winter bloom (LWB, Braun, 1980; Arístegui *et al.*, 2001). The formation of this bloom is more similar to the autumn bloom (nutrient-limited) rather than the spring bloom (light-limited) in temperate seas (Barton *et al.*, 1998). Mesozooplankton biomass also exhibits an annual maxima during this LWB and often with a ~2-3 weeks lag in relation to the first chlorophyll peak (Hernández-León, 1988; Hernández-León *et al.*, 2004).

The present study is the first long-term sampling to report ichthyoplankton results in the Canary Islands, where little is known about the spawning times and temporal associations of the fish species inhabiting these waters. Assuming the potential of fish larvae as indicators of the future recruitment in adults (Houde, 1987, 2008), this work constitutes a first step towards understanding the Canary Islands fish community, of paramount importance for fisheries management.

Material and methods

Weekly sampling was carried out from January 2005 to June 2007 during daylight hours on board the R.V Solana II at a sampling station near Las Palmas de Gran Canaria, Gran Canaria Island (Fig. 1). This station was located ~3 nm offshore in the 100 m isobath, at the edge of the island shelf. Due to technical problems, no sampling was performed during September 2005. Temperature, salinity and fluorescence (CTD) casts were performed with a SBE25 (Sea-Bird Electronics Inc., Bellevue, WA, USA). Phytoplankton chlorophyll was derived from depth profiles of in-situ fluorescence, calibrated with samples collected at 15 m with a Niskin bottle. Samples of 500 ml of seawater were filtered through Whatman GFF filters and preserved in liquid nitrogen until analyzed. Chlorophyll *a* pigments were measured using the fluorometric method (Yentsch and Menzel, 1963). NOAA-16 AVHRR and SeaWiFS satellite-derived images of Sea Surface Temperature (SST) and chlorophyll were obtained through the Physical Oceanography and Remote Sensing Group of the University of Las Palmas de Gran Canaria (http://www.webs.ulpgc.es/orpamcanarias/static/imag_index.html) and the Earth Observation, Remote Sensing and Atmosferic Department (CREPAD) of the Spanish National Institute for Aerospace Technology (INTA).

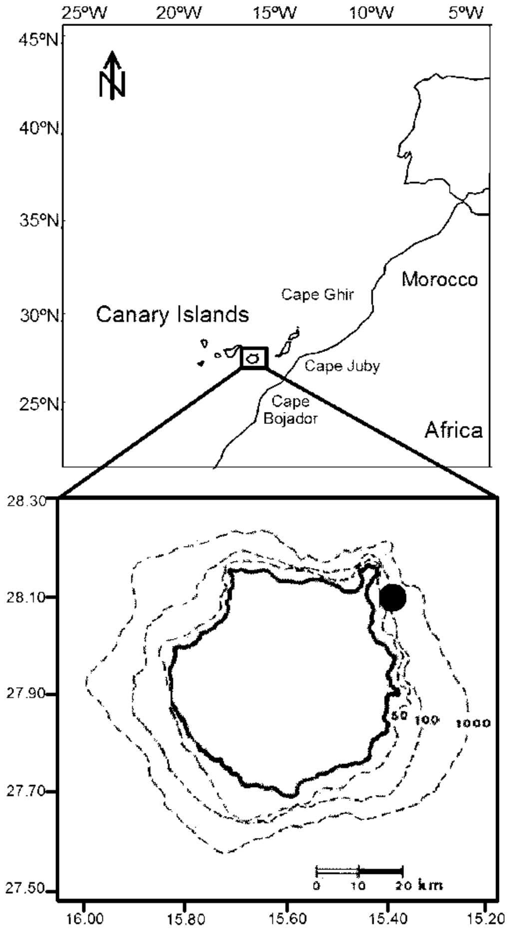

Figure 1. Location of the study area. Dot shows the location of the sampling station in front of Las Palmas de Gran Canaria (Northeast Subtropical Atlantic).

Plankton samples were obtained using bongo net tows (oblique, surface to 90 m, speed 2-3 knots). Nets were fitted with 200 µm mesh and a flowmeter (General Oceanics) to measure the volume of filtered water. The first sample was fractionated by a 1000 µm sieve to quantify the dry weight biomass of small (200-1000 µm) and large mesozooplankton (>1000 µm) following the method of Lovegrove (1966). The second sample was quickly preserved in 4% buffered formaline and used for ichthyoplankton analyses. All fish larvae were sorted and identified to the lowest taxonomic level possible using Greenwood classification (CLOFETA, Check-List Of the Fishes of the Eastern Atlantic, Queró *et al.*, 1990). Following Rodriguez *et al.* (1999), larvae were divided into three categories (Neritic, Oceanic and Other) in relation to the behaviour of juveniles and adults of the species and/or group.

Temporal evolution of abiotic (i.e., temperature, salinity,) and biotic (i.e., ichthyoplankton abundance, mesozooplankton biomass, chlorophyll concentration) variables was analyzed using the Statistica 7.0 software package (StatSoft Inc.). Spearman's rank correlation was conducted to test the relationships between the different variables during the sampling period. In addition, Kruskall-Wallis ANOVA was conducted to analyze inter-annual differences in abiotic and biotic environmental variables across the LWB period (January-May). Non-parametric tests were applied since most of the variables did not meet the underlying conditions of normality (Kolmogorov-Smirnov) and homogeneity of variances (Levene´s test).

The variability of the composition and structure of larval fish assemblages were studied using the PRIMER 6.0 software package (Plymouth Routines in Multivariate Ecological Research, (Clarke and Warwick, 2005). To avoid the noise-derived effects of rare species, only species with positive presence for at least two years and contributing >0.1% total larval abundance were included in the analysis. Gobiidae larvae were analyzed as unique taxa due to the high contribution of this family to the total abundance of larvae and their homogeneity as all species share a similar ecological niche. Also, monthly averages were used instead of single samples during the whole data treatment to avoid the substantial noise derived from plankton patchiness. Prior to building the similarity matrix using the Bray-Curtis index, data were standardized and log (x+1) transformed to down-weigh the importance of highly abundant taxa. A two-way layout analysis of similarities (Nested ANOSIM) was performed on the species resemblance matrix to examine temporal differences between months within years and between years. Once this temporal variability was highlighted (see Results), multivariate clustering and ordination techniques were applied. A hierarchical agglomerative clustering was conducted from the species resemblance matrix, using group-average linkages to find *natural groupings* (i.e., assemblages) of samples. The resulted dendrogram was cutted to produce ecologically interpretable clusters. The significance of the cluster groups was then confirmed by two methods: (1) a series of similarity profile (SIMPROF) permutation tests which resulted in the characterization of discrete, significant larval fish assemblages; (2) superimposing the clustering results on a non-metric, multi-dimensional scaling (MDS) plot generated from the same similarity matrix (Clarke, 1993). In order to identify the role of individual taxa in contributing to the separation between the cluster groups, a similarity percentages routine (SIMPER) was applied. SIMPER decomposes average Bray-Curtis dissimilarities between all pairs of samples into percentage contributions from each species.

On the other hand, multivariate analysis of the environmental variables (temperature, salinity, chlorophyll *a*, small and large zooplankton biomass) was carried out on the Euclidean-distance matrix created from normalized data. Hierarchical clustering and a Principal Components Analysis (PCA) ordination were performed, so patterns in the environmental data across samples were displayed in an analogous way to species data. Afterwards, the BEST (Bio-Env) routine was applied in order to find the “best” match between multivariate among-sample patterns of a larval assemblage and that from environmental variables associated with those samples. Maximum temperature (at 15-75 m depth) and salinity in the mixed layer (20-30 m depth) were chosen instead of average temperature and salinity, respectively, because they returned the higher correlations in structuring the larval fish assemblage.

Results

Although seasonality was not very strong in the Canary waters, a typical weak seasonal variation in water temperature was observed (Fig. 2a). There was no clear seasonal pattern in salinity (Fig. 2b) and lower values were recorded in summer 2005 due to the arrival of two upwelling filaments to the eastern shore of Gran Canaria Island

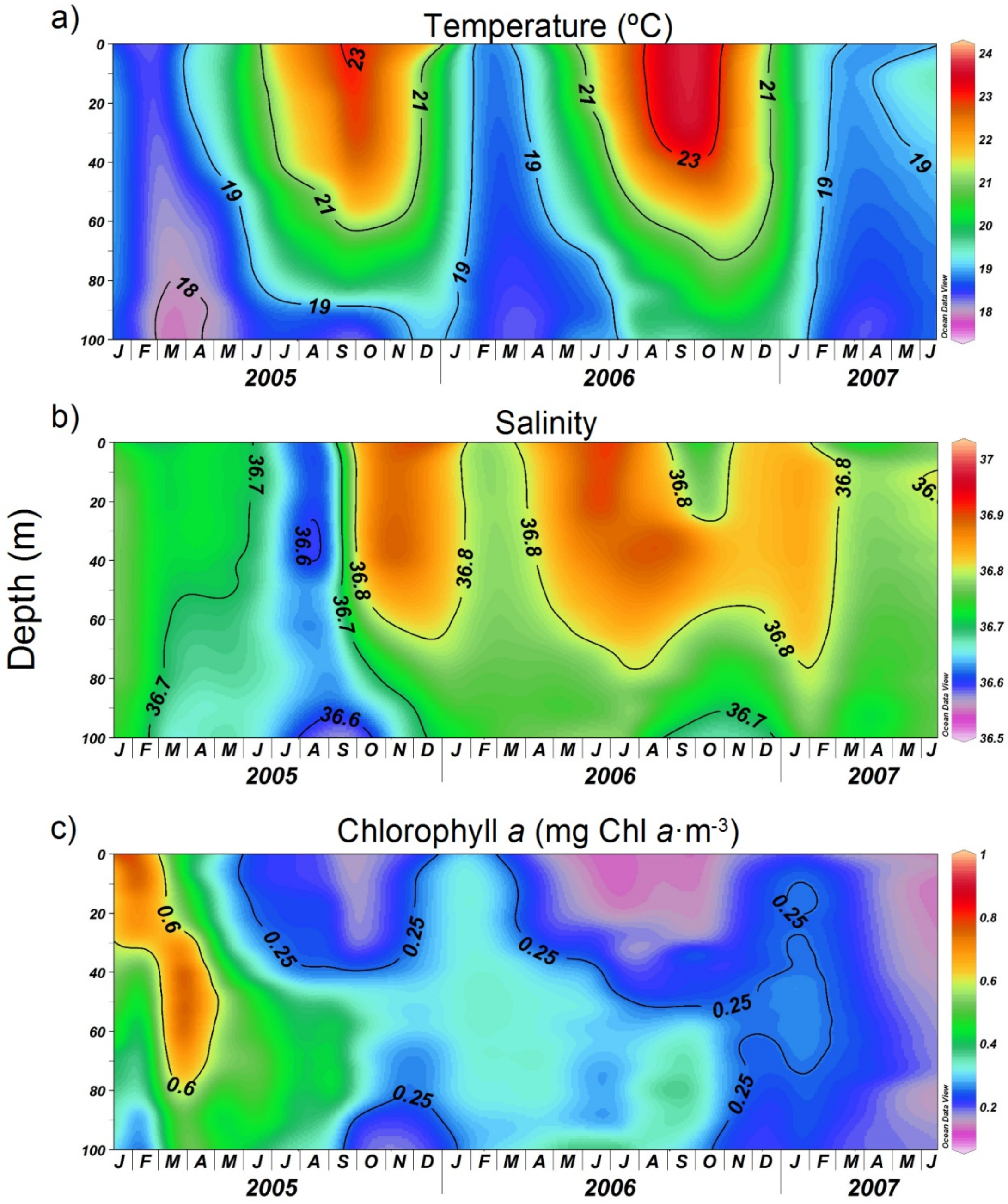

Figure 2. Sections up to 100 m depth, showing the temporal evolution of a) temperature (ºC), b) salinity, c) chlorophyll *a* (mg chl *a*·m^{-3}).

(Moyano *et al.*, 2009). Stratification of the water column persisted during most of the year until surface waters started to cool off and temperatures fell below 19ºC, promoting the mixing period. As a consequence of this vertical mixing, nutrients were pumped up to surface waters enhancing phytoplankton growth, as observed from the increase in chlorophyll *a* concentration (Figs. 2c, 3a). This was considered the start of the LWB period that often lasts until May. The phytoplankton bloom started in surface waters, deepening as it evolved, and exhibited a typical two-peak structure of chlorophyll *a* concentration during the bloom (Fig. 3a). Coupled with chlorophyll concentration, but often with 2-3 weeks-lag, mesozooplankton biomass also exhibited an annual maximum during this bloom (Fig.3b). Neither neritic nor oceanic larval abundance were linked to this annual production cycle (Fig.3c).

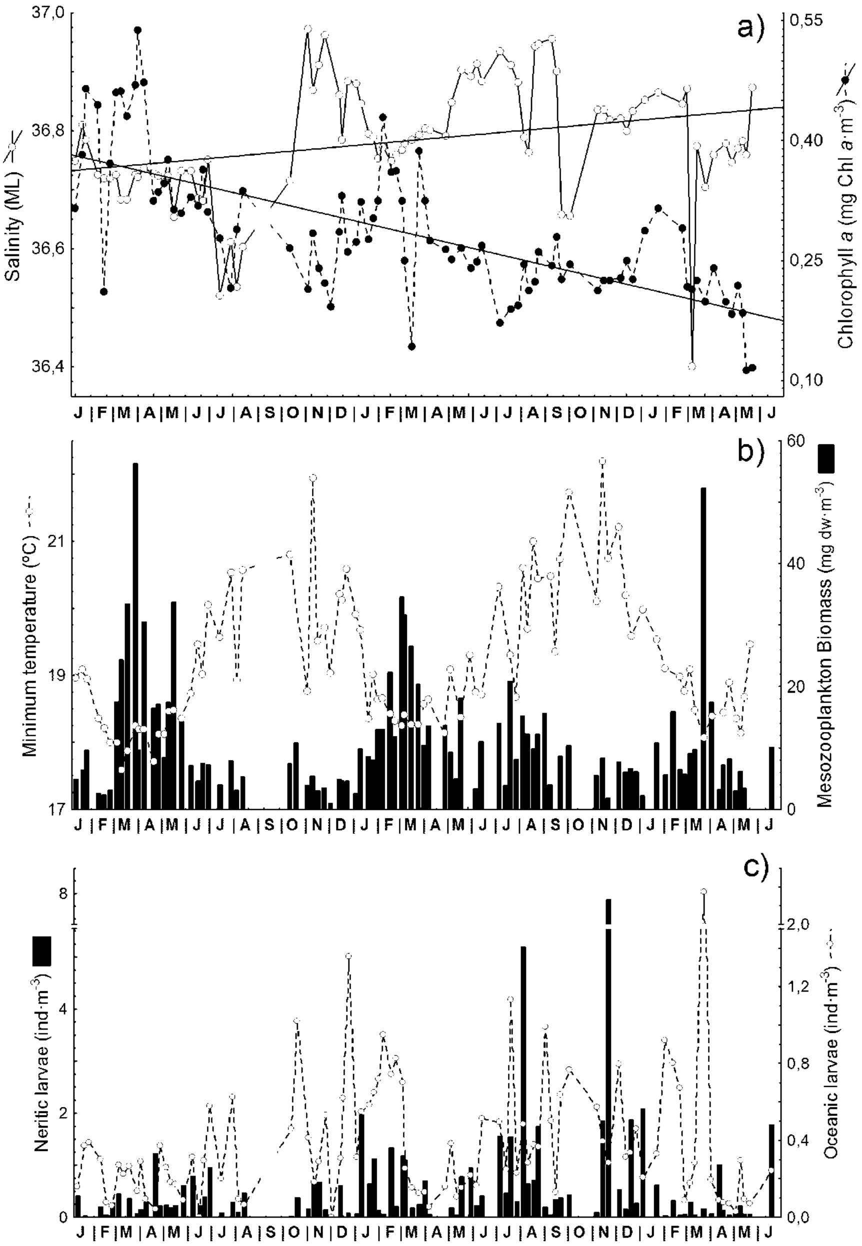

Figure 3. Temporal evolution of **a)** Average salinity in the mixed layer (ML) and chlorophyll a (mg chl $a{\cdot}m^{-3}$), both displaying their linear fit; **b)** Minimum temperature (ºC) and total mesozooplankton biomass (mg dry weight·m^{-3}); **c)** Neritic and oceanic larvae (no. individuals·m^{-3}).

Total mesozooplankton biomass and larval fish abundance were correlated more highly to minimum temperature than to any other environmental variable (Table 1). Neritic larval abundance was significantly correlated to small mesozooplankton biomass, while oceanic larval abundance was significantly correlated to large mezooplankton biomass and salinity (Table 1).

Significant interannual variability was observed in the environmental and biological variables during the late winter bloom period (January-May) (Fig. 4). During 2005, the mixing of the water column was already started in January while in 2007 the mixing period was delayed by one month. Minimum temperature and salinity exhibited higher values in 2007 (KW-ANOVA, $p<0.001$). On the other hand, higher chlorophyll concentrations were reported in 2005, while 2007 registered very low values for this area (KW- ANOVA, $p<0.001$). Low mesozooplankton biomass was also recorded in 2007 (KW- ANOVA, $p<0.001$). Nevertheless, the small mesozooplankton size-fraction exhibited a subtle increase in 2006 (Fig. 4c), while the large size-fraction gradually decreased since 2005 (Fig. 4b). Total larval fish abundance was not influenced by this decreasing pattern and showed significantly higher abundances in 2006 (KW- ANOVA, $p<0.05$).

Table 1. Matrix showing the Spearman´s correlation coefficients for environmental and biotic variables. Abreviations: T min (Minimum temperature, ºC), T max (maximum temperature, ºC), T ML (average temperature in the mixed layer, 20-30 m depth, ºC), S ML (average salinity in the mixed layer), Chl *a* (Chlorophyll *a*, mg Chl *a*·m^{-3}), Sm. Zoop, Lg. Zoop. (Small and Large Zooplankton size fraction Biomass, mg dry weight·m^{-3}), Fish L (Fish Larvae, no·m^{-3}), Neritic L, Oceanic L (Neritic and Oceanic Larvae, no·m^{-3}).

	T min	T max	T ML	S ML	Chl a	Sm Zoop	Lg Zoop	Zoop	Fish L	Neritic L
T min										
T max	0.775**									
T ML	0.796**	0.994**								
S ML	0.361**	0.360**	0.371**							
Chl *a*	-0.338**	-0.355**	-0.341**	-0.368**						
Sm Zoop	-0.330**	-0.196	-0.213	-0.220*	0.168					
Lg Zoop	-0.381**	-0.374**	-0.361**	-0.058	0.260*	0.615**				
Zoop	-0.424**	-0.329**	-0.337**	-0.190	0.255*	0.909**	0.850**			
Fish L	0.419**	0.286**	0.304**	0.301**	-0.056	0.178	0.140	0.164		
Neritic L	0.219*	0.262*	0.266*	0.171	0.024	0.224*	0.076	0.189	0.784**	
Oceanic L	0.339**	0.128	0.174	0.196	0.021	0.125	0.278**	0.177	0.613**	0.140

* ($p<0.05$), ** ($p<0.01$)

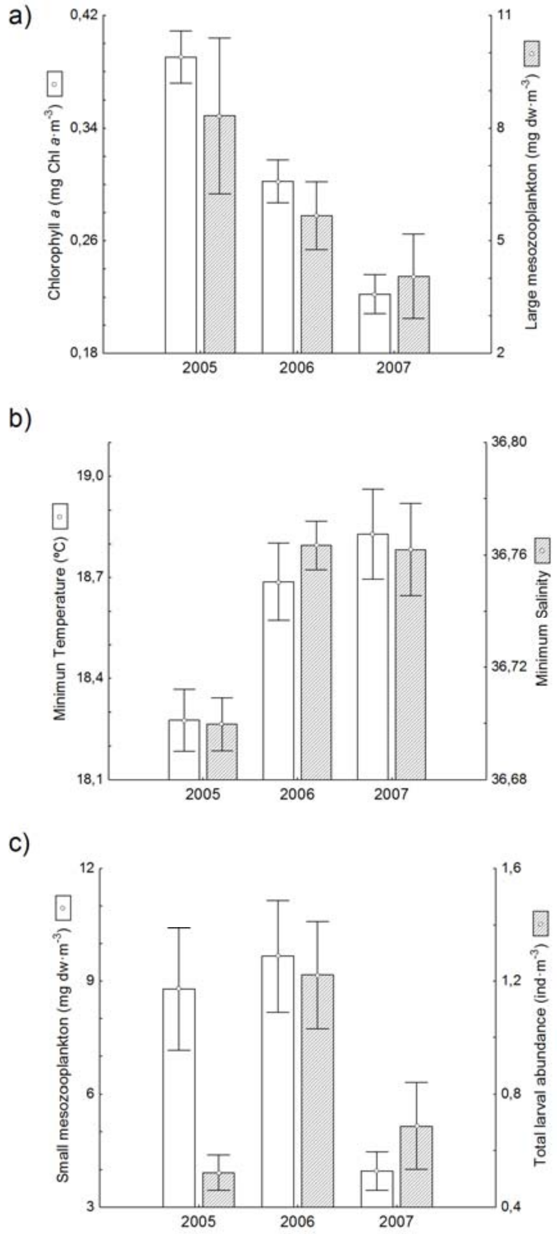

Figure 4. Annual differences in the average values during the late winter bloom period (January-May) of **a)** minimum temperature (ºC) and minimum salinity; **b)** chlorophyll *a* (mg chl *a*·m^{-3}) and large mesozooplankton biomass >1mm (mg dry weight·m^{-3}); **c)** small mesozooplankton biomass <1mm (mg dry weight·m^{-3}) and total larval abundance. Note the inverse pattern between variables included in a) and b).

Ichthyoplankton taxonomic composition

The high diversity in these subtropical waters was reflected in the high number of taxa collected during the study period that included 49 families, 69 genera and 100 species (Table 2). Clupeids and Myctophids contributed almost one half of the total number of larvae collected, 21.9% and 20.5%, respectively. It was also remarkable that only 9 families accounted individually more than 1% to total captured larvae. Also, neritic families were more abundant (50.6% of total larvae) than oceanics (32.8%), with high contributions of sparids (9.8%), gobids (7.3%) and pomacentrids (4.6%).

Sardinella aurita was the most abundant species (17.5% of total larvae collected), followed by *Cyclothone braueri* (6.0%), *Boops boops* (6.0%) and Pomacentridae sp2 (4.1%). Myctophids was the most diverse family, mainly represented by *Lampanyctus* sp (1.8%) and *Notoscopelus* species (1.3%). Similarly to results at family level, only 10 species out of 100 contributed >1% to total number of larvae collected.

Larval fish assemblage structure

ANOSIM routine using a two-way layout nested design for months within years revealed significant differences among months (R=0.281, p=0.001) but not between years (R=0.033, p=0.246). Pairwise tests of months averaged across years identified four different groups: winter (December, January, February, March), spring (April, May, June), summer (July, August, September) and autumn (October, November). However, months belonging to winter and summer were more closely related than those belonging to spring or autumn categories.

This clear temporal pattern was reflected in the clustering and ordination techniques (Fig. 5). Dendrogram was cut at a 40% similarity (Fig. 5a), creating two groups: winter-spring and summer-autumn. March 2007 may be considered as an outlier but August 2005 was clearly different from the summer assemblage average larval composition. The significance of these assemblages was confirmed by SIMPROF. Superimposing the clustering results to the MDS plot re-confirms the validity of the two groups (Fig. 5b). Winter and summer months were more similar to each other than the spring (i.e. May and April) and autumn months (i.e. October and November) whose larval community was a transition between both periods. Although the distance between samples was not perfectly preserved in two dimensions (stress value was high, 0.18), the ordination may be considered valid (Clarke, 1993). After defining the two main assemblages, SIMPER routine was performed in order to describe the species contributing to separate these groups. This analysis revealed that the annual community

Table 2. Taxonomic list of fish larvae collected showing the presence/absence during the year. The percentage contribution of each taxa to the total amount of larvae collected during the study (January 2005-June 2007) is also shown. Hypothesized spawning periods are shaded for those species whose abundances were relatively significant.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	%
FAM.NETTASTOMIDAE													
Nettastoma melanurum (Rafinesque, 1810)							X						0.03
FAM.CLUPEIDAE													
Sardina pilchardus (Walbaum, 1972)	X			X				X					0.17
Sardinella aurita (Valenciennes, 1847)	X	X	X	X	X	X	X	X	X	X	X	X	17.5
Sardinella maderensis (Lowe, 1838)	X					X		X	X	X	X	X	0.78
FAM.ENGRAULIDAE													
Engraulis encrasicolus (Linnaeus, 1758)											X	X	0.24
FAM.BATHYLAGIDAE													
Bathylagidae sp1	X	X										X	0.31
FAM.GONOSTOMATIDAE													
Cyclothone acclinidens (Garman, 1899)							X		X		X	X	0.24
?*Cyclothone alba* (Brauer, 1906)							X						0.03
Cyclothone braueri (Jespersen & Tåning, 1926)	X	X	X	X	X	X	X	X	X	X	X	X	6.04
Cyclothone microdon (Günther, 1878)										X			0.03
Cyclothone pseudopalida (Mukhacheva, 1964)											X		0.03
Cyclothone spp		X			X		X	X		X			0.44
Gonostoma atlanticus (Norman, 1930)							X						0.03
Gonostoma spp					X								0.03
FAM.STERNOPTYCHIDAE													
Argyropelecus hemigymnus (Cocco,1829)		X											0.1
Maurolicus muelleri (Gmelin, 1789)		X											0.07
FAM.CHALIODONTIDAE													
Chauliodus spp		X											0.07
FAM.STOMIIDAE													
Idiacanthus fasciola (Peters, 1877)												X	0.03
Stomias boa ferox (Risso, 1810)	X	X								X		X	0.27
Stomias sp.A	X			X									0.1
Unidentified spp		X											0.14
FAM.PHOTICHTHYDAE													
Vinciguerria attenuata (Cocco, 1938)				X									0.03
Vinciguerria nimbaría (Jordan & Williams, 1896)	X		X	X	X	X							0.24
Vinciguerria poweriae (Cocco, 1938)	X	X			X	X	X				X	X	0.55
Vinciguerria spp	X	X	X	X	X	X					X	X	1.02
FAM.CHLOROPHTHALMIDAE													
Chlorophthalmus sp1					X								0.03
FAM.NOTOSUDIDAE													
Scopelosaurus lepidus (Krefft & Maul, 1955)			X										0.03
FAM.SYNODONTIDAE													
Synodontidae sp.B								X					0.14
FAM.MYCTOPHIDAE													
Benthosema suborbitale (Gilbert, 1913)		X			X								0.07
Ceratoscopelus maderensis (Lowe, 1839)				X	X	X	X						0.41
Ceratoscopelus warmingi (Lütken,1892)	X		X	X	X	X	X	X	X	X	X	X	2.25
Diaphus brachycephalus (Taning,1928)												X	0.03
Diaphus holti (Taning, 1918)										X			0.07
Diaphus metopoclampum (Cocco, 1829)					X				X				0.07
Diaphus mollis (Taning, 1928)	X				X								0.07
Diaphus rafinesquii (Cocco, 1838)										X			0.14
Diaphus spp	X	X			X	X	X	X		X		X	0.55
Diogenichthys atlanticus (Tåning, 1918)	X	X	X	X	X		X		X		X		0.78

Table 2 (cont.)

Gonichthys cocco (Cocco, 1829)	X												0.03
Hygophum benoiti (Cocco, 1838)		X					X			X	X	X	0.55
Hygophum benoiti (Cocco, 1838)		X					X			X	X	X	0.55
Hygophum hygomii (Lütken, 1892)	X	X	X							X	X	X	0.55
Hygophum macrochir (Günther, 1864)	X		X				X	X			X	X	0.48
Hygophum reinhardtii (Lütken, 1892)	X			X	X		X		X		X	X	0.41
Hygophum taaningi (Becker, *1965*)	X		X		X			X			X	X	0.44
Hygophum spp	X	X							X	X		X	0.34
Lampadena spp	X	X			X		X	X	X	X	X	X	1.02
Lampadena sp1	X												0.1
Lampanyctus sp.A	X									X			0.1
Lampanyctus spp	X	X	X	X	X	X	X	X	X	X	X	X	1.84
Lepidophanes guentheri (Goode & Bean, 1896)		X					X		X		X		0.27
Lobianchia dofleini (Zugmayer, 1911)	X	X	X		X	X						X	0.82
Lobianchia gemellarii (Cocco, 1938)	X	X	X	X	X							X	0.58
Lobianchia spp	X	X	X								X	X	0.82
Myctophidae sp.A					X								0.03
Myctophidae sp.B					X	X	X						0.34
Myctophidae sp.C		X	X										0.07
Myctophidae sp.D				X	X	X			X				0.82
Myctophidae sp.D										X			0.1
Myctophidae sp.E	X												0.1
Myctophum nitidulum (Garman, 1899)		X								X	X	X	0.27
Myctophum selenops (Tåning, 1928)		X						X			X		0.17
Nannobrachium atrum (Tåning, 1928)											X	X	0.07
Nannobrachium lineatum (Tåning, 1928)		X				X		X					0.14
Notolychnus valdiviae (Brauer, 1904)									X				0.03
Notoscopelus resplendens (Richardson, 1845)	X	X	X										0.24
Notoscopelus spp	X	X	X	X	X	X	X			X		X	1.33
Symbolophorus spp	X	X	X	X	X								0.2
FAM.EVERMANELLIDAE													
Evermanella balbo (Risso, 1820)		X										X	0.1
FAM.PARALEPIDAE													
Lestidiops jakari pseudospyraenoides (Ege, 1918)	X												0.03
Lestidiops spp									X				0.07
Sudis hialina (Rafinesque, 1810)	X	X						X					0.17
FAM.LOPHIIDAE													
Lophius piscatorius (Linnaeus, 1758)	X												0.03
FAM.GADIDAE													
Phycis sp												X	0.03
FAM.CENTRISCIDAE													
Macroramphosus scolopax (Linnaeus, 1758)	X	X							X				0.24
FAM.MELAMPHAIDAE													
Melamphaes simus (Ebeling, 1962)	X								X			X	0.17
FAM.CENTRISCIDAE													
*Capros ape*r (Linnaeus, 1758)	X											X	0.1
FAM.SERRANIDAE													
Anthias antias (Linnaeus, 1758)	X		X	X	X	X	X	X	X	X	X	X	1.71
Serranus cabrilla (Linnaeus, 1758)					X	X		X				X	0.24
Serranus sp.		X	X	X	X						X		0.27
SERRANIDAE SP 1	X		X										0.07
FAM.APOGONIDAE													
Apogon imberbis (Linnaeus, 1758)							X	X					0.07
FAM.CARANGIDAE													
Trachurus pictoratus (Bowdich, 1825)	X	X	X										0.14
FAM-CORYPHAENIDAE													
Coryphaena hippurus (Linnaeus, 1758)			X		X			X					0.2
FAM.MULLIDAE													
Mullus barbatus (Linnaeus, 1758)					X								0.03
FAM.BRAMIDAE	X	X											0.17

Table 2 (cont.)

FAM.SPARIDAE													
Boops boops (Linnaeus, 1758)	X	X	X	X	X	X	X				X	X	6.04
Diplodus spp	X	X	X	X	X		X	X		X			1.84
Oblada melanura (Linnaeus, 1758)					X				X				0.34
?*Pagellus acarne* (Risso, 1826)	X			X									0.17
Pagellus bogaraveo (Brünnich, 1768)	X			X							X	X	0.44
Pagellus erythrynus (Linnaeus, 1758)	X												0.03
Pagellus spp		X											0.03
Pagrus pagrus (Linnaeus, 1758)	X				X	X							0.17
FAM.CENTRACANTHIDAE													
Centracanthus cirrus (Rafinesque, 1810)	X									X			0.07
FAM.SPHYRAENIDAE													
Sphyraena sp.							X						0.03
FAM.LABRIDAE													
Coris julis (Linnaeus, 1758)		X			X	X	X	X					0.31
LABRIDAE		X					X	X					0.24
Thalassoma pavo (Linnaeus, 1758)	X										X		0.07
FAM.SCARIDAE													
Sparisoma cretense (Linnaeus, 1758)								X					0.07
FAM.POMACENTRIDAE	X	X	X	X								X	0.51
Pomacentridae sp1					X	X	X	X	X	X	X		4.09
Pomacentridae sp2													
FAM.CHIASMODONTIDAE												X	0.03
Chiasmodon niger (Jonhson, 1864)													
FAM.TRACHINIDAE								X					0.03
Trachinus draco (Linnaeus, 1758)				X									0.03
Trachinus spp													
FAM.GEMPYLIDAE	X	X	X				X	X				X	0.24
Diplospinus multistriatus (Maul, 1948)								X				X	0.07
Nealotus tripes (Jonhson, 1865)					X		X						0.1
Unidentified spp													
FAM.TRICHIURIDAE	X											X	0.14
Benthodesmus elongatus (Clarke, 1879)													
FAM.SCOMBRIDAE		X										X	0.07
Sarda sarda (Bloch, 1793)	X	X		X									0.17
Scomber colias (Houttuyn, 1792)													
FAM.BLENNIDAE			X	X	X	X	X	X		X			0.99
Ophioblennius atlanticus (Valenciennes, 1836)						X							0.03
Scartella cristata (Linnaeus, 1758)													
FAM.GOBIIDAE					X		X						0.07
Lebetus guilletii (Le Danois, 1913)	X			X				X				X	0.17
Lebetus sp	X	X	X	X	X	X	X	X	X	X	X	X	7.09
Unidentified spp													
FAM.OPHIDIDAE								X					0.03
Paraophidion vassali (Risso, 1810)							X	X	X				0.17
Unidentified spp													
FAM.NOMEIDAE							X						0.07
Nomeidae sp.1													
FAM.TETRAGONURIDAE												X	0.03
Tetragonurus atlanticus (Lowe, 1839)													
FAM.SCORPAENIDAE								X				X	0.14
Scorpaena porcus (Linnaeus, 1758)	X				X		X	X				X	0.38
SCORPAENIDAE	X					X							0.07
FAM.TRIGLIDAE													
FAM.BOTHIDAE							X		X				0.07
Arnoglossus thori (Kyle, 1913)								X					0.07
Arnoglossus spp							X			X			0.1
Bothus podas (Delaroche, 1809)								X		X			0.27
Bothus spp													
FAM.MONACANTHIDAE								X					0.03
Stephanolepis hispidus (Linnaeus, 1766)						X	X	X		X			0.65
FAM.TETRAODONTIDAE													

was mainly composed by *C. braueri*, *S. aurita*, *Lampanyctus* spp, *Notoscopelus* spp, *Ceratoscopelus warmingii* and Gobidae species. The changes in abundance of these species constituted a fundamental character distinguishing each assemblage, as well as presence/absence of some characteristic species of each group. Therefore, the winter assemblage was basically distinguished by the presence of *Boops boops* (23.3% contribution to the Bray-Curtis similarity within the assemblage) and the relatively high abundances of *C. braueri* (20.6%), *S. aurita* (13.2%), *Notoscopelus* sp (7.0%) and lower values of Gobidae species (13.1%). Also, the presence of *Lobianchia dofleini* and Pomacentridae sp1 typify this group. The absence of *S. aurita* in March 2007 made it different from the other years. On the other hand, the summer assemblage was dominated by Gobiid species (20.7% contribution to the Bray-Curtis similarity within the assemblage), *C. braueri* (20.4%) and *C. warmingii* (14.8%). Also, the presence of

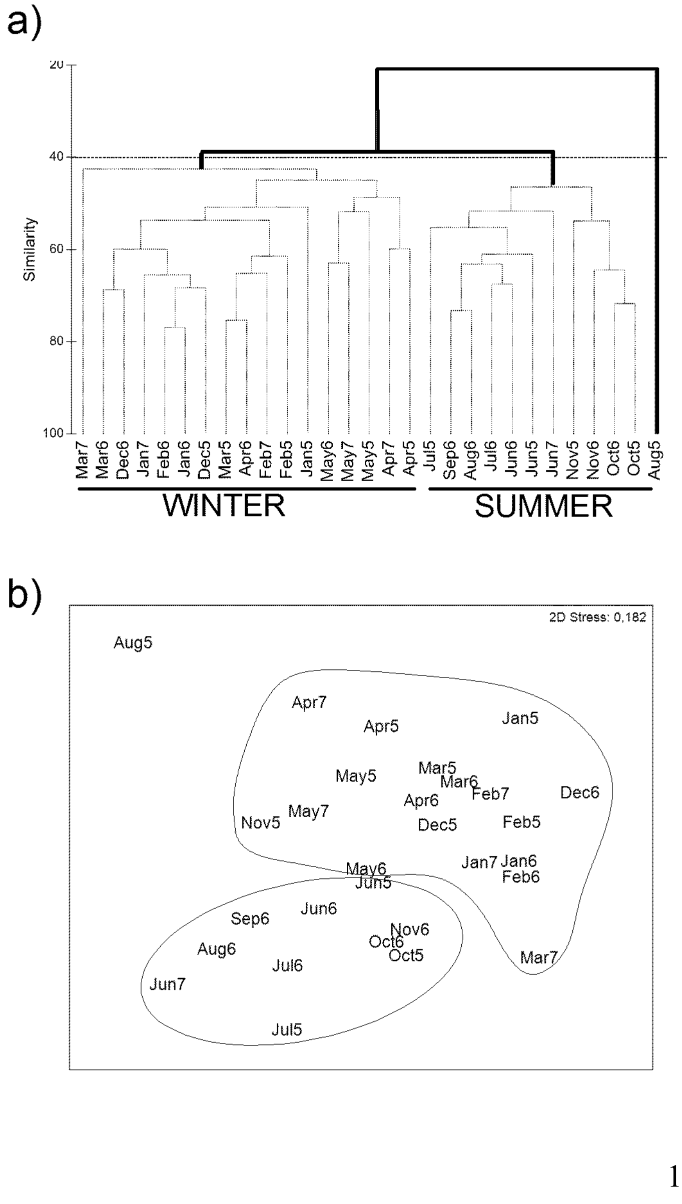

Figure 5. Clustering and ordination representations of the larval fish assemblage from January 2005 to June 2007. **a)** Hierarchical cluster from the species density matrix. Three groups are identified (darker line) according to the similarities profile results (SIMPROF): winter, summer and August 2005. **b)** Multidimensional scaling (MDS) showing the distribution of the samples within the same three groups as 4a.

Pomacentridae sp2 and *Anthias anthias* differentiate this group. The larval composition during August 2005 was quite different from that of the typical summer assemblage since this month was characterized by the presence of a suite of Myctophid species and other species such as *Sardina pilchardus* and *Engraulis encrasicolus*.

Cluster and PCA plots also revealed patterns in the environmental variables with time (Fig. 6). Cluster representation (Fig. 6a) identified 4 groups: (1) Winter-spring; (2) Summer-autumn; (3) months of upwelling filaments arrival to the eastern shores of Gran Canaria; and (4) LWB period. Subsequently, PCA was used to highlight the contribution of maximum temperature and salinity on the mixed layer to explain the variability of the samples (Table 3). PC1 explained more than 50% of the variance and was mainly composed by temperature. Though, PC2 (19.8%) was defined by salinity. The four groups generated in the cluster (Fig. 6a) were also well separated in the PCA representation (Fig. 6b): (1) The Winter-spring samples displayed low to moderate values of temperature and salinity; (2) Summer-autumn was characterized by high water temperatures; (3) the Upwelling group was identified by low salinity values in the mixed layer; and (4) LWB exhibited high chlorophyll and zooplankton values. Although upwelling filaments found in summer 2005 were perfectly detected by remote sensing (Moyano *et al.*, 2009), in that of February 2007, cloud cover precluded any conclusion. As expected considering PCA results, BEST Bio-Env returned the highest correlation in a combination of maximum temperature and salinity in the mixed layer (0.416 $p<0.01$), while only temperature explained the variability in a 37.1%.

Table 3. Eigenvalues for the two principal components (PC) axes derived from the principal components analysis (PCA) on the 5 environmental variables analyzed in the study.

Environmental variables	PC1	PC2
Maximum Temperature	0.702	-0.083
Salinity Mixed Layer	0.166	-0.765
Chlorophyll *a*	-0.476	0.229
Small Mesozooplankton	-0.346	-0.486
Large Mesozooplankton	-0.365	-0.345

Discussion

The present study has recorded a larval fish community similar to that found in other studies in the region, in terms of larval abundance and composition (Bécognée *et al.*, 2006; Moyano *et al.*, 2009). Nevertheless, the contribution of neritic larvae was slightly higher than in previous works (Moyano *et al.*, 2009) due to the location of the sampling area, near a retention spot for neritic species upstream of the island (Rodríguez *et al.*, 2001). In addition, total larval abundance did not show any seasonality, suggesting that shorter time-scales might have stronger effects on this temporal planktonic community (e.g. hydrography, local productivity, lunar phase).

The high fish diversity in the area is typical from subtropical waters (Longhurst and Pauly, 1987). This diversity would influence the larval fish assemblage structure, as membership would be dynamic, similarly to what has been reported in the highly diverse coastal area off SW Australia (Gray and Miskiewicz, 2000) and Northern Chile (Rodríguez-Graña and Castro, 2003). Both of those studies reported a seasonal pattern with the presence of some larvae characteristic of a particular season whereas other dominant taxa persisted year-round (which may or may not display seasonal peaks). This is also the case of Gran Canaria Island where a few abundant taxa dominate the annual assemblage: *C. braueri, S. aurita* and Gobiidae larvae. *C. braueri* was found every month. Although *C. braueri* is known to spawn from April to October in Mediterranean waters (CLOFNAM), McKelvie (1989) concluded that in lower latitudes this spawning period might be extended. *S. aurita* spawns year-round off Gran Canaria displaying larval abundance peaks in winter, supporting data reported by Bécognée *et al*. (2006). Although Gobids' spawning strategies differed between species, higher abundances were found in warmer months during this study.

Two seasonal larval fish assemblages were identified in this work: winter-spring and summer-autumn. These assemblages corresponded to annual variations in temperature. A winter assemblage was found when the water column was mixed and characterized by low water temperature, medium salinity and medium-high values of chlorophyll concentration and mesozooplankton abundance (LWB period). Regarding the larval fish community, *S. aurita*, *C. braueri* and *B. Boops* were the most abundant during this period. The former two species are year-round components of the larval

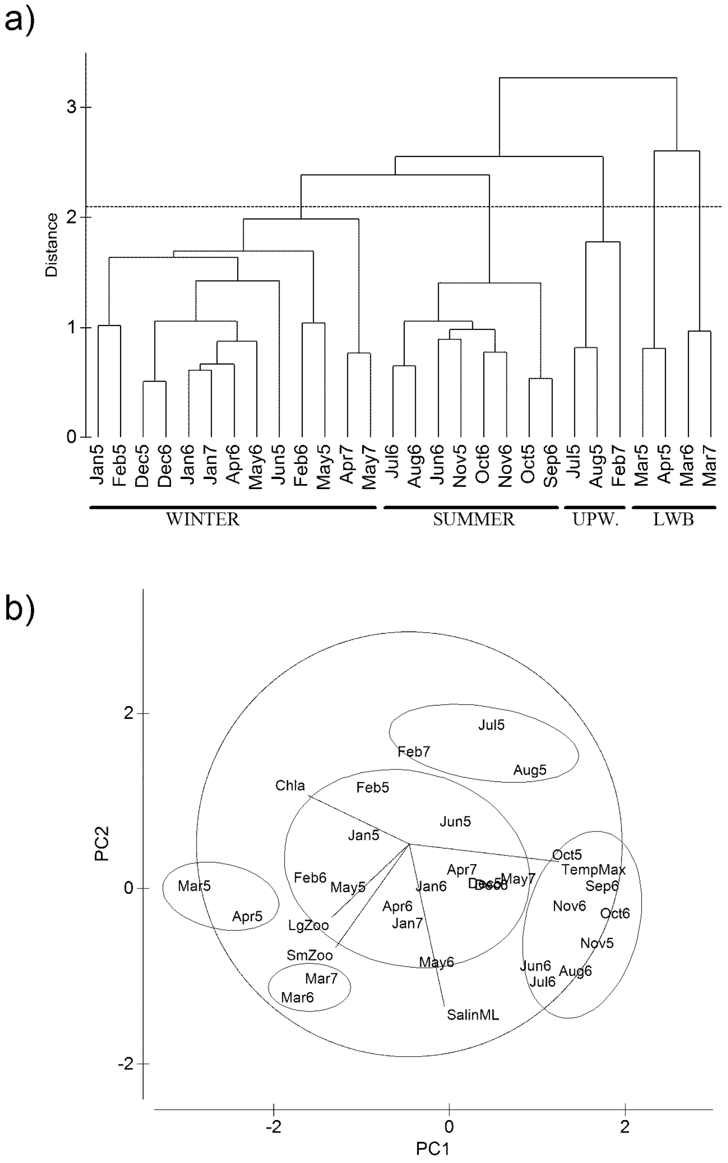

Figure 6. Clustering and ordination representations of the environmental variables from January 2005 to June 2007. **a)** Hierarchical cluster from the environmental data matrix. Four groups are identified: winter-spring (WINTER), summer-autumn (SUMMER), samples in which the influence of upwelling filaments reaching the eastern shore of Gran Canaria was registered (UPW.) and late winter bloom (LWB). **b)** Principal components analysis (PCA) ordination for all sampled months, displaying the vectors for the five studied variables. TempMax: Maximum temperature. SalinML: Salinity in the mixed layer. SmZoo: Small Zooplankton. LgZoo: Large zooplankton. Chla: chlorophyll *a*.

assemblage while the latter is a winter spawner (November-March in Gran Canaria Island, Franquet and Brito, 1995). In addition, this assemblage was also characterized by Pomacentridae sp1 and *Lobianchia dofleini*, as well as the presence of some typical winter spawners such as *Pagellus bogaraveo* (Bauchot and Hureau, 1986; Stockley *et al.*, 2005). The presence of *Stomias* sp and *Bathylagus* sp also characterized this group despite their low concentrations. However, species belonging to each of those genera may not display the same reproductive strategies. In this sense, Rodríguez (2000) and Rodríguez *et al.* (1999; 2004) found both genera during summer and autumn in the oceanic region of the African-Canaries coastal transition zone. Therefore, the conditions in the water column around Gran Canaria in winter are somehow suitable for these offshore species, seeming to contribute to the annual larval assemblage in the oceanic region.

Despite the strong Trade Winds, the summer assemblage occurred when the water column was stratified and surface waters were characterized by high salinity, and low chlorophyll and mesozooplankton values. Gobids and *C. braueri* were important components of this assemblage, but it is the higher abundance of *Ceratoscopelus warmingii*, Pomacentridae sp2, *Lampanyctus* spp and *Anthias anthias* that characterizes this season. *C. warmingii* presents a broad worldwide distribution pattern in tropical areas (Bekker, 1983) and its larvae contributed year-round to the ichthyoplankton of the Central North Pacific (Loeb, 1980). Little is known about their reproduction in Canary waters, but this species seems to spawn during the whole year peaking in the warmer months in Azores (Sobrinho-Gonçalves and Isisdro, 2001), which is in accordance with our results. A similar spawning strategy was displayed by *Anthias anthias*, a species found in high abundances together with *Engraulis encrasicolus* larvae during summer by Rodríguez *et al.* (2001; 2004), what would support our findings. Some other species were only found during these warmer months, such as *Trachinus draco*, *Arnoglossus thori* and Tetraodontidae sp1. In the Mediterranean, *T. draco* is also known to be a summer spawner (Sabatés, 1990; Hoşusu and Ak, 2002) while *A. thori* spawns during summer and autumn (Sabatés, 1990; Macpherson and Raventos, 2006), which is in agreement with our results.

In August, trade winds reach their maximum intensity in the area (Barton *et al.*, 1998) and thus very likely influence variability in upwelling mesoscale features and the zoo- and ichthyoplankton composition in the Canaries. The influence of trade winds was reflected by the giant upwelling filaments that reached the eastern shores of Gran Canaria during July and August 2005 (Moyano *et al.*, 2009). Although another upwelling filament was also detected in February 2007, variations in the local larval community were only detected in samples from August 2005. During this month, a higher contribution of mesopelagic species and also the presence of *Sardina pilchardus* and *Engraulis encrasicolus* (Moyano *et al.*, 2009) were registered compared to months included in the summer assemblage. The contribution of those transported clupeoid larvae to the island's local populations has been debated in several works (Rodríguez *et al.*, 1999; Rodríguez *et al.*, 2004; Bécognée *et al.*, 2006; Moyano *et al.*, 2009). However, the present study is the first work to demonstate that the arrival of an upwelling filament to Gran Canaria significantly influenced the island's summer larval fish assemblage. Nevertheless, more intensive sampling, both temporal and spatially may be needed to adequately assess the ultimate effects that these mesocale structures have on the local community.

Interannual variability

Environmental variables exhibited a remarkable interannual shift during the LWB period. However, their influence on total larval abundance was not clear. Average annual temperatures in 2005 seemed to be within the range of those found previously in the area (Bécognée *et al.*, 2006), while salinity was lower. Similarly, chlorophyll a concentrations recorded during 2005 were similar to those previously documented in studies in the area (Arístegui *et al.*, 2001), but the decreasing values of the subsequent years were remarkable (Fig. 3). Total mesozooplankton biomass was also in the range of previous studies (Hernández-León *et al.*, 2004; Hernández-León *et al.*, 2007), although their average annual values also showed a slight fall due to the decline of the large size-fraction (Fig. 4). Therefore, this interannual variability is evident considering the increasing trend of minimum temperature and salinity and the inverse pattern for chlorophyll and mesozooplankton biomass. According to our results, the magnitude of the LWB seems to vary depending on temperature, being those <19ºC within the mixed layer a good indicator. During colder years, the mixing period starts earlier, promoting the beginning of the bloom and so, phytoplankton and zooplankton biomass may reach higher values. This would be the case in 2005. On the other hand, during warmer years such as 2007, the LWB started later and may cause lower plankton densities during this period. The case of 2007 is specially striking because the mixing period started in mid February when it often begins in January (Arístegui *et al.*, 2001; Hernández-León *et al.*, 2004). This delay together with the subtle temperature increase in early March that lasted a couple of weeks, made the phytoplankton kick-off less effective than before (as deduced from the low chlorophyll concentrations).

In order to explain this interannual variability, the North Atlantic Oscillation (NAO) index was considered. The winter NAO index was 0.21 in 2005,0.24 in 2006 and 0.63 in 2007, which can be inversely correlated with the average LWB biomass of small mesozooplankton (January-May) (Fig. 4c). This relationship has been previously mentioned (Fromentin and Planque, 1996; Fernandez de Puelles *et al.*, 2004; Fernández de Puelles *et al.*, 2007). In our study, the monthly NAO index was better correlated to small mesozooplankton biomass (R=-0.33, p<0.05), as reported in the Balearic Islands (Fernández de Puelles and Molinero, 2007). In relation to fish larvae, the longer life cycles of fish do not have the same immediate response to changes in temperature compared to zooplankton. Thus, the higher abundances during 2006 may be a consequence of the enhanced production during 2005. Although this is the first time that the influence of the NAO is found in the planktonic community in the Canary Islands, the influence of this index on decadal *Sardina pilchardus* productivity in the NW African upwelling region has been proposed several times (Borges *et al.*, 2003; Santos *et al.*, 2005). Therefore, longer time series may shed some light on the interannual variability of this bloom and the possible consequences on the planktonic and fish communities in the Canary Islands.

In conclusion, this work revealed that the larval fish assemblage off Gran Canaria Island exhibited a clear seasonal variation in accordance with the physical and/ or biological properties of the water column. Assemblages are specific, multispecies grouping that reflect the synchrony and cohesion in the spawning pattern of adults (Frank and Leggett, 1983). Thus, in our study region, the dynamics of larval fish assemblages found can be explained by both high species diversity and the extended spawning periods of most of the species inhabiting these subtropical waters. This study has revealed some useful trends in the understanding of the seasonality of the planktonic community off Gran Canaria Island and the Canaries archipelago. It also provides a basis for future studies on ichthyoplankton in the area, emphasizing the unique contribution of the early life stages and their linkage to adult spawning pattern for fisheries and marine reserves management purposes off the Canary Islands.

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CHAPTER V

MESOSCALE DISTRIBUTION OF CLUPEOID LARVAE IN AN UPWELLING FILAMENT TRAPPED BY A QUASI-PERMANENT CYCLONIC EDDY OFF NORTHWESTERN AFRICA

P. Bécognée, M. Moyano, C. Almeida, J.M. Rodríguez, E. Fraile-Nuez, A. Hernández-Guerra, S. Hernández-León (2009) Mesoscale distribution of clupeoid larvae in an upwelling filament trapped by a quasi-permanent cyclonic eddy off Northwest Africa. *Deep Sea Research I* 56(3): 330-343.

Abstract

The distribution of fish larvae in relation to a filament shed from the Northwest African coastal upwelling was studied in February 2001. During the cruise, the filament was located between 27ºN and 28º N, extending from the African coastal upwelling zone to the south of Fuerteventura Island (Canary Islands). This filament was trapped and remained over the quasi-permanent cyclonic eddy observed in previous studies. Almost all *Sardina pilchardus*, *Engraulis encrasicolus* and *Sardinella aurita* larvae caught during the cruise were associated with upwelled waters and filament structures. The sampled larval fish assemblage was composed by 12.6% of clupeoid larvae. These were distributed as follows: 73.9% were *S. pilchardus*, 20.7% were *E. encrasicolus* and 5.4% were *S. aurita*. Their distribution suggested that the coastal upwelling filament is a mechanism of transport from the upwelling area to oceanic waters, but its junction with the generated cyclonic eddy may not always work as a retention structure for those transported larvae, as described in previous studies. Physiological studies based on gut fluorescence and ETS activity of clupeoid larvae, as proxies for grazing and respiration, respectively, denoted a switch from pigmented food near the upwelling zone to unpigmented food toward the ocean. This pattern agrees with observed mesozooplankton feeding along an upwelling filament in previous studies. Therefore, this work confirms the close relationship between clupeoids distribution and mesoscale circulation, as well as constitutes the first assessment of the metabolic activity of those larvae in the region.

Key words: fish larvae, clupeoids, filament, cyclonic eddy, Canary Islands.

Introduction

The Canary Islands Archipelago is located on the eastern flank of the North Atlantic subtropical gyre in the main path of the Canary Current. This current has been described as a weak flow in a south-southwest direction, fed by the Azores Current (Stramma and Siedler, 1988; Hernández-Guerra *et al.*, 2001). The Canary Islands act as a barrier to the Canary Current giving rise to mesoscale oceanographic processes (Hernández-Guerra *et al.*, 1993; Arístegui *et al.*, 1994; Hernández-León *et al.*, 2001). Much of the mesoscale variability in the region, such as cyclonic and anticyclonic eddies, is related to the perturbation of the mean incident flow by the island chain, forming Von Karman vortex street (Arístegui *et al.*, 1994, 1997; Barton *et al.*, 1998, 2004). This kind of eddy generation can also be favoured by the perturbation of the trade winds through Ekman pumping in the islands′ wakes (Barton *et al.*, 2000). Another factor that favours cyclogenesis is potential vorticity conservation as the flow encounters deeper waters on leaving the channels between the islands as observed by Navarro-Pérez and Barton (1998) and Barton *et al.* (2004) south of Fuerteventura Island.

Other mesoscale features described for this area are the upwelling filaments originating in the upwelling system off Northwest (NW) Africa between Cape Juby and Cape Bojador (Borges *et al.*, 2004). These filaments are elongated features consisting of colder and fresher upwelled water, rich in nutrients, shed from the coastal upwelling waters into the open ocean. They are originated either (1) by the presence of mesoscale eddies that draw recent upwelled water away from the coast or (2) by the meandering of the upwelling front, which entrains coastally upwelled waters nearshore and creates filaments of cold water (Ramp *et al.*, 1991; Strub *et al.*, 1991). Upwelling filaments were described in different upwelling areas such as California (Traganza *et al.*, 1980; Kosro and Huyer, 1986; Brink and Cowles, 1991), Benguela (Schillington *et al.*, 1990; Nelson *et al.*, 1998) and NW Africa (Hagen *et al.*, 1996; Barton *et al.*, 1998; Navarro-Pérez and Barton, 1998).

In the NW Africa region, Barton *et al.* (1998) and Navarro-Pérez and Barton (1998) found that a quasi-permanent cyclonic eddy, trapped between the African coast and the Canary Islands, promoted the formation of filaments. These filaments are considered to be an offshore transport mechanism for nutrients and phytoplankton

(García-Muñoz *et al.*, 2004), zooplankton (Hernández-León *et al.*, 2001, 2002) and ichtyoplankton (Rodríguez *et al.*, 1999, 2004). These structures can frequently reach the eastern islands of the Canary Archipelago (La Violette, 1974; Van Camp *et al.*, 1991; Hernández-Guerra *et al.*, 1993; Barton *et al.*, 1998; Navarro-Pérez and Barton, 1998; Bécognée *et al.*, 2006). Therefore, upwelling filaments play a fundamental role in the horizontal distribution of African neritic larvae in the region. Moreover, those larvae transported offshore by the filament are likely to be entrained around the trapped cyclonic eddy, which may return the larvae to the nearshore region, not far from their place of origin. This was the case found by Rodríguez *et al.* (1999), who observed a high concentration of clupeoid larvae (*Sardina pilchardus*, *Sardinella aurita* and *Engraulis encrasicolus*) inside a filament. However, a small number of larvae may be recruited into the Canary Island waters, thereby refreshing the island populations (Bécognée *et al.*, 2006). The recurrence of the quasi-permanent cyclonic eddy suggests that the filament and the associated eddy may constitute an "ocean triad" (Bakun, 1998). Three major physical processes are combined to yield a favourable reproductive area for African coastal pelagic species: enrichment (upwelling system), concentration (eddy) and retention within this appropriate habitat (filament-cyclonic eddy complex).

The aim of this work was to study the dynamics of transport of neritic larvae from the upwelling zone to the open ocean or to the eastern islands of the Canary Archipelago. This transport was carried out by an upwelling filament that, in this case, was trapped by a quasi-permanent cyclonic eddy, maintaining the larvae in the oceanic domain. The study is focused on three clupeoid species, *S. pilchardus*, *E. encrasicolus* and *S. aurita*. *S. pilchardus* constitute the backbone of the fisheries industry of Morocco since 1920s (Kifani, 1998) and represents on average >70% of total fish catches (FAO, 2005) in the NW African upwelling, while *E. encrasicolus* account for 2.0% (FAO, 2005). *S. aurita*, on the other hand, is less commercially important. Decadal fluctuations in small pelagic fishes in the Canary upwelling system were related to environmental changes (e.g. Kifani, 1998; Santos *et al.*, 2005). The latter authors showed a decrease in the *S. pilchardus* catches (70-40%) and an increase of *S. aurita* (0-20%) during 1994-1995 due to an abrupt increase in the upwelling intensity. Also, Rodríguez *et al.* (2004) found a higher contribution of *E. encrasicolus* during summer 1999 in relation to a previous survey in 1993 (Rodríguez *et al.*, 1999) which was attributed to higher values of sea-surface temperature (SST) in 1999. In the Canary Islands, these three species are an important commercial resource, mainly because of their use as live bait for tuna fishing (Ramos *et al.*, 1995). Their scarcity causes serious problems to local fisheries as they are unable to capture the more valuable species. Insights of spawning periods, recruitment and other physical environmental conditions influencing fish populations, such as the transport of fish larvae from the upwelling area to the islands, are thus essential for fisheries management around the archipelago. However, such studies are scarce or lacking in the region, and there is an important gap in the comprehension of the dynamics of the marine fish populations in the Canary Islands. In the present work, a preliminary assessment of the metabolic activity of larvae was also performed. The objective was to provide new insights into larval condition as these organisms are advected away from the upwelling area.

Materials and Methods

Sampling was carried out from February 20th to March 2nd. 2001 onboard R.V. “García del Cid” during the cruise “Pelagic 0102”. The oceanographic survey consisted of 18 stations located between the Canary Islands and the upwelling area off NW Africa. Stations were distributed in four transects crossing the cyclonic eddy (transects 2-4) and the associated filament (transect 1), south of Fuerteventura Island (Fig. 1).

At every station, conductivity, temperature, depth (CTD) and fluorescence casts were carried out from surface to 2000 m depth with a Neil Brown Mark-III probe. Sea-surface temperature images from the advanced very-high-resolution radiometer (AVHRR) sensor on board the NOAA-16 satellite were processed using the algorithm developed by Eugenio *et al*. (2005). Chlorophyll concentration images from the Sea-viewing Wide-Field-of-view Sensor (SeaWiFS) on board the SeaStart satellite were processed using Seadas software. Time series of the component of the velocity vector in the direction of the maximum variance (southwestward) were calculated from a current meter mooring located at 28º44’N, 13º28’W, in the Lanzarote passage at 291m depth (Hernández-Guerra *et al.*, 2003).

Zooplankton and ichtyoplankton samples were collected with a Longhurst–Hardy Plankton Recorder (LHPR, Longhurst and Williams, 1976) equipped with a 200 μm mesh net and a flowmeter to measure the volume of filtered water. Hydrographic

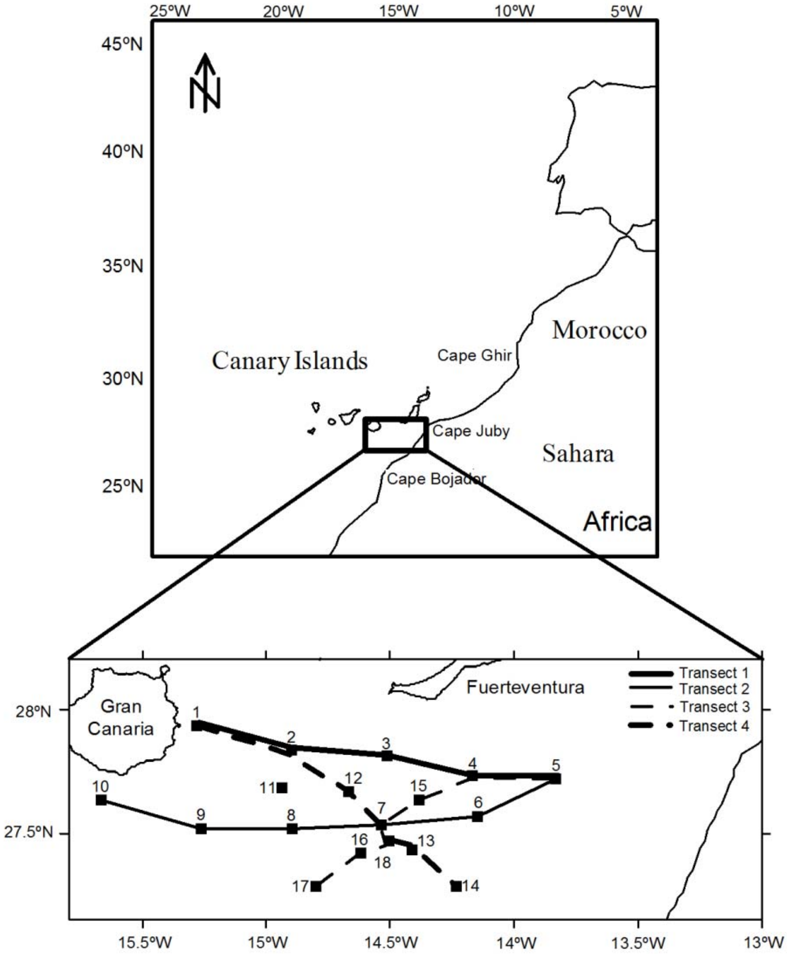


Figure 1. Location of the study area and sampling stations.

conditions (conductivity, temperature, fluorescence and depth) were also measured by a CTD sensor coupled to the LHPR. Tows were conducted at 3 knots for almost 1h. The 200 µm mesh screen in the sampler was programmed to increment at 2-minute intervals during the descent of the net. About 14–18 samples (representing 14–18 layers with a vertical resolution of about 10–20 m) were obtained in each haul from subsurface to 200 m. The volume of water filtered by the net varied between 4 and 35 m^3 per sample. Total fish larvae and larvae of clupeoid species (*S. pilchardus*, *S. aurita* and *E. encrasicolus*) were sorted. Also, from each sample, a subsample of zooplankton, total larvae and those clupeoid species were picked and stored in liquid nitrogen (-196 ºC) for further studies of the indices of grazing (gut fluorescence–GF), respiration (electron

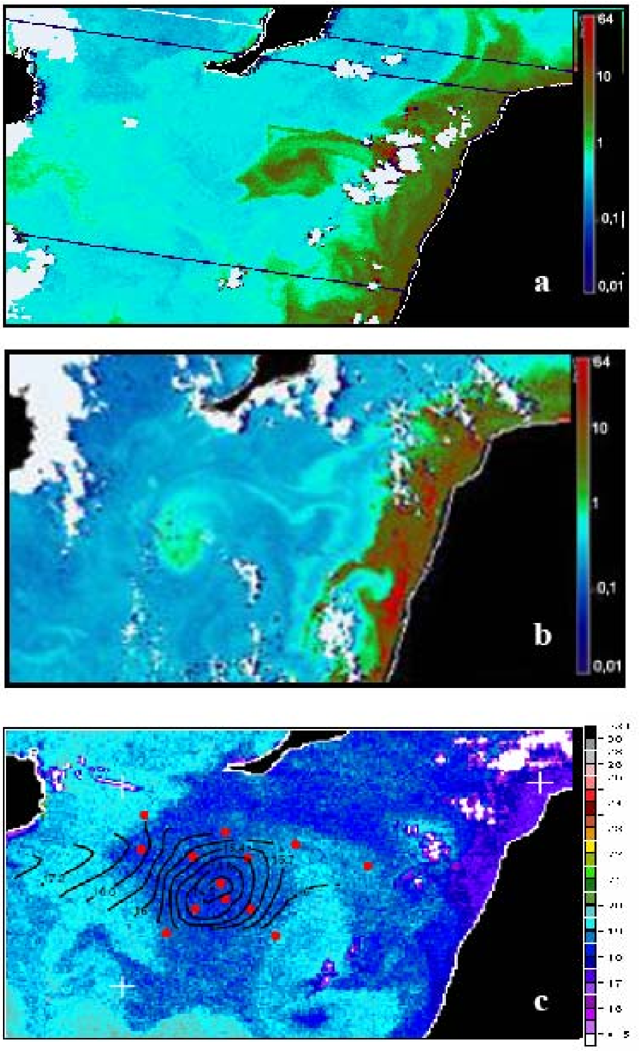


Figure 2. (a) Phytoplankton pigment distribution (mg chlorophyll·m^{-3}) from the Sea-Viewing Wide-Field Sensor (SeaWiFS) for February 13th, 2001 and **(b)** February 27th, 2001. (c)Sea-surface temperature (SST) forMarch 2nd, 2001 together with the temperature (ºC) contour at 175m depth during the cruise. Notice the upwelling filament waters trapped by a cyclonic eddy south of Fuerteventura Island.

transfer system (ETS) activity), growth (aminoacyl-tRNA synthetase (AARS) activity) and protein content. The remaining samples were preserved in 4 % buffered formaldehyde for further taxonomic analysis.

Once in the laboratory, the larval subsamples were homogenized by an ultrasonic processor (Cole Parmer) for protein, ETS, AARS and GF analysis, while in the zooplankton subsamples only protein analysis was carried out. In both cases, protein content, used as an index of biomass, was assayed following the method proposed by Lowry *et al.* (1951) modified by Rutter (1967) using bovine serum albumin (BSA) as standard. ETS activity was measured according to Kenner and Ahmed (1975) with the modifications introduced by Gómez *et al.* (1996). Details of this procedure are also given in Hernández-León and Gómez (1996). In order to assure a proper comparison between respiration rate and ETS, the enzymatic activity was recalculated for the *in situ* temperature using the Arrhenius equation and an activation energy of 15 $\text{kcal}\cdot\text{mol}^{-1}$ (Packard *et al.*, 1975). AARS activity was measured using the colorimetric method of Chang *et al.* (1984) modified by Yebra and Hernández-León (2004). GF was measured from the crude homogenates, following Yebra *et al.* (2004). Pigments were calculated from the Strickland and Parsons (1972) equations modified by Hernández-León *et al.* (2001).

Statistical analysis was carried out to study differences in the metabolic rates among stations. When data did not follow a normal distribution, then Kruskal–Wallis (K–W) ANOVA was applied for all cases. The Statistica 7.0 (Statsoft Inc.) software package was used for this procedure.

Results

Hydrography

An upwelling filament originating on the African continental shelf was observed between 27ºN and 28ºN. The evolution and extension of this filament and the quasi-permanent cyclonic eddy were observed in SeaWifs and AVHRR images (Fig. 2a–c). The upwelling filament ended over the quasi-permanent cyclonic eddy (Barton *et al.*, 1998, 2004) trapped south of Fuerteventura Island between the African shelf edge and Gran Canaria Island (Fig. 2b).

The current meter mooring located in the Lanzarote passage showed a southward flow every winter from January 1997 to January 2001 (Hernández-

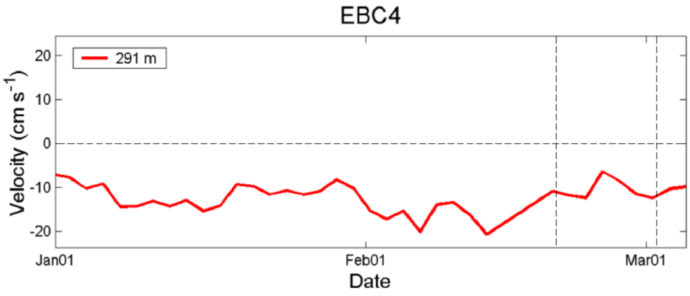


Figure 3. Time series of the velocity at 291m depth in the direction of the maximum variance (southwestward) from January 2001 to March 2001 in the Lanzarote passage. Vertical dashed lines show the start and the end time for the cruise.

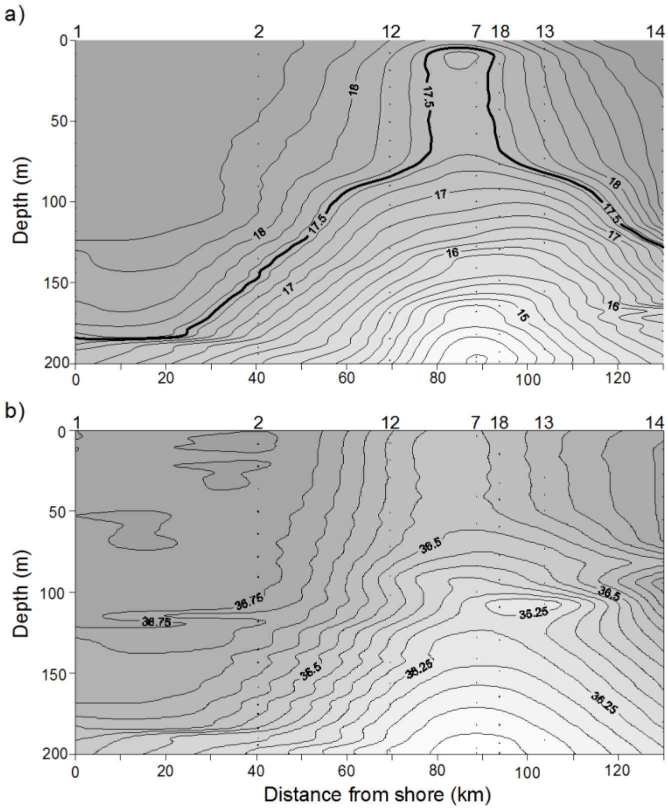


Figure 4. Vertical profiles of (a) temperature and (b) salinity in the upper 200m for transect 4. Dashed lines represent each station profile.

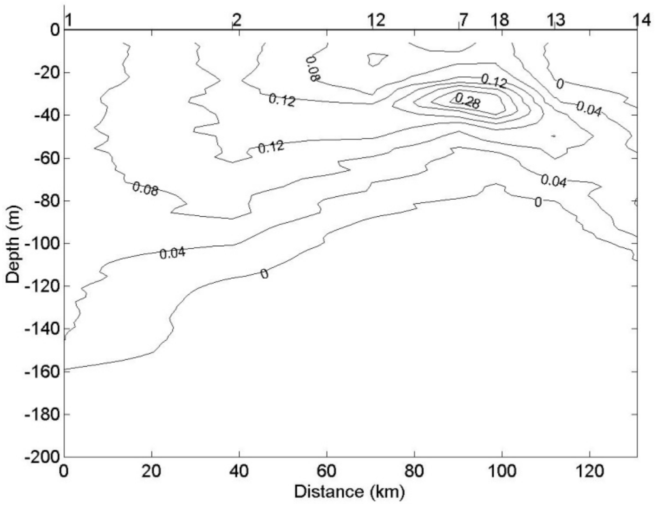


Figure 5. Fluorescence section in the upper 200m for transect 4. Note the eddy presence in the upward doming of the isolines.

Guerra *et al.,* 2003). Figure 3 displays the times series of velocity in the direction of the maximum variance (southwestward) before and during the cruise with a mean velocity >10 cm·s^{-1}. The result of this southwestward flow is a cyclonic eddy, due to the conservation of the potential vorticity, located south of Fuerteventura Island during the period studied. The upward doming of the isotherms and isohalines (Fig. 4a, b) clearly shows the cyclonic eddy, also evident in the fluorescence pattern (Fig. 5). The vertical section of differential temperature anomaly (DTA, Fig. 6a), defined as the maximum DTA (Simpson and Lynn, 1990), showed the extension and intensity of the eddy. Its core was located at 175 m depth (-1.2ºC maximum negative anomaly) and the eddy signal is visible to 450–500 m depth (Fig. 6a). The SST image shown in Fig 2c is presented with a contour of temperature at 175 m that resembles the sea-surface pattern. Geostrophic velocity for transect 3 (Fig. 6b) shows the cyclonic signal of the eddy. This velocity was calculated by taking into account the possible existence of a layer without movement when two opposite flows are present. This is the case for the Canary Island region, where the North Atlantic Central Water (NACW) flows southward and the Antarctic Intermediate Water (AAIW) flows northward (Hernández-Guerra *et al.*, 2001).

The main parameters used for the description of different eddies sampled in the Canary Islands correspond to those used by Patzert (1969) for Hawaiian eddies. Table 1 displays a comparison between the cyclonic eddies generated south of Gran Canaria Island by the Von Karman process (Arístegui *et al.*, 1994) and the one observed in the present work (Pelagic 0102) generated by the potential vorticity conservation. In both cases, eddies exhibited a general elliptical shape (high eccentricity indices, 0.76 for Pelagic 0102 eddy), that indicated that the structures were in their early stage of formation. Pelagic 0102 eddy showed the highest eddy radii, the half major axis and half minor axis at the 16ºC isotherm representation (31, 38.3 and 25.1 km, respectively), when compared to the other eddies. The depth of the 16ºC isotherm at the center and periphery of the eddy was 130 m and 165 m, respectively. The maximum negative DTA was -1.2ºC while the eddy doming/depression index was 1.2. Both parameters justify that Pelagic 0102 eddy had larger dimensions but lower intensity than the eddies produced by the island effect studied by Arístegui *et al.* (1994).

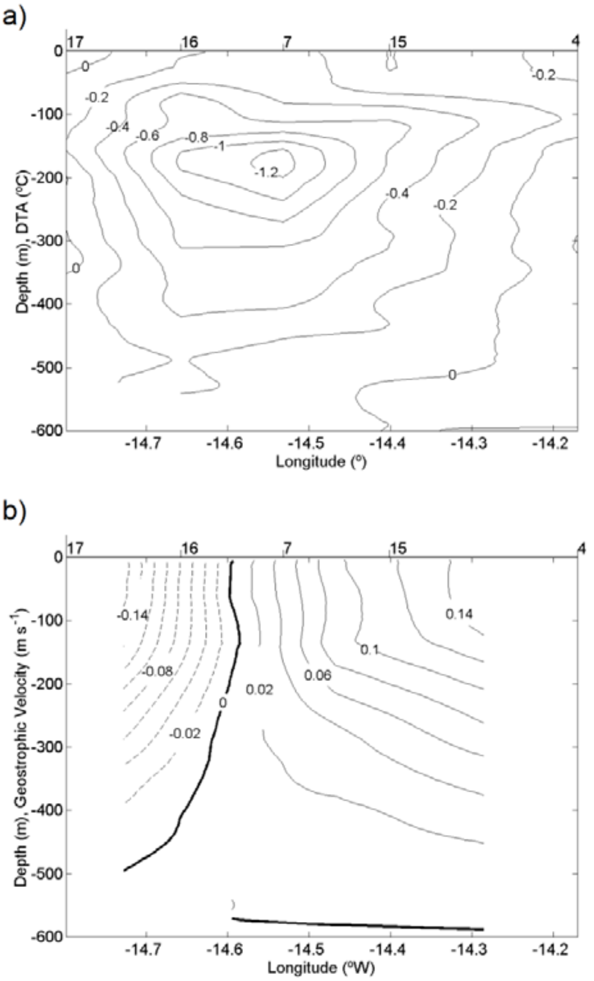


Figure 6. (a) Vertical section of differential temperature anomaly (DTA) for transect 3. **(b)** Geostrophic velocity (ms_1) along the major axis of the eddy for the same transect (positives go into the page).

Table 1 – Estimates of eddy parameters from different CTDs samplings.

Code	Pelagic 0102[a]	CM89[b]	CM 90[b]	CJ 90[b]
Eddy type	Cyclonic	Cyclonic	Cyclonic	Cyclonic
Sampling date	20 February. 2001	5 May 1989	24 May 1990	5-11 June 1990
Data type	CTDs	CTDs	CTDs	CTDs
Half major axis at 16ºC isotherm (km)	38.3	29	24	24
Half minor axis at 16ºC isotherm (km)	25.1	15	18	19
Radius at 16ºC, r_{16} (km)	31	21	24	21
Depth (16ºC) at eddy center (m)	130	130	155	145
Depth (16ºC) at eddy periphery (m)	165	190	180	180
Δd_{16} in m	35	60	25	35
Eccentricity (e)	0.76	0.9	0.6	0.6
Depth of eddy core (m)	175	175	125	150
mDTA in ºC	-1.2	-2.5	-1.5	-1.5
HDT in ºC	-1.5	-1.6	-0.5	-0.7
Eddy doming/depression index (i)	1.2	2.9	1.0	1.7

Here r_{16} the eddy radius, calculated from the depth of the 16ºC isotherm; $r=(a.b)^{1/2}$, where a and b are minor and major axes lengths of the approximating ellipse, respectively; Δd_{16}: difference between the depth of the 16ºC isotherm at the center and periphery of each eddy and e the eccentricity of the eddy, $e = (a^2-b^2)^{1/2}/a$. Depth of eddy core calculated from the DTA plots, represents the mean depth where the positive or negative anomalies are the highest. mDTA: maximum, positive or negative, differential temperature anomaly. DTA is calculated from the formula used by SIMPSON and LYNN (1990): $DTA(r,p)=T_e(r,p)-T_{ff}(r,p)$ the measured vertical profile of temperature at an eddy station some radial distance r from the eddy's center, $T_{ff}(p)$ is the reference vertical profile of temperature obtained from the arithmetic average of all temperature profiles, and p the pressure. HDT: horizontal differential temperature. The difference in temperature values between the periphery and the center of the eddy at the depth of each eddy core (where DTA is maximum); i: index of the doming or depression intensity in eddies. $i = \Delta d_{16}/ r_{16}$.

[a] This study [b] from Arístegui et al. (1994)

Ichthyoplankton composition and distribution

A total of 730 fish larvae were caught during this cruise of which 12.6% were clupeoids. Three species from this group were collected: *Sardina pilchardus* (73.9% of total clupeoid catches), *Engraulis encrasicolus* (20.7%) and *Sardinella aurita (5.4%).*

All of them were caught in the oceanic region, beyond the 200 m isobath, which is considered as the boundary of their typical distribution over the African shelf.

Total larval abundance was not affected by upwelled waters because of the high contribution of mesopelagic larvae to the assemblage in oceanic waters (Fig. 7a). On the other hand, clupeoids were found in stations strongly influenced by upwelled waters near the African coast and in the cyclonic eddy, which were characterized by temperatures under 18 ºC at 50 m. Most of the *S. pilchardus* (97.6 %) and all *E. encrasicolus* and *S. aurita* larvae were caught at those stations (Fig. 7b). The remaining 2.4% of *S. pilchardus* larvae were sampled near the coast of Gran Canaria Island. Total fish larvae exhibited a gradient in their vertical distribution (Fig. 8) with maximum abundances coinciding with locations where mesozooplankton biomass was high. Both

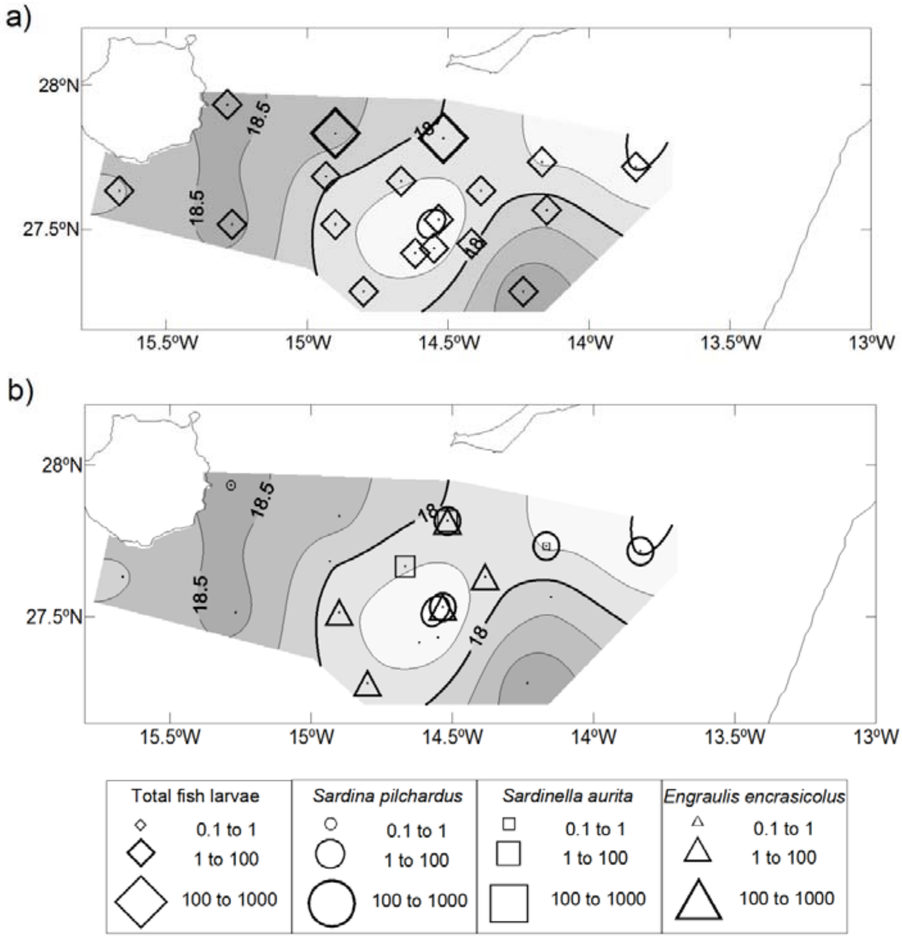


Figure 7. Temperature isolines at 50 m and horizontal distribution of larval fish abundance (individuals·m^{-3}) of **(a)** total fish larvae (◊); **(b)** *Sardina pilchardus* (O), *Sardinella aurita* (□) and *Engraulis encrasicolus* (Δ) larvae.

groups showed shallower distributions near the upwelling area (Station 5) and deeper offshore (Station 2). Clupeoid larvae appeared in the upper 120 m along the four sampled transects (Fig. 9), coinciding with the filament and the region of lower temperature of the eddy. This is especially clear for transects 2 and 4. Only a few of these larvae were found in deeper layers, such as some *E. encrasicolus* larvae at Stations 3 and 7 and some *S. pilchardus* larvae at station 5.

The vertical distribution of specific ETS activity in fish larvae increased at the westernmost stations (Fig. 10a), while specific GF showed higher values in the shallower layer near the upwelling area (Fig. 10b). ETS specific activity coincided with zooplankton biomass vertical distribution (Fig. 8). Specific AARS did not show any clear pattern (Fig. 10c).

For clupeoid larvae, no significant differences (K–W ANOVA, $p > 0.05$) were observed for the indices of respiration and growth when stations were grouped in relation to the distance to the upwelling area (Fig. 11). However, respiration showed a tendency to increase as the distance from the African coast increased. In contrast, the grazing index, measured as chlorophyll *a* and total pigments, exhibited significant differences among stations (Fig. 11c, d; $p < 0.01$ and $p < 0.05$, respectively). A clear gradient appeared from the African coast toward the ocean, where respiration tends to

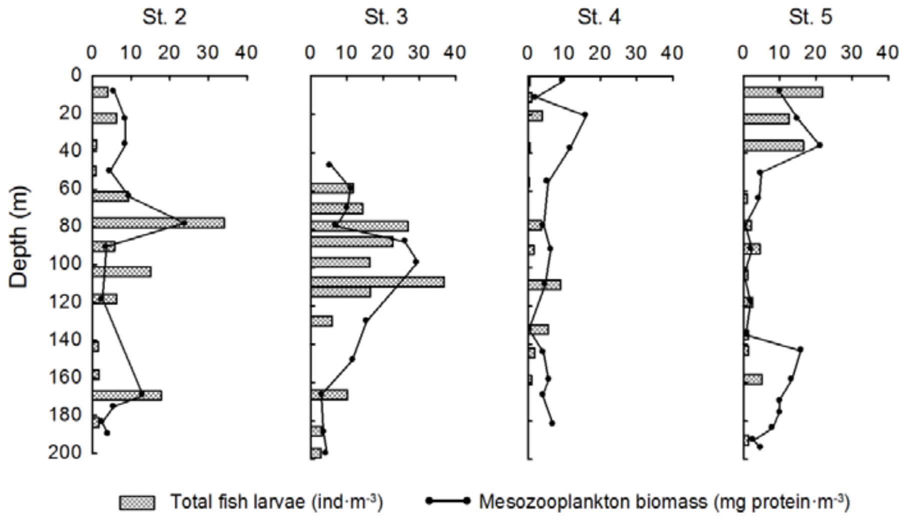


Figure 8. Vertical distribution of total fish larvae abundance (individuals·m^{-3}) and zooplankton biomass (mg protein·m^{-3}) for transect 1(Stations2–5).

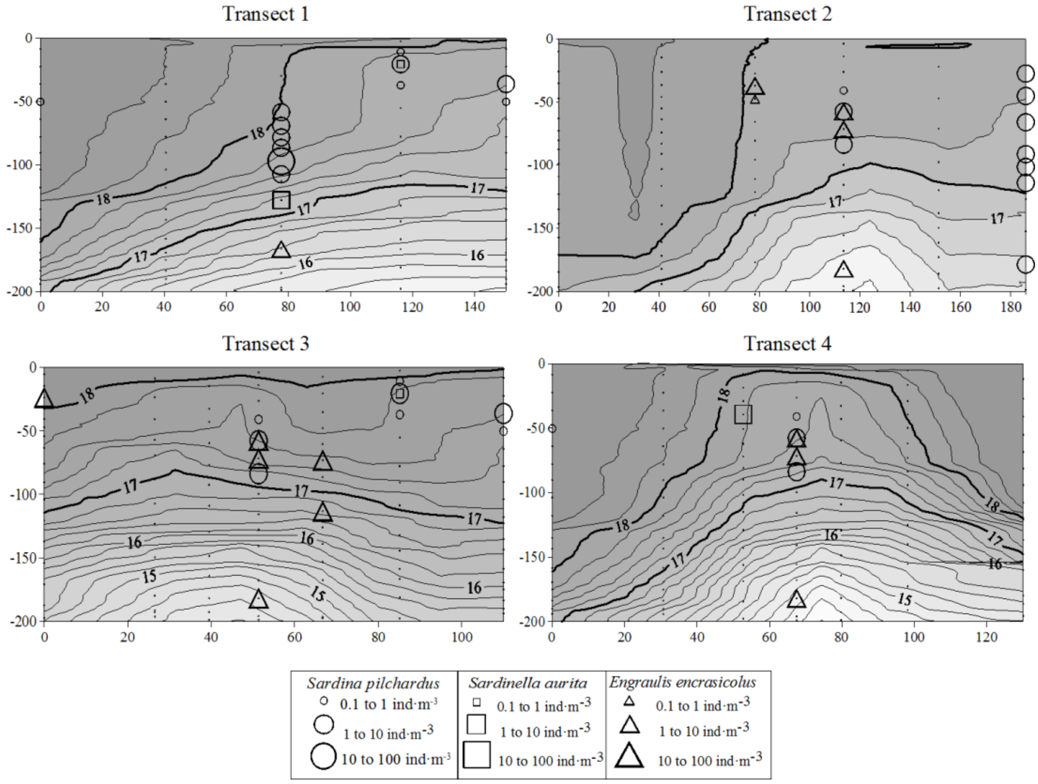


Figure 9. Vertical profiles of temperature (ºC) and vertical distribution of larval densities (fish larvae·m^{-3}) of *Sardina pilchardus* (O), *Sardinella aurita* (□) and *Engraulis encrasicolus* (Δ) larvae along transects **(a)** 1, **(b)** 2, **(c)** 3 and **(d)** 4.

rise while grazing decreases. The AARS showed a different pattern (Fig. 11b), with higher values near the filament structure and lower values related to the center of the trapped cyclonic eddy.

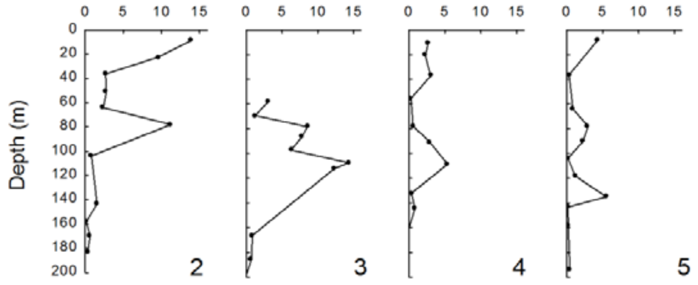
Discussion

The results of this work confirm the close relationship between clupeoid distribution and oceanographic processes, such as upwelling filaments as already suggested by Rodríguez *et al.* (1999, 2004) and Bécognée *et al.* (2006). In the present study, horizontal and vertical distribution patterns support the transport of three clupeoid species within upwelling filaments. The presence of *Sardina pilchardus* (73.9% of total clupeoids) in the filament and the cyclonic eddy suggests a transport of locally spawned larvae from the African shelf. Pilchard spawns primarily during winter along the NW African coast, but reproduces also during summer (Roy *et al.,* 1989; Ettahiri *et al.*, 2003). In this sense, Rodríguez *et al.* (1999) considered *S. pilchardus* to be a good tracer of the movement of upwelled waters in this region in summer 1993.

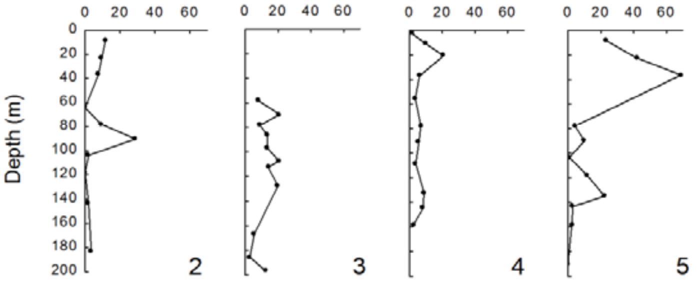
E. encrasicolus and *S. aurita* are also known to spawn north of Cape Juby (Furnestin and Furnestin, 1959) but mainly during the summer period (Ettahiri, 1996; Ettahiri *et al.*, 2003). This is the explanation for its lower contribution to total clupeoids in the present work. Indeed, larval transport of anchovy in upwelling filaments was recorded by Rodríguez *et al.* (2004) during summer. Neritic larvae were found in the upwelling filament (0–120 m depth), characterized by lower temperature and salinity and high concentrations of chlorophyll (Fig. 2a). Upwelling filaments are also known to transport high concentrations of zooplankton (Hernández-León *et al.*, 2002; Hernández-León *et al.*, 2007). During this study, fish larvae and zooplankton biomass displayed a similar pattern spatially and in their vertical distribution (Fig. 8). Thus, ambient food should assure larval survival during their transport within the filament. In fact, Rodríguez *et al.* (1999) found an increase in the size of *S. pilchardus* from the African coast to the ocean along the filament structure.

However, in this case, the transport is stopped by the quasi-permanent cyclonic eddy structure (Barton *et al.*, 1998, 2004; Rodríguez *et al.*, 2004) causing the upwelled waters, and therefore fish larvae, to be retained in the oceanic area. This feature is rather different from the larval transport within filaments previously studied in the area. Rodríguez *et al.* (1999) observed that neritic larvae were transported offshore by the filament and the latter was likely to be entrained around the eddy, returning many of the larvae nearshore, not far from their place of origin. This would provide a nursery area, increasing the recruitment off the African coast. In contrast, Bécognée *et al.* (2006) confirmed the transport of pilchard larvae within a filament that reached Gran Canaria Island. In this second case, larval transport in the upwelling filaments can lead to an African connection between the fisheries in the upwelling area and the Canaries, certainly serving to maintain the unidirectional genetic flow towards the archipelago. The third case observed in this area is related to the drift of the filament waters to the open ocean south of the Canary Archipelago (Rodríguez *et al.*, 2004). Then, coastal fish larvae should be lost for any recruitment or, on the other hand, they could be trapped by

a) Specific *in situ* ETS activity (µl O_2·mg protein^{-1}·h^{-1})



b) Specific GF (ng pigments·mg protein^{-1})



c) Specific AARS (nmPP$_i$·mg protein^{-1}·min^{-1})

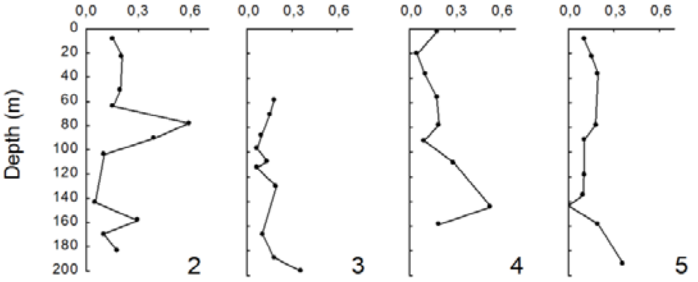


Figure 10. Vertical distribution of **(a)** the specific *in situ* ETS activity (µl O_2·mg^{-1} protein·h^{1}); **(b)** specific GF (ng pigments·mg^{-1} protein); and **(c)** specific AARS (nmPP$_i$·mg^{-1} protein·min^{-1}) of the ichthyoplankton in the upper 200 m for transect 1 (Stations 2–5).

eddies shed by the Canary Islands with some probability of reaching them and be recruited there. Finally, our results show a fourth case in the development of filaments in which the fate of this structure and the fish larvae remained in the oceanic realm. These early stages of fish are transported far from any shelf waters. Their chance to reach the islands or the African shelf as they grow into juveniles will remain, but it is supposed that the absence of transport to suitable areas will allow heavy predation pressure by diel vertical migrants in the ocean (Hopkins and Gartner, 1992; Hernández-León*,* 1998), and hence a progressive decline and disappearance of larvae.

Feeding of the three clupeoid species studied showed a phytoplankton-based ingestion decreasing offshore, as observed from GF (Fig. 11). In contrast, although highly variable, the respiration index showed an increasing pattern from the upwelling to the ocean. Despite most studies reporting that *S. pilchardus* diets during its early stages consist of copepod nauplii and copepodite (Fernández and González-Quirós, 2006), other investigations have revealed the importance of phytoplankton community contribution to the diet in the highly productive waters of the Gulf of Lions (Rasoanarivo *et al.*, 1991) and in the NW Mediterranean (García *et al.*, 2006; Mercado *et al.*, 2007).

García et al (2006) recorded significantly higher carbohydrate content in sardine larvae from a comparison between the Alboran and the Catalonian Sea, with higher phytoplankton contribution in the latter. This omnivory trend is maintained during the adult stage, being able to prey on a broad size spectrum with high efficiency (Garrido *et al.*, 2007). In fact, Garrido *et al.* (2008) observed a phytoplankton contribution of >74%

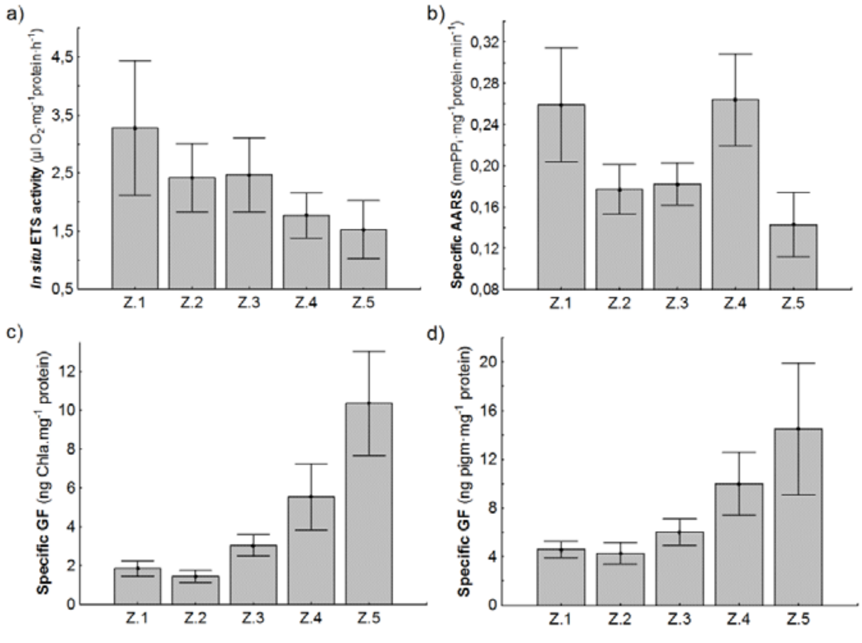


Figure 11. Mean values and standar Error for clupeoid larvae of **(a)** in situ ETS activity (µl $O_2 \cdot mg^{-1}$ protein$\cdot h^{-1}$); **(b)** specific AARS (nmPP$_i \cdot mg^{-1}$ protein$\cdot min^{-1}$); **(c)** specific GF as chlorophyll *a* (ng pigments chl $a \cdot mg^{-1}$ protein$\cdot h^{-1}$) and **(d)** specific gut fluorescence as total pigments (ng total pigments$\cdot mg^{-1}$ protein$\cdot h^{-1}$). Stations were grouped into five zones to evaluate the offshore gradient: zone 1 (Stations 1, 9, 10), zone 2 (Stations 2, 8, 11, 17), zone 3 (Stations 3, 7, 12, 13, 16, 18), zone 4 (Stations 4, 6, 14) and zone 5 (Station 5).

of the dietary carbon of adult sardine collected in Portugal in relation to summer upwelling events. The vertical distribution of larval–specific ETS activity coincided with the vertical distribution of zooplankton biomass, supporting at least in part, the switch from herbivory to omnivory. In this sense, Hernández-León *et al.* (2002) observed a similar feeding pattern for mesozooplankton, with a decrease in the importance of pigmented food and an increase in unpigmented food (protists) toward the open ocean. Our preliminary results about feeding and metabolism in fish larvae indicate that these organisms could also be affected by the transition of the planktonic community from the eutrophic to the oligotrophic regime. The increment in the proxy for growth activity was not detected as clearly as for zooplankton in Hernández-León *et al.* (2002). However, a maximum value was found in the eastern flank of the eddy, similar to the pattern previously observed for zooplankton on the edge of a cyclonic eddy by Hernández-León *et al.* (2001).

In summary, our results confirm that (i) there is an offshore transport of *S. pilchardus* (considered to be a good tracer of the movement of upwelled waters) from the upwelling area within filaments, (ii) other neritic larvae such as *S. aurita* and *E. encrasicolus* are also transported and might also be good tracers of upwelled waters during winter, (iii) the quasi–permanent cyclonic eddy is a mechanism of retention of this transport, and (iv) the conditions of food, temperature and salinity in the filament and the cyclonic eddy may be favourable for the transported neritic larvae, but their survival will depend on whether their dispersal is produced toward suitable areas for recruitment (Rodríguez *et al.*, 1999) or to the open ocean (this work).

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DISCUSSION

SYNTHESIS OF RESULTS AND GENERAL DISCUSSION

The goal of this thesis is to analyze the ecology of the larval fish assemblage in the easternmost area of the Canary Islands. First of all, an extensive review considering all the previous studies on ichthyoplankton in the Canaries-African Coastal Transition Zone was done (Chapter I). Considering the absence of long-term studies in the area, temporal and spatial variability of the larval fish community was analyzed using an ichthyoplankton time series (>2 years) off the eastern and southern Gran Canaria Island coast (Chapters III and IV). Seasonal larval fish assemblages were identified (Chapter IV) as well as retention spots for certain neritic families up- and downstream of the island (Chapter III).

An important component of this thesis involved the analysis of larval transport of some commercial target species (mainly Clupeoids, sardine and anchovy) within upwelling filaments originated in the African coast. The combination of larval sampling in fixed stations off Gran Canaria and remote sensing analysis revealed a transport of sardine larvae to the island (Chapter II). On the other hand, the study of the development of a filament during winter in the Canaries-African CTZ suggested a situation in which fish larvae were retained in the oceanic realm without any chance to be recruited either in the African or Canarian coasts (Chapter V).

Larval fish assemblages off Gran Canaria Island

Seasonality and composition of larval fish assemblages

Larval fish assemblages around islands in tropical and subtropical environments are composed by a high number of fish species (Leis, 1991) with different ecological roles in their adult stage (i.e, mesopelagic, coastal-pelagic). In the case of the Canary Islands, few studies have dealt with the complete larval fish community (Rodríguez *et al.*, 1999, 2000, 2001, 2004) and all of them were carried out during short cruises. As a result, the temporal evolution of the ichthyoplankton in the Canaries remains almost completely unknown. The studies included in this thesis (Chapters II, III and IV) reveal some interesting temporal trends.

The larval fish community off Gran Canaria shows a high diversity (more than 150 taxa identified) and is composed almost equally by neritic and oceanic species (see Annex II). This is similar to reports from previous studies carried out in the region (Rodríguez *et al.*, 2001) and around other oceanic islands (Leis *et al.*, 1976; Leis, 1991; Boehlert *et al.*, 1992). Clupeids, Sparids and Gobids were the most important neritic families, whereas Myctophids, Gonostomatids and Photichthids prevailed in the oceanic group. No significant differences in the temporal patterns of these families were observed, probably because of the relatively low seasonality of the water column variables (temperature, salinity and chlorophyll). In tropical and subtropical areas, the absence of dramatic changes in environmental factors results in the lengthening of fish spawning periods (Lowe-McConnell, 1987). For this reason, a high percentage of fish species spawn during several months or all year round in the Canaries. As for larval densities, they were similar to those found in other oligotrophic regions (Alemany *et al.*, 2006; Muhling *et al.*, 2008).

Despite the above arguments, two main seasonal larval assemblages were found off Gran Canaria: winter-spring and summer-autumn (Chapters III and IV). Temperature was the most important environmental variable explaining assemblage variability. Also salinity and small-sized mesozooplankton biomass had a slight influence in structuring assemblages. Then, we could affirm that those assemblages correspond to the two typical conditions in the annual cycle in the Canary Island waters, the mixing and stratification periods, respectively.

The *winter assemblage* occurs during the mixing period of the water column that includes the late winter bloom. This period is characterized by lower water temperatures, average salinity and higher chlorophyll and mesozooplankton concentrations. *Sardinella aurita*, *Boops boops* and *Cyclothone braueri* dominate the larval assemblage during this period. The presence of Pomacentridae sp1, *Lobianchia dofleini* and some typically winter spawners such as *Pagellus bogaraveo, Trachurus picturatus and Scomber colias* contribute to characterize this assemblage.

On the other hand, the *summer assemblage* occurs during the warmer months, when the water column is well-stratified (i.e. higher temperatures and salinities, lower chlorophyll and mesozooplankton concentrations), the larval assemblage is dominated by Gobidae species and *Cyclothone braueri*. But the species that characterize this assemblage were *Ceratoscopelus warmingii*, Pomacentridae sp2, *Lampanyctus* spp and *Anthias anthias*. Some other species (e.g., *Trachinus draco* and Tetraodontidae sp1) were only found during this warmer period.

Using all data from the temporal series off Gran Canaria (Chapters II, III and IV), a table with the most important species, either due to their high contribution to total larval abundance (e.g. *Cyclothone braueri, Vinciguerria poweriae*) or their commercial importance (e.g., *Scomber colias, Sarda sarda, Trachurus pictoratus*), was built (Table 1). In this table, the reported spawning periods based on biometric studies carried out on adult fish species of the Canaries region are shown. In the cases where no data were available (e.g., *Arnoglossus thori, Trachinus draco*), studies from the Mediterranean or North Atlantic were used. Although those studies were conducted in temperate ecosystems that are fairly different from that of the Canaries, they may be a useful reference to infer the thermal spawning ranges for different species. Then, the lengthening of the spawning periods observed in warm waters (Lowe-McConnell, 1987) was observed for some species compared to the Mediterranean. *Arnoglossus thori* reproduces in summer in the Mediterranean but in the Canaries this period extends to early winter. *Trachinus draco* larvae are found in autumn as well as summer off Gran Canaria, where as in the Mediterranean this species is considered a summer spawner. However, it is worth mentioning that larvae of species considered as summer spawners in the Mediterranean are present during winter (*Scomber colias, Trachurus picturatus*) or during the whole year (*Sardinella aurita*, *Hygophum hygomii*) in the Canary waters.

Table 1. Presence of the most important larvae collected in the Gran Canaria time series (January 2005 – June 2007) and their suggested spawning periods in the Canaries or similar regions.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	References
Anthias anthias	X	X	X	X	X	X	X	X	X	X	X	X	Fage (1918)[a]
Apogon imberbis							X	X					Tortonese (1986)[a]
Arnoglossus thori	X						X		X	X	X	X	Sabatés (1990)[a]; Macpherson & Raventos (2007)[a]
Bathylagidae sp1	X	X	X									X	
Boops boops	X	X	X	X	X	X	X				X	X	Franquet & Brito (1995)
Bothus podas							X	X		X			Nash *et al.* (19991)[b]
Ceratoscopelus warmingi	X	X	X	X	X	X	X	X	X	X	X	X	Loeb (1980)[c]
Cyclothone braueri	X	X	X	X	X	X	X	X	X	X	X	X	Jespersen & Taning (1926)[a]
Engraulis encrasicolus					X			X			X	X	Frunestin & Furnestin (1959)[a]
Lampanyctus spp	X	X	X	X	X	X	X	X	X	X	X	X	
Lobianchia dofleini	X	X	X	X	X	X	X					X	Taning (1918)[a]
Mullus barbatus					X	X							Hureau (1986)[a]
Mullus surmuletus					X		X						Pajuelo *et al* (1997)
Pagellus bogaraveo	X	X	X	X							X	X	Bauchot & Hureau (1986)[d]
Pagrus pagrus	X		X		X	X							Pajuelo & Lorenzo (1996)
Pomacentridae sp1	X	X	X	X	X					X		X	
Pomacentridae sp2					X	X	X	X	X	X	X		
Sarda sarda		X	X									X	Collete & Nauer (1983)[e]
Sardina pilchardus	X		X	X	X			X				X	Méndez-Villamil *et al.* (1997)
Sardinella aurita	X	X	X	X	X	X	X	X	X	X	X	X	Bécognée *et al*. (2006)
Sardinella maderensis	X				X	X		X	X	X	X	X	Whitehead (1985)
Scomber colias	X	X	X	X		X							Franquet & Brito (1995)
Stomias boa ferox	X	X	X		X					X		X	Ege (1934)[a]
TETRAODONTIDAE						X	X	X		X		X	
Trachinus draco						X		X		X	X		Sabatés (1990)[a]; Hoşusu & Ak (2002)[a]
Trachurus pictoratus	X	X	X		X								Franquet & Brito (1995)
Vinciguerria poweriae	X	X	X	X	X	X	X	X		X	X	X	Franquet & Brito (1995)

[a] Mediterranean Sea, [b] Azores, [c] Central North Pacific, [d] Morocco, [e] Eastern Atlantic, [f] Western Central North Atlantic

Some larvae of *Sardina pilchardus* were found outside of their spawning period described for the area (Table 1). Those larvae are thought to be transported from the NW African coast (discussed below). In addition, the relationships between *Sardinella aurita* (round sardinella), *Sardina pilchardus* (sardine) and *Engraulis encrasicolus* (anchovy) larval population sizes suggest a change over the last 15 years (Table 2). Results from 2005 and 2006 suggest that the round sardinella population may be increasing while sardine and anchovy populations seem to be decreasing. Round sardinella is a thermophilic small pelagic species that extends in tropical and subtropical waters of the western and eastern Atlantic Ocean, the Pacific Ocean and the Mediterranean Sea (Bauchot, 1987). These species are highly mobile, rely on short plankton-based food chains, are highly fecund and have plasticity in growth, survival and other life history traits (Alheit and Hagen, 1997). Thus, these authors argue that these small pelagic schooling fish can respond dramatically and quickly to climatic variations, changing in abundance and in their distribution. This is the case of the round sardinella in the Mediterranean, where this species is currently successfully reproducing further north than 20 years ago (Sabatés *et al.*, 2006). Also, they pointed out that sardine and anchovy landings have declined in the region during the last 15 years. These authors found a clear link between this change in distribution and increased water temperature (~1.1ºC in surface waters and 0.7ºC at 80 m depth since 1970).

Table 2. Comparison of the larval contribution of three Clupeoid species in three studies off Gran Canaria Island.

	Sardinella aurita	*Sardina pilchardus*	*Engraulis encrasicolus*
October 1991 [a]	83.9%	8.1%	8.1%
July 2000-June 2001 [b]	92.9%	4.7%	2.4%
January -December 2005 [c]	95.4	2.7	1.93

[a] Rodríguez *et al*. (2001) [b] Bécognée *et al*. (2006) [c] Data from Chapters II and III

Recent observations indicate that during the last 23 years, the warming trend in the Canary Current region (north of Cape Blanc, 20 ºN) has been the most intense of all the eastern boundary upwelling systems (Arístegui *et al.*, *in press*). This warming may explain the dramatic increase of round sardinella and the decrease of sardine population sizes in the Canary Island waters. However, the ultimate factors governing this shift, if real, are unknown. The absence of fisheries' historical records precludes any conclusion about a sardine stock depletion in the Canary Islands, considering the stock in the African coasts is in good-condition (FAO, 2009).

In addition, two species of Pomacentrids (Pomacentridae sp1 and Pomacentridae sp2) were relatively abundant in the samples. There is a seasonal segregation between the two: Pomacentridae sp1 was more abundant in winter-spring, while Pomacentridae sp2 was more abundant in summer (Table 1). This temporal distribution is in agreement with the spawning periods of *Chromis limbata* (winter-spring) and *Abudefduf luridus* (summer) (A. Brito, *pers. comm.*). Only three species of Pomacentrids inhabit the Canarian waters (Brito *et al.*, 2002): *Chromis limbata*, *Abudefduf luridus* and *Abudefduf saxatilis*. The first two species are abundant, while the third one is very rare in the region (Brito *et al.*, 2002). Considering the abundance and the seasonal distribution, it is highly probable that Pomacentridae sp1 is *Chromis limbata* and Pomacentridae sp2 is *Abudefduf luridus*. However, we acknowledge that further morphological analysis of the larvae is needed in order to describe the early larval stages of both species since, to our knowledge, only the newly hatched-larvae of *Abudefduf luridus* are described (Ré, 1980).

Horizontal distribution of fish larvae off Gran Canaria Island

It is well known that fish larvae usually accumulate leeward of oceanic islands (Leis, 1991; Boehlert *et al.*, 1992; Boehlert and Mundy, 1993). Off Gran Canaria Island, fish eggs and neritic larvae showed higher abundances in two stagnation areas, upstream and downstream of the island (Rodríguez *et al.*, 2001). During the temporal series carried out in that island, we confirmed retention for fish eggs and neritic larvae in those regions on a finer time scale (Chapters II and III). The pattern found for total neritic larvae was mainly due to two families, Clupeidae and Gobiidae. On the other hand, oceanic larvae showed slightly higher values in the eastern flank of the island, where the flow is enhanced.

Nevertheless, although this accumulation up- and downstream seems to be effective for fish eggs and total neritic larvae, it seems that only has a marginal effect on the annual assemblage composition. During an intensive 8-month study, no significant differences were found on the composition of the larval fish assemblage among sites in five eastern and southern sites of the island (Chapter III).

Does lunar illumination influence larval abundance?

The temporal variability of the larval fish assemblage structure was mainly dependent on temperature (Chapter IV). However, total larval abundance did not seem to follow any temporal pattern, as neither species seems to take advantage of the zooplankton outburst during the late winter bloom (Chapter III).

Nevertheless, an interesting relationship between neritic larval abundance and small mesozooplankton (<1000 µm) was found, which may be coupled with the lunar cycle (Chapter III). Small mesozooplankton exhibited a monthly periodicity that has already been explained by Hernández-León (1998) as the result of the predator pressure exerted by diel vertical migrants (DVMs). This author hypothesized that during the low lunar illumination period (new moon), DVMs are able to reach the upper layers of the water column and predate on epipelagic mesozooplankton. On the other hand, during the illuminated period of the lunar cycle (full moon), these DVMs are absent from upper layers and allow the epipelagic zooplankton to grow.

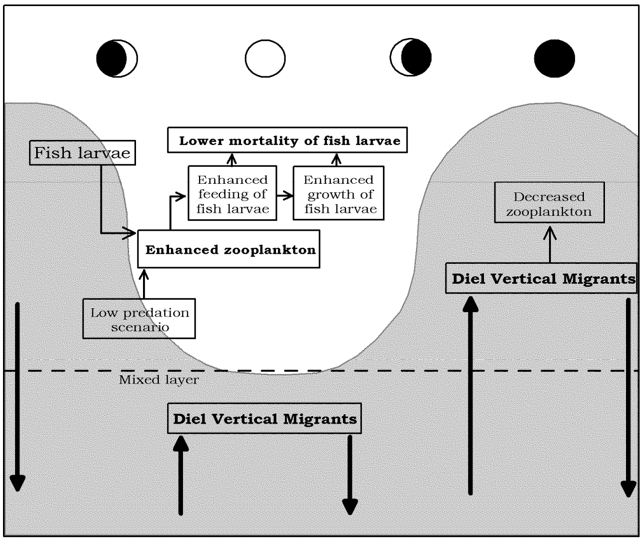


Figure 1. Schematic illustration of the mortality, feeding and growth of fish larvae, under the influence of the lunar cycle. Redrawn from Hernández-León (2008).

According to the results shown in this thesis, neritic larval abundance might also be controlled by this predation cycle, showing lower values during the new moon (Fig. 1). In this sense, Hernández-León (2008) hypothesized that fish larvae may also be influenced by this DVMs predation cycle, arguing that this pattern may constitute a short-term version of the match-mismatch hypothesis (Cushing, 1990). This author purports that this coupling would be explained as a result of (1) the lower predatory pressure on fish larvae, (2) the enhanced feeding of adult fish promoted by the increase in zooplankton concentration during the lunar cycle insofar as this energy intake would be converted into reproduction products; and (3) the enhanced feeding of fish larvae on zooplankton during the lunar cycle. Our results only support the first assertion. Further research is needed to assess the ultimate causes responsible for this variability. Is the lunar cycle influencing total neritic larval abundance in subtropical waters? If so, is it only a result of higher mortality during new moon? Or is there a real reproductive strategy, i.e., to avoid the high predation pressure during the new moon?

The Canaries-African Coastal Transition Zone

The Canary Current System (CCS) is one of the 49 large marine ecosystems of the world (Sherman, 1993). Like other eastern boundary upwelling ecosystems, it is characterized by an intense mesoscale oceanographic activity in the transition region between the cool, nutrient-rich coastal waters and warmer, oligotrophic waters of the open ocean. Off NW Africa (north of 25ºN), the upwelling season occurs from July to September, although small-scale and short-time upwelling events may arise at any time (Mittelstaedt, 1991; Van Camp *et al*., 1991). The CCS shows the singularity that the presence of the Canary Islands interrupts the Canary Current and trade wind flows, generating mesoscale oceanographic structures south of the islands (warm wakes and cyclonic/anticyclonic eddies).

A review of the ichthyoplankton of the Canaries-African Coastal Transition Zone (Canaries-African CTZ) was carried out (Chapter I). The larval fish community that inhabits this region has some identifying characteristics, such as exhibiting a high diversity, typical of subtropical areas (Longhurst and Pauly, 1987). Mesopelagic species contributed significantly to the community. Myctophidae was the most diverse family, but *Cyclothone braueri* was the most abundant species. Adults of this species were also found to be very abundant in a nearby oceanic area (Badcock, 1970; Badcock and Merret, 1976).

During summer, the Canaries-African CTZ larval fish community was dominated by clupeoid larvae transported in filaments (i.e, *Sardina pilchardus, Engraulis encrasicolus*). During winter and spring, other island neritic species (i.e., *Boops boops, Sardinella aurita*) were more important.

The presence of larvae of some tropical species (e.g. *Hygophum macrochir*, and *Vinciguerria nimbaria*) may support the *tropicalization* of the ichthyofauna of the Canary archipelago as suggested by Brito *et al.* (2005). However, further research is needed in order to give evidence of this phenomenon.

Larval dynamics in the Canaries-African Coastal Transition Zone

Mesoscale structures generated south of the Canary Islands have a profound effect on larval dynamics, both for larval dispersal and retention. The functioning of warm wakes as retention areas for fish eggs and larvae of the neritic fish population of Gran Canaria is well-known (Chapters II and III). Also cyclonic eddies may play the same role south of the islands (Rodríguez *et al*., 2001). However, the effect of this drift on larval survival within the Canary Current or island-generated eddies is still unknown (Chapter I). There is some evidence that island-generated eddies transport larvae to the open ocean (e.g., *Anthias anthias*) (Chapter I). The evolution of those eddies will determine the fate of the larvae. If eddies shed from the upstream archipelagos (i.e, Madeira, Azores) reach other islands downstream, larvae could survive, as suggested by Rodríguez *et al.* (2000). The participation of oceanic currents and eddies in larval fish transport has already been suggested (Lobel and Robinson, 1986; Hutchings and Pearce, 1994).

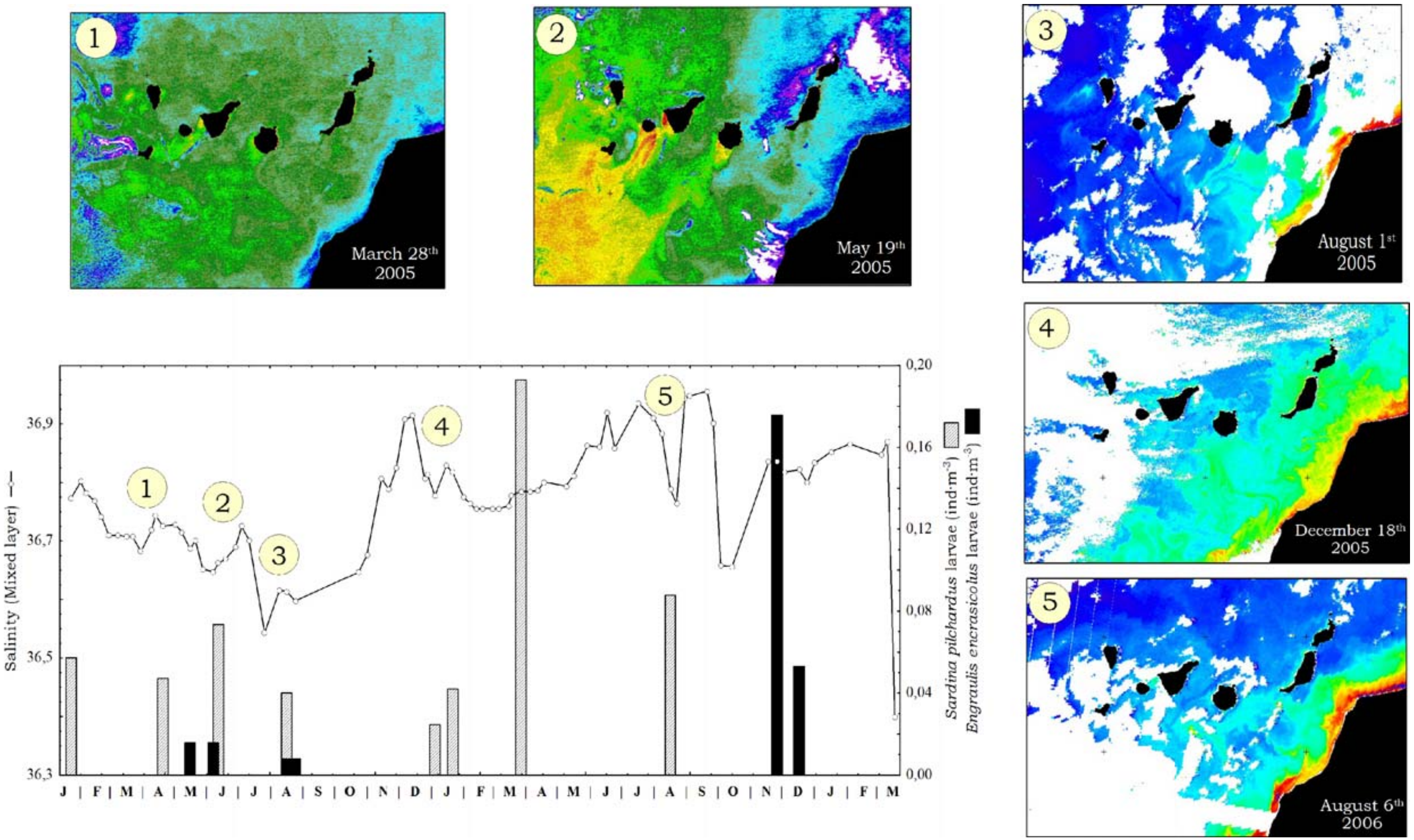
Larval transport in upwelling filaments from the NW African coast has been studied only a few times (Rodríguez *et al*., 1999, 2004; Bécognée *et al*., 2006). These studies focused mainly on two clupeoid species, sardine and anchovy. Both species are considered as good tracers of these upwelling filaments (Rodríguez *et al*., 1999, 2004).

They spawn during the whole year in the NW African upwelling region, but the sardine shows the spawning peak in winter (Ettahiri *et al*., 2003) while the anchovy spawns in summer (Furnestin and Furnestin, 1959; Berraho, 2007). Within the upwelling filament, the dominance of one species over the other in summer seems to depend on sea surface temperature in the African upwelling region (Chapter I). On the other hand, sardines seem to prevail in winter (Chapter V), although more data is needed to confirm this finding.

The development of these filaments might result in larval retention off the African coast, dispersal to the eastern shores of the Canary Islands or dispersal to the open ocean (Rodríguez *et al*., 1999, 2004, Bécognée *et al*., 2006). Our results suggest a pattern in which the fate of the filament-eddy complex and fish larvae within was to remain in the oceanic realm (Chapter V). In this case, larvae will be lost for fish populations due to the high predation pressure exerted by DVMs in the open ocean (Hopkins and Gartner, 1992; Hernández-León, 1998). There is little chance that they grow up to juveniles inside the eddy system and are recruited to the African neritic region or the Canaries.

In addition, we have evaluated for the first time the metabolic activity of Clupeoid larvae transported within an upwelling filament (Chapter V). Electron Transfer System activity (ETS activity) and Gut Fluorescence (GF) were measured as proxies for respiration and grazing, respectively. ETS activity and GF revealed an inverse gradient in their spatial distributions. GF was higher near the African coast, while ETS activity increased towards the ocean. Growth (measured as AminoAcyl-tRNA synthetase, AARS activity) showed higher values near the filament structure and lower in the eddy core. These results suggest that fish larvae might be affected by the transition of the planktonic community from the eutrophic to the oligotrophic regime.

Figure 2. Temporal evolution of salinity in the mixed layer and *Sardina pilchardus* and *Engraulis encrasicolus* larvae collected off Gran Canaria Island. The presence of *S. pilchardus* larvae coincide with the arrival of upwelling filaments from NW Africa to Gran Canaria.



Sardine and anchovy larval transport to Gran Canaria Island

The transport of sardine larvae within upwelling filaments from the African coastal upwelling region to the Gran Canaria coast was confirmed by Bécognée *et al.* (2006). This dispersal mechanism was also analyzed considering fish larvae collected during the ichthyoplankton time series included in this thesis (data from Chapters II, III and IV, compiled in Fig. 2). Sardine larvae were not very abundant, contributing less than 0.5% to total larvae collected during this >2-year study period. The presence of these larvae off Gran Canaria, coinciding with the arrival of upwelling filaments, confirms a larval dispersal from elsewhere during the whole year. The arrival of these filaments to the island was detected by remote sensing and confirmed by low salinity values measured in the mixed layer. Nevertheless, this larval drift is particularly evident in May and August, when the sardine is outside of its spawning season in Gran Canarian waters (December-March, Méndez-Villamil *et al.*, 1997).

The anchovy is considered as an occasional species in the Canaries Archipelago (Brito *et al.*, 2002). This species spawns all year round, peaking in summer, in the African shelf (Furnestin and Furnestin, 1959). There is no information on their spawning periods in the Canary Islands waters. Relatively large quantities of anchovy eggs were found during May and June, south of Gran Canaria Island (Moyano, unpublished data), suggesting that their spawning peak may occur during late spring and summer. Nevertheless, it is likely that this species spawns all year round off Gran Canaria since its larvae were found during autumn-winter (November-February 2001, Bécognée *et al.*, 2006; November-December 2007, Table 1). Typical annual temperatures found off Gran Canaria match with the thermal range of spawning registered for this species in the NW African upwelling (Berraho, 2007). But it is worth mentioning that the coincidence of anchovy larvae off Gran Canaria, with the arrival of upwelling filaments to this island (Fig. 2, May and August 2005), suggests that larval transport within these structures may contribute to the local populations.

Recently, Brochier *et al.* (2008) attempted to model this larval transport both for sardine and anchovy. Two main characteristics arose from this model: (1) the majority of particles that reach the eastern islands of the Canaries mainly come from the Moroccan region located between Cape Draa and Cape Juby, an important spawning area for both clupeoid species (particularly for anchovy in summer); (2) the arrival of these particles off Gran Canaria displays two peaks, the biggest one in late winter (March-April) and the second one in July-August. These data fit our observations on the arrival of sardine larvae off Gran Canaria coast that peaked in March-April and in August (Fig. 2). However, the release area for those larvae was believed to be located between Cape Juby and Cape Bojador, instead of Cape Juby-Cape Draa. Therefore, it is obvious that further research is needed in order to assess the real magnitude of this connectivity and so improving fisheries management in the region. In this sense, high-resolution hydrodynamic models that include other factors that play key roles for habitat, spawning grounds and nurseries definition (temperature, food, homing…) should be considered.

CONCLUSIONS

The conclusions that arise from this thesis are:

1. The larval fish community off Gran Canaria Island is highly diverse, typical from subtropical waters in oceanic islands. Neritic and oceanic species equally contribute to the larval assemblage. Clupeidae, Sparidae and Gobidae are the most abundant neritic families, while Myctophidae, Gonostomatidae and Photichthydae dominate in the oceanic group.

2. Two temperature-dependent seasonal larval fish assemblages are found off Gran Canaria:

    - The winter-spring larval assemblage occurs during the mixing of the water column and the late winter bloom (i.e. low water temperatures, medium salinity and medium to high chlorophyll and mesozooplankton values). This assemblage is characterized by relatively high abundances of *Sardinella aurita*, *Boops boops* and *Cyclothone braueri* and the presence of Pomacentridae sp1, *Lobianchia dofleini, Pagellus bogaraveo, Trachurus pictoratus and Scomber colias*.

    - The summer-autumn larval assemblage occurs during the stratification period of the water column (i.e. higher temperature and salinity, low chlorophyll and mesozooplankton values). This assemblage is characterized by relatively high abundances of larvae of Gobidae species and of *Cyclothone braueri*., *Ceratoscopelus warmingii*, Pomacentridae sp2, *Lampanyctus* spp and *Anthias anthias*, and also by the presence of *Trachinus draco* and Tetraodontidae sp1.

3. The stagnation regions up- and downstream of Gran Canaria are confirmed as accumulation areas of eggs and neritic fish larvae (Clupeidae and Gobidae). Nevertheless, the composition of the larval assemblage in those retention areas is not significantly different from other island sites.

4. There is a strong relationship between mesoscale oceanographic processes and fish larvae, especially between upwelling filaments and two clupeoid species (*Sardina pilchardus* and *Engraulis encrasicolus*).

    - Filaments transport larvae of African neritic fish species into the oceanic region and towards the Canary Islands

    - This larval transport within upwelling filaments is responsible for the high abundances of neritic larvae recorded in the oceanic realm during summer.

    - Clupeoid larvae transported to Gran Canaria Island enhanced the size of local larval fish populations. The importance for local fisheries, although may seem obvious, needs further research.

    - Upwelling filaments may be trapped by the quasi-permanent cyclonic eddy located between the Canaries Archipelago and the African coast. This filament-eddy complex may act as a retention structure for fish larvae but sometimes also as a dispersal mechanism, maintaining those larvae in the oceanic domain.

5. A first assessment of the metabolic activity of clupeoid larvae during an upwelling filament event revealed that grazing decreased offshore, from the coastal upwelling region, while respiration increased. Then, fish larvae might be affected by the transition of the planktonic community from the eutrophic to the oligotrophic regime, as previously observed in zooplankton.

FURTHER RESEARCH

Results presented in this thesis constitute the basis for future studies on larval fish assemblages, their temporal and spatial variations and their relationship with the environmental variables in the easternmost region of the Canary Islands. Ichthyoplankton studies in the region should be extended to monitoring, in order to improve fisheries management and marine reserves design in the Canaries region.

Knowledge of the connectivity among organisms of marine populations is vital for a correct resource management (Cowen *et al.*, 2000). Then, multidisciplinary studies carried out in coordination with physical oceanographers and modelers are essential to produce coupled biophysical models to understand the interacting factors influencing early life stages of fish of target species (i.e., *Sardina pilchardus, Engraulis encrasicolus, Scomber colias*) in the easternmost region of the Canary Islands. Quality data is required as inputs for a good-quality model. This implies the combination of laboratory experiments to analyze energetic, trophic, growth and behavioral issues, and field studies to determine larval distributions on a real environment. In this sense, data from Chapters II, III and IV will be included in a model to analyze sardine larval transport in upwelling filaments (Brochier *et al.*, *in prep.*)

In addition, genetic analysis, biomarkers or otolith microchemistry would be interesting approaches to evaluate the connectivity between clupeoid species population of the African coastal upwelling and of the Canary Islands. Preliminary studies carried out with sardine adults caught off Tenerife Island and off the Moroccan coasts do not seem to show significant differences in concentrations of any trace element characterizing each population. Nevertheless, a clear periodicity was found in the Moroccan sardines, suggesting that it may be related to the upwelling index.

Lastly, we should take advantage of the mild annual water temperatures off Gran Canaria and promote underwater sampling combined with light traps. This type of sampling allows the collection of larger larvae to experiment with and opens a range of new potential studies.

SPANISH SUMMARY

INTRODUCCIÓN

Generalidades del ictioplancton

Se considera al ictioplancton un elemento del meroplancton formado por los huevos y larvas de peces teleósteos. A pesar de que con frecuencia son considerados partículas inertes, las larvas de peces son elementos activos del ecosistema (Cowen, 2002; Fuiman, 2002). La mayoría de los peces tienen una fase pelágica, cuya duración puede oscilar entre semanas y meses (Brothers *et al.*, 1983; Victor, 1986). A lo largo de este período larvario se producen importantes cambios en intervalos de tiempo muy cortos, por lo que el crecimiento y los procesos que favorezcan la supervivencia van a ser determinantes para el éxito del reclutamiento (Cushing, 1975; Cowan and Shaw, 2002). Así, por ejemplo, muchos peces aumentan su peso cinco órdenes de magnitud a lo largo de su vida, tres de los cuales tienen lugar durante la fase larvaria (Werner and Gilliam, 1984; Houde, 1987; Miller *et al.*, 1988). Este rápido incremento en biomasa en el relativamente corto período de vida larvario, pone de manifiesto el potencial de esta fase como regulador del reclutamiento, a través de las tasas de crecimiento (Cushing, 1975; Cowan and Shaw, 2002).

Un factor crítico en la etapa larvaria de un pez es la mortalidad. Las larvas han de enfrentarse a tasas de supervivencia normalmente menores al 1% (Houde, 1987; Chambers and Trippel, 1997). El estudio de las variaciones en la abundancia de los stocks ha fascinado a pescadores y científicos desde finales del siglo XIX. Hjort (1914, 1926) fue el primero en intentar explicar este fenómeno, a través de dos hipótesis: (1) falta de alimento en la transición a la etapa de alimentación exógena (*Hipótesis del Período Crítico*), y (2) la existencia de corrientes que puedan transportar las larvas a zonas desfavorables para su desarrollo (en inglés, Aberrant Drift Hypothesis). La primera hipótesis de Cushing básicamente propone que el tamaño de una clase anual estará determinado al inicio de la fase larvaria, poco después de la absorción del vitelo, cuando la larvas deben encontrar el tipo y cantidad de presas planctónicas adecuadas (Fig. 1). Si no son capaces de encontrar este alimento, esto llevaría a mortalidades masivas.

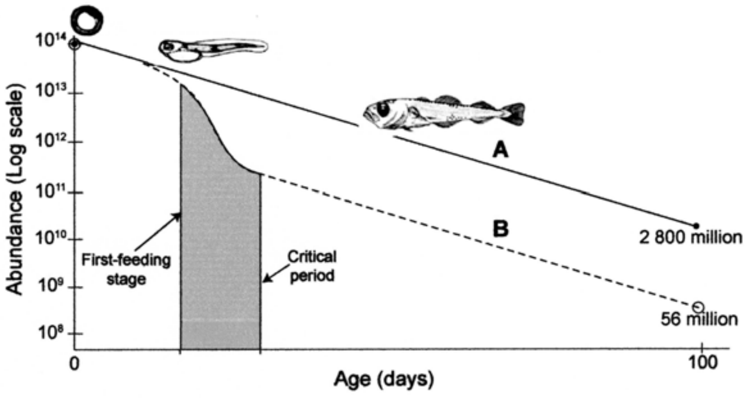


Figura 1. Curvas de supervivencia mostrando la influencia del "período crítico" (Hjort, 1914) en la abundancia de supervivencia 100 días después de la eclosión. De Houde (2008).

Las hipótesis de Hjort constituyeron el trabajo de base para posteriores estudios de reclutamiento, principalmente basados en la hipótesis del período crítico (Cowan and Shaw, 2002; Houde, 2008). Cushing (1975) combinó las dos hipótesis de Hjort en la *Hipótesis del match-mismatch* (del inglés, Match-mismatch Hypothesis). Este autor propone que un período fijo de puesta acoplado a blooms planctónicos variables en el tiempo, generará una supervivencia variable y, por lo tanto, un reclutamiento variable. En esta hipótesis, (1) la limitación de alimento en cualquier momento del período larvario, junto con (2) los factores abióticos que regulan la mezcla de la columna de agua y (3) el inicio y la intensidad de los ciclos estacionales de producción, contribuirán en gran medida a explicar la variabilidad del reclutamiento. Posteriormente, Lasker (1981) sugirió la *Hipótesis del Océano Estable* (del inglés, Stable Ocean Hypothesis). En ésta, el autor plantea que la presencia de períodos de calma en ecosistemas de afloramiento (conocidos como Lasker events) potencian la estratificación de la columna de agua y, por tanto, la agregación de las larvas de peces y sus presas; esto se traducirá en mayores tasas de alimentación, supervivencia y reclutamiento. Cury y Roy (1989) ampliaron la hipótesis de Lasker con el modelo de la *Ventana Ambiental Óptima* (del inglés, Optical environmental window). Estos autores hipotetizaron que los niveles de reclutamiento en sistemas de afloramiento tienen una forma de campana, donde el mayor éxito se produce con niveles de viento medios, en los que se optimizan las pérdidas por advección y el beneficio alimenticio para las larvas derivado de las turbulencias (mayor tasa de encuentro entre las larvas y sus presas). La *Hipótesis del Contacto Planctónico* (del inglés, Plankton contact hypothesis) de Rothschild y Osborn (1988) también apunta la importancia de las micro-turbulencias para el éxito en la alimentación. Estos autores propusieron que las larvas de peces pueden sobrevivir en ambientes con bajas densidades de presas, si las tasas de encuentro entre ambas aumentan debido a turbulencias generadas por el viento a pequeña escala.

Una extensión de la segunda hipótesis de Hjort fue la *Hipótesis de la Retención Larvaria* (del inglés, Larval Retention or Member/Vagrant Hypothesis). Estos autores plantearon que la retención física es crítica en el proceso de reclutamiento y que ésta depende de que la puesta se realice en áreas favorables para la retención de huevos y larvas. Esta hipótesis tiene, a su vez, afinidades con la *Hipótesis del Triángulo Migratorio* (Harden-Jones, 1968; Cushing, 1975), ya que ambas están basadas en el hecho de que los procesos físicos determinan el éxito del reclutamiento, a través de la deriva larvaria y las zonas de puesta.

Para las regiones tropicales, los estudios de reclutamiento son más complicados que en las zonas templadas (Sale, 2004). A pesar de esto, diferentes trabajos han demostrado que los peces de los arrecifes coralinos no son diferentes de los de otras regiones, ya que también presentan un éxito variable en el reclutamiento (Doherty and Williams, 1988). Sale (1978) propuso la *Hipótesis de la Lotería* (del inglés, Lottery Hypothesis), que afirma que la prioridad en la llegada de las post-larvas listas para asentarse en el arrecife es más importante a la hora de determinar la presencia de las especies en un determinado lugar, que las necesidades o habilidades de los adultos. Por lo tanto, los procesos que tienen lugar después del asentamiento controlarán el reclutamiento. En la actualidad, se considera que tanto los procesos previos como posteriores al asentamiento influenciarán al reclutamiento (Jones, 1991; Doherty, 2002). Además, el hecho de que las poblaciones de peces en los arrecifes sean un sistema cerrado o abierto es una cuestión que sigue en el aire (ej., Cowen *et al.*, 2000; Mora and Sale, 2002; Cowen *et al.*, 2006), por lo que aún es necesario seguir investigando para cuantificar con precisión la conectividad y los mecanismos de auto-reclutamiento.

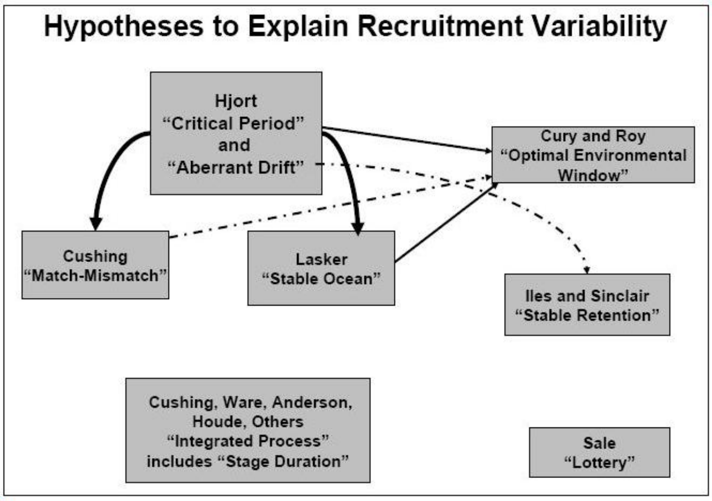


Figura 2. Hipótesis que explican la variabilidad del reclutamiento en peces marinos y su relación con las hipótesis de Hjort (1914). Las flechas contínuas indican relaciones directas, y las discontínuas, indirectas. El ancho de las flechas indica la intensidad de la relación. De Houde (2008).

Todas las hipótesis anteriores consideraban la inanición y los procesos físicos como los mayores responsables de la variabilidad en el reclutamiento. Pero, actualmente, la predación está reconocida como el mayor factor de mortalidad que influye al reclutamiento (Hunter, 1981; Bailey and Houde, 1989), aunque su acción está modulada por varios factores: (1) *Temperatura*, que influye en la fisiología, actividad metabólica, comportamiento y crecimiento de los primeros estadios de desarrollo larvario (Blaxter, 1992), actuando en todas las escalas temporales y espaciales relevantes (desde el nivel celular a las grandes cuencas oceánicas); (2) *Procesos físicos* (difusión, advección y dispersión), cuya importancia ya queda reflejada en algunas hipótesis de reclutamiento (Cushing, 1975; Heath, 1992); (3) *Presas*. Una buena cantidad de presas se asocia con una mayor supervivencia y un mejor crecimiento de las larvas (Zenitani *et al.*, 2007), aunque a bajas densidades de presa, la presencia de micro-turbulencias incrementa las tasas de encuentro entre las larvas de peces y sus presas (MacKenzie *et al.*, 1994); y (4) *Estado nutricional y tasas de crecimiento* influenciarán la predación, a través de la talla de la larva y su tasa de crecimiento (ej., Meekan and Fortier, 1996; Vigliola and Meekan, 2002). Así podríamos decir que "Cuanto más grande, mejor" y "Cuanto más rápido crezca, mejor" (del inglés, *The faster you get bigger the better*) (Houde, 1987). Muchos factores que influencian el comportamiento y la fisiología de las larvas de peces tienden a ser talla-dependientes (Hunter, 1981). Las larvas de pequeño tamaño serán más susceptibles a la inanición y, por lo tanto a la depredación, debido a que sus reservas energéticas son limitadas (saco vitelino de pequeño tamaño).

En definitiva, en la actualidad se considera que la variabilidad en el reclutamiento es el resultado de un proceso integrado que actúa durante todo el período anterior al reclutamiento (Fig. 3). De hecho, se afirma que el éxito del reclutamiento no se determina durante un estadio ontogenético preciso (ej., cambio de alimentación endógena a exógena, como aseguraba Hjort), sino que varía en función de la especie, de la población o de las condiciones ambientales (Houde, 2008).

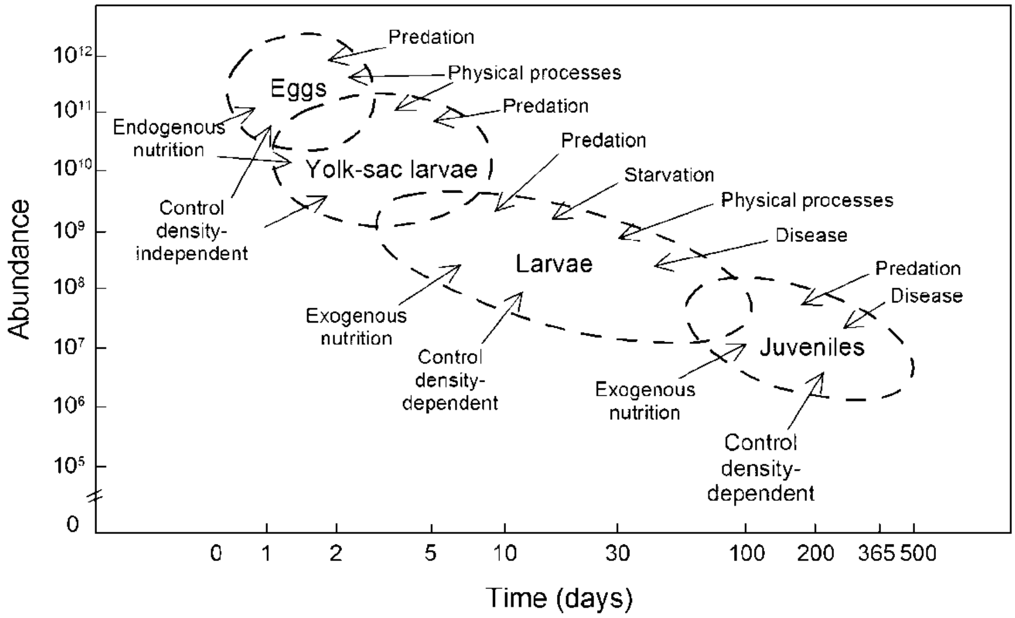


Figura 3. Esquema conceptual de los diferentes procesos que actúan en las cuatro primeras etapas de desarrollo de un pez marino (huevo, larva con saco vitelino, larvas y juveniles). Notése como la predación actúa en todos los niveles. Redibujado de Houde (1987).

La incorporación de nuevas tecnologías como las imágenes de satélite (Platt *et al.*, 2007), simulaciones de dispersión acopladas a modelos basados en el individuo (Werner *et al.*, 2001; Daewel *et al.*, 2008; North *et al.*, 2009) o técnicas de grabación *in situ* (Leis, 2007) han posibilitado tanto testar viejas hipótesis a escalas adecuadas (Platt *et al.*, 2003), al tiempo que se modificaban ciertas creencias sobre la importancia del control hidrodinámico sobre la conectividad y estructura de las poblaciones (Hamilton *et al.*, 2008). Así, aunque en la actualidad la mayor parte de los conceptos básicos sobre reclutamiento y conectividad siguen siendo válidos, se tiende a combinar datos de diversa índole (datos de campo, laboratorio y modelos) provenientes de diferentes disciplinas (climatología, ecología, oceanografía, acuicultura) para lograr optimizar la información. Así se puede, de forma integrada, resolver hipótesis desde el nivel individual al ecosistémico (Cury *et al.*, 2008).

Las fluctuaciones naturales (ej., variaciones climáticas a gran escala o interanuales) son una fuente de incertidumbre en los modelos clásicos de evaluación de stocks pesqueros (Sharp, 2004). Es por esto que el estudio del reclutamiento y, por ende, de las primeras fases de desarrollo de los peces se están convirtiendo en una línea prioritaria de investigación sobre los recursos marinos a escala mundial, como se observa en el incremento de las publicaciones sobre esta temática en las dos últimas décadas (Fig. 4). Los estudios sobre estas fases de los peces (huevos, larvas y juveniles) abarcan múltiples vertientes, como variabilidad en el reclutamiento (Govoni, 2005; Houde, 2008), conectividad (Cowen *et al.*, 2006), cambio global y biodiversidad (Boeing and Duffy-Anderson, 2008), impacto de sustancias tóxicas (Norcross *et al.*, 1996), taxonomía (Richards, 2006) o funcionamiento del ecosistema (Mollmann *et al.*, 2008).

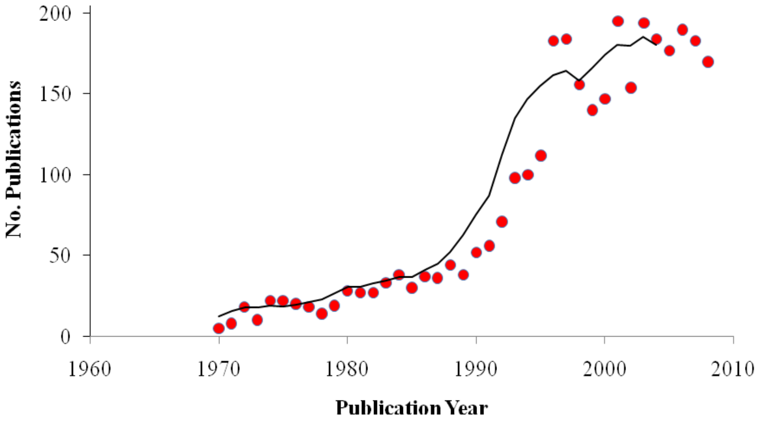


Figura 4. Artículos o revisiones publicadas entre 1970 y 2008 que contienen las palabras *ichthyoplankton* o *fish larva/fish larvae* en el título, resumen o palabras clave. Fuente: Scopus.

Asociaciones de larvas de peces

Las *asociaciones de larvas de peces* se pueden definir como el conjunto de larvas que son capturadas en un momento determinado en un área determinada (Miller, 2002). Así, por definición, son asociaciones transitorias y no suponen que entre las especies que se encuentran asociadas, necesariamente existan procesos de convergencia evolutiva o interacciones biológicas (ej., competición, predación). Así, estas asociaciones simplemente suponen que un determinado grupo de especies han encontrado la misma solución para una determinado periodo de su vida (Miller, 2002).

En la formación y mantenimiento de las asociaciones de larvas de peces participan un conjunto de procesos físicos y biológicos sobre un amplio rango de escalas temporales y espaciales (Tabla 1). Durante la formación, estas asociaciones reflejan la sincronía y cohesión del comportamiento de puesta de los adultos (Frank and Leggett, 1983) y el de las larvas (ej., Gray and Miskiewicz, 2000). Además, se encuentran normalmente asociadas a determinadas masas de aguas (Grothues and Cowen, 1999; Hare *et al.*, 2001), mostrando una distribución de especies que refleja los procesos oceanográficos tanto perpendiculares como paralelos a la costa.

Tabla 1. Descripción de los factores que afectan a la formación, mantenimiento y disgregación de las asociaciones de larvas de peces según Boehlert y Mundy (1993).

Type of factor	Influencing formation	Influencing maintenance	Influencing disruption
Adult behaviour	Spawning location Spawning time (tidal, diel, lunar, seasonal)	None	Predation (cannibalism) Influences on settlement
Egg development	Buoyancy (demersal Vs. Pelagic eggs, egg density) Incubation time Hatching location Hatching time	None	None
Larval behaviour	Buoyancy at hatching Swimming ability at hatching	Habitat preference (temperature, salinity, light, depth) Vertical migration	Ontogenetic changes in vertical distribution Metamorphosis (settlement, schooling)
Biotic environment	Predation (absence will create "ecological safe sites")	Prey presence	Predation Prey absence (starvation)
Abotic environment	Convergence Fronts	Eddies (Taylor columns) Upwelling Downwelling Internal waves Convergences Fronts	Diffusion Mixing Advection

El mantenimiento de estas asociaciones dependerá de la presencia de unas condiciones que favorezcan el crecimiento y la supervivencia de las larvas, y de los procesos físicos que contrarresten los mecanismos que causarían la disrupción de las asociaciones, como flujos ciclónicos (Werner *et al.*, 1993) o frentes (Galarza *et al.*, 2009). Los procesos físicos dispersivos, como los remolinos de núcleo cálido (Drinkwater *et al.*, 2000), los filamentos de afloramiento (Rodríguez *et al.*, 2004), o procesos de difusión (Fortier and Legget, 1985) son factores disruptivos importantes. Por otro lado, los factores biológicos disruptivos más importantes son la metamorfosis y la predación. Esta última es el factor de mortalidad más importante, ya que, con una mortalidad diferencial, la composición de las asociaciones de larvas puede variar fácilmente.

En los últimos años se han llevado a cabo numerosos estudios para conocer la variación temporal y espacial en la estructura y composición de las asociaciones de larvas de peces en determinadas zonas como el mar Mediterráneo (Sabatés, 1990; Somarakis *et al.*, 2002), mar Cantábrico (Rodríguez, 2008), California (Aceves-Medina *et al.*, 2004), Benguela (Olivar and Shelton, 1993) o Australia (Gray and Miskiewicz, 2000; Muhling *et al.*, 2008). Sin embargo, estas variaciones en estas asociaciones son totalmente desconocidas en aguas de las Islas Canarias. La inexistencia de series temporales en la zona ha impedido hasta el momento analizar cuál es la relación entre las diferentes especies a lo largo del año y bajo diferentes condiciones ambientales.

Hidrología y estacionalidad en aguas de Gran Canaria y su efecto sobre la población de larvas de peces

Gran Canaria es una de las islas mayores del Archipiélago Canario (Fig. 5), situada a 28-29º N, muy cercana al afloramiento costero de NO África. Está bañada por la Corriente de Canarias, que es la extensión natural de la Corriente de Azores (Stramma, 1984). A medida que la Corriente de Azores se acerca al margen este del Atlántico Norte, gira hacia el sur forzada por los vientos y el bloqueo del continente africano, constituyendo la Corriente de Canarias. Al llegar a la latitud Cabo Blanco, la Corriente de Canarias se separa de la costa africana, convirtiéndose en la Corriente Ecuatorial del Norte (Fedoseev, 1970; Mittelstaedt, 1991; Fiekas *et al.*, 1992; Paillet and Mercier, 1997; Barton, 2001). Por otro lado, la recirculación más al sur de los 20ºN parece ocurrir todo el año, mientras que en otoño e invierno, el flujo sub-superficial hacia el polo (AAIW, Antarctic Intermediate Water) aflora en superficie pudiendo incluso alcanzar el archipiélago canario (Barton, 2001; Hernández-Guerra *et al.*, 2003).

La estacionalidad en aguas del archipiélago no es tan marcada como en las zonas templadas, debido a su situación subtropical. Así, ésta se manifiesta por una estratificación de las capas superficiales de la columna de agua relativamente fuerte y un máximo de clorofila en profundidad durante la mayor parte del año (Hernández-León *et al.*, 2007). La termoclina estacional se rompe durante el invierno cuando el agua de superficie se enfría (<18.5º C), impulsando el flujo de nutrientes hacia la zona eufótica. Este proceso deriva en la formación del denominado *bloom de finales de invierno* (De León and Braun, 1973; Braun, 1980) durante el que se incrementan los valores de clorofila y de producción primaria. Por lo tanto, este bloom típico de zonas subtropicales (Menzel and Ryther, 1961) depende del aporte de nutrientes, a diferencia del bloom primaveral en zonas templadas que depende de la disponibilidad lumínica.

Los valores anuales de clorofila oscilan normalmente entre 0.05-0.2 $mg \cdot m^{-3}$ en superficie y 0.2-0.3 $mg \cdot m^{-3}$ en el máximo profundo de clorofila, mientras que durante el bloom pueden alcanzar los 1.0-1.5 $mg \cdot m^{-3}$ en las capas superficiales (Hernández-León et al., 2007). Arístegui *et al.* (2001) estudiaron en profundidad la evolución de este bloom en aguas de la isla de Gran Canaria observando que el incremento en la producción primaria se debía principalmente a células grandes (>2 µm) durante la primera parte del bloom, mientras que las células más pequeñas (<2 µm) eran más abundantes al final de éste. Igualmente, encontraron un fuerte control de la biomasa del fitoplancton por pastaje del microzooplancton (o mesozooplancton para las células más grandes). Así, concluyeron que el inicio del bloom dependerá de la disponibilidad de nutrientes, mientras que durante el desarrollo del mismo, el control lo ejercerá la presión predadora del microzooplancton. Este control top-down ha sido confirmado por Schmoker *et al.* (*in prep.*).

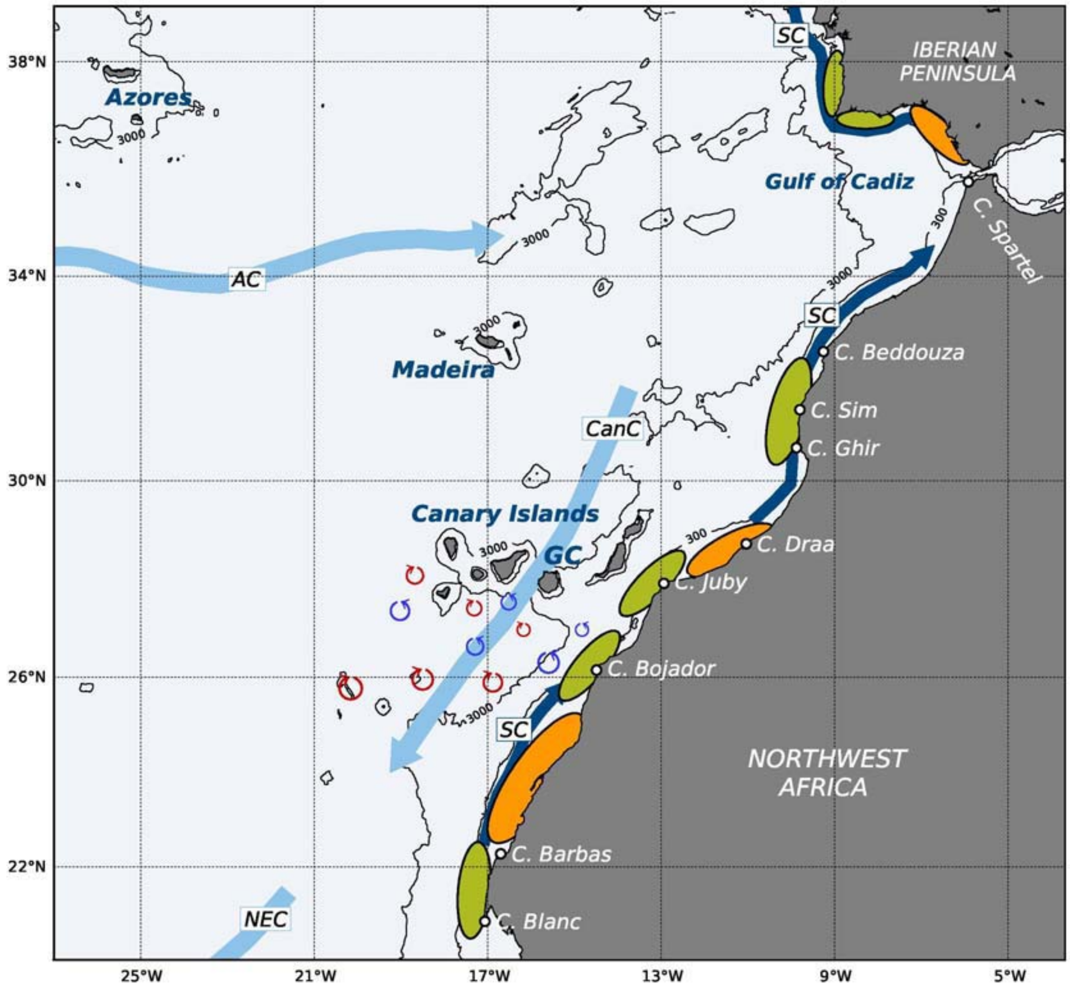


Figura 5. Esquema de la Cuenca Canaria mostrando los cabos más importantes, los diferentes archipiélagos (Azores, Madeira, Canarias) y la isla de Gran Canaria (GC). Además, se muestran las corrientes (azul claro, corrientes superficiales; azul oscuro, corriente de talud), remolinos de mesoscala (azul, ciclónicos; rojo, anticiclónico) y zonas de retención (naranja) y dispersión (verde) en la región costera. AZ: Corriente de Azores, CanC: Corriente de Canarias, NEC: Corriente Ecuatorial del Norte, SC: Corriente de talud. Redibujado de Arístegui *et al.* (2009) por E.Mason.

Por otro lado, el mesozooplancton también muestra máximos anuales durante el mencionado bloom (Hernández-León *et al.*, 1984; Hernández-León, 1988). Estos máximos suelen presentarse con un retraso de dos o tres semanas con respecto al primer máximo de clorofila. Al igual que la clorofila, los valores de biomasa de mesozooplancton también oscilan durante el bloom. Hernández-León *et al.* (2004) afirmaron que el mesozooplancton presenta normalmente dos o tres picos durante el bloom. Esto lo asociaron a la presión predadora ejercida por los migradores verticales (del inglés, *Diel Vertical Migrants*, DVM) de las capas de reflexión profunda. Según estos autores, la evolución del bloom de mesozooplancton en zonas subtropicales está ligada al ciclo lunar, debido a que están acoplados al ciclo de los DVM. Así, durante las épocas de mayor iluminación (luna llena), los DVM se mantienen en capas más profundas, mientras que en las noches de menos luz (luna nueva), son capaces de alcanzar zonas más superficiales y ejercer un control sobre la población de epizooplancton.

En la región canaria, la evolución del ictioplancton durante este bloom era desconocida hasta el momento. Así, resultaba muy interesante evaluar el acoplamiento entre la producción primaria, el zooplancton y las larvas de peces durante el bloom de finales de invierno en esta zona. Ésta sería una manera de comprobar la hipótesis del match-mismatch (Cushing, 1975), originalmente propuesta para aguas templadas, en una zona subtropical.

Comunidades larvarias en islas oceánicas: el caso de Gran Canaria

Las poblaciones de peces neríticos en islas oceánicas necesitan desarrollarse en zonas donde sean capaces de evitar las corrientes que les arrastren lejos de las islas, ya que sino sus larvas se perderían para el reclutamiento. El auto-reclutamiento se considera como el factor más importante a la hora de mantener estas poblaciones en islas oceánicas (Jones *et al.*, 1999; Swearer *et al.*, 1999; Paris and Cowen, 2004). Su importancia resulta evidente si consideramos la existencia de especies endémicas en islas (Wing *et al.*, 1998). Además, éste puede verse potenciado por la presencia de barreras para la dispersión, como los frentes (Galarza *et al.*, 2009), o el propio comportamiento larvario (Leis, 2007). A pesar de esto, Cowen *et al.* (2006) sostienen que el aporte externo de larvas es necesario para el mantenimiento de determinadas poblaciones de peces en islas. Además, estos autores también destacan que una escala relevante de dispersión para larvas de varias especies se debe estimar entre 10-100 km.

La influencia del régimen de corrientes sobre la comunidad de larvas de peces ha sido estudiada en diferentes islas. Hammer and Hauri (1981) registraron altas concentraciones de zooplancton corriente-arriba de la isla, donde diverge el flujo incidente, en Pandora Reef, en la Gran Barrera de Coral (Australia). Del mismo modo, Miller (1979) y Leis (1986) encontraron también mayores densidades larvarias en esa región en Oahu (Hawaii) y Lizard Island (Gran Barrera de Coral, Australia), respectivamente. Por otro lado, Boehlert *et al.* (1992) hallaron altas concentraciones de huevos y larvas de peces a sotavento de Johnston Atoll (Hawaii). Cowen and Castro (1994) obtuvieron mayores densidades de larvas de peces muy cercanas a costa, en zonas con flujo superficial reducido, en Barbados. La presencia de estructuras oceanográficas de mesoscala, como los remolinos, pueden contribuir a la retención de las larvas cerca de la costa (Sale, 1970; Leis, 1982).

En el caso de las Islas Canarias, la presencia del archipiélago bloqueando los flujos oceánicos y atmosféricos, produce una gran variabilidad oceanográfica de mesoscala, con la formación de remolinos ciclónicos y anticiclónicos y estelas cálidas a sotavento (Fig. 6), en el sur de las islas (Arístegui *et al.*, 1994; Barton *et al.*, 1998). Los remolinos derivan con el flujo general de la corriente de Canarias (Fig. 5) formando una *calle de remolinos* (Chopra and Hubert, 1964; La Violette, 1974). La duración de estos remolinos puede ser de varios meses o incluso superior a un año (Sangrá *et al.*, 2005; Sangrá *et al.*, 2007). Estas estructuras están presentes al sur de todas las islas del archipiélago (Fig. 5) e influenciarán la distribución del plancton alrededor de éstas.

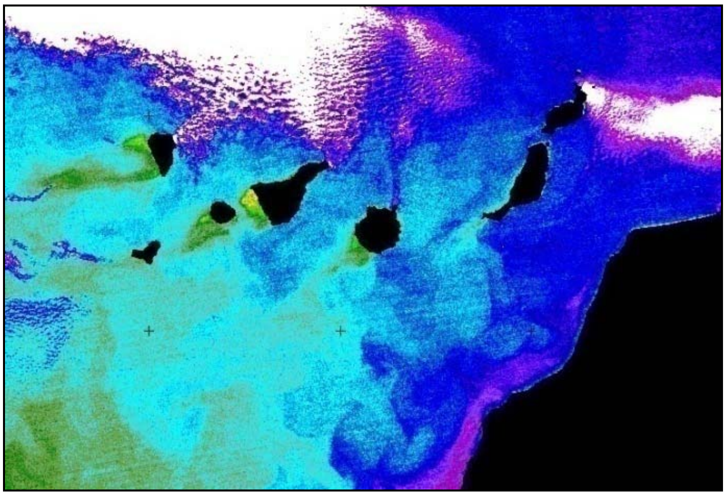


Figure 6. Imagen de temperature superficial del agua mostrando el Archipiélago Canario y las estelas cálidas a sotavento de varias islas.

Durante los primeros años de estudio de la distribución del plancton alrededor de Gran Canaria se centró en las zonas sur y este de la isla (Hernández-León and Miranda-Rodal, 1987; Hernández-León, 1988; Arístegui *et al.*, 1989). Hernández-León (1991) utilizó el término de *efecto de masa de isla* (Doty and Oguri, 1956) para explicar el modelo de distribución del zooplancton alrededor de la isla de Gran Canaria. Así, este autor encontró en la estela cálida de la isla, valores de biomasa zooplactónica hasta 10 veces superiores a los habituales para las aguas oligotróficas de la región. Sin embargo, su potencial metabólico era menor que en las zonas batidas por el viento, lo que sugería que ese aumento de biomasa era debido a la acumulación, más que al aumento de la productividad la estela.

Posteriormente, Rodríguez *et al.* (2001) desarrollaron un modelo de simulación basado en la circulación geostrófica alrededor de la isla de Gran Canaria para explicar la distribución del plancton alrededor de la misma (Fig. 7). Estos autores identificaron dos puntos de retención para zoo- e ictioplancton debido a este efecto de masa de isla: (1)*N-NE a barlovento de la isla*, donde se forma una región de flujo mínimo o nulo, donde la Corriente de Canarias choca con la isla; y (2) *S-SW a sotavento de la isla*, donde se encuentra la estela cálida que generalmente presenta corrientes de poca intensidad. Sin embargo, los márgenes de esta estela están caracterizados por unos gradientes de viento horizontales muy fuertes, así, se produce divergencia y convergecia de Ekman en el oeste y este, respectivamente.

Sin embargo, en los flancos de la isla, el flujo desviado al chocar con la isla se acelera. En el oeste, éste es ayudado por la canalización del flujo causada por la proximidad a de la isla de Tenerife. Además de esto, en la zona sur de la isla se produce una interacción con fenómenos de mesoscala: (1) remolinos generados al SO; y (2) la llegada de filamentos procedentes del afloramiento africano en el SE, que aceleran las corrientes al chocar con el flujo general de la Corriente de Canarias.

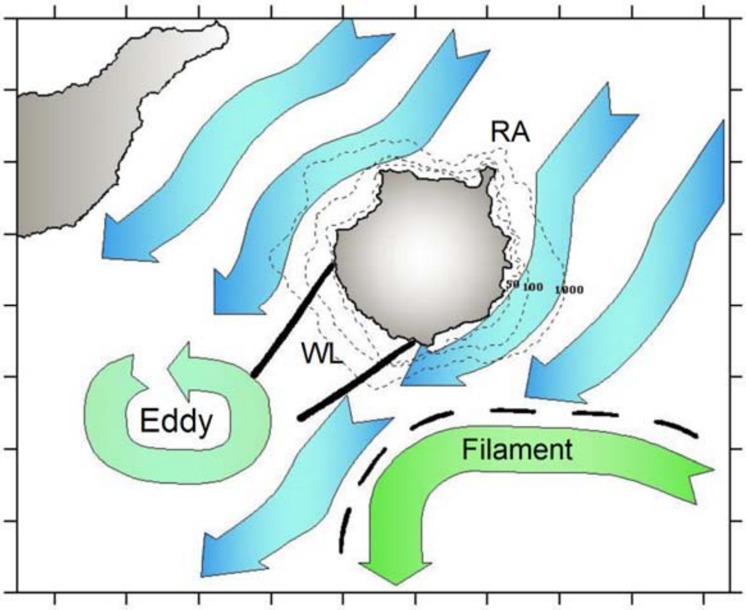


Figura 7. Esquema mostrando los principales elementos hidrográficos que afectan a la isla de Gran Canaria. WL: warm lee; RA: Retention area. Redibujado de Rodríguez *et al*. (2001).

Rodríguez *et al*. (2001) concluyeron que estas zonas de retención son beneficiosas, incluso para organismos con una mínima capacidad de natación, es decir, partículas pasivas que quedarían retenidas en la estela cálida. Sin embargo, a pesar de la importancia de este modelo para el conocimiento de la hidrografía básica que influencia la distribución larvaria cerca de la isla, éste necesitaría mejorarse con la inclusión de los movimientos verticales de las partículas (modelo 3D) y de velocidades de natación y pautas de comportamiento vertical más específicas.

La Zona de Transición Costera Canario-Africana: influencia de la actividad de Mesoscala

El Archipiélago Canario se encuentra situado entre 90-500 km de las costas del NO Africa, donde se localiza uno de los cuatro grandes afloramientos. Así, se sitúa en la zona de transición entre las frías y muy productivas aguas del afloramiento africano y las aguas oligotróficas de mar abierto. De este modo, esta área se conoce como Zona de Transición Costera de Canario-Africana (ZTC Canario-Africana, del inglés *Canaries-African Coastal Transition Zone*).

Los *filamentos de afloramiento* son estructuras frecuentes en los sistemas de afloramiento (Flament *et al.*, 1985). Éstas son unas estructuras superficiales de agua fría y que normalmente no tienen más de 100 km de ancho, pero que son capaces de extenderse desde costa hasta cientos de kilómetros, conectando el afloramiento costero con el océano abierto (Brink and Cowles, 1991). Estas estructuras se estudiaron por primera vez en las imágenes de satélite por infrarrojos de la región de California (Traganza *et al.*, 1980; Traganza *et al.*, 1981). Estos autores comprobaron que los filamentos poseían unas características químicas y biológicas propias. Posteriormente, se comprobó que estas estructuras eran frecuentes en todas las corrientes de frontera este: Benguela (Shillington *et al.*, 1990; Ducombe-Rae *et al.*, 1992; Nelson *et al.*, 1998), Humbolt (Sobarzo and Figueroa, 2001); y NO Africa (ej., Nykjaer *et al.*, 1988; Van Camp *et al.*, 1991; Hernández-Guerra *et al.*, 1993; Barton *et al.*, 1998).

Según Strub *et al.* (1991), los filamentos pueden originarse por: (1) el efecto de la convergencia de diferentes masas de agua cerca de costa, que crea lenguas de agua con un flujo unidireccional hacia el océano (Ikeda and Emery, 1984); (2) la presencia de remolinos que se muevan paralelos a costa y dirijan el agua aflorada hacia el océano (Mooers and Robinson, 1984); (3) por el serpenteo del frente de afloramiento que desplaza el agua aflorada fuera de costa (Strub *et al.*, 1991)

En el caso de la región canaria, la recurrencia de los filamentos en la zona de Cabo Juby está relacionada con la presencia de un remolino ciclónico cuasi-permanente localizado entre Gran Canaria y la costa africana (Barton *et al.*, 1998; Barton *et al.*, 2004). Estos autores afirman que un filamento aparecerá siempre que el afloramiento sea lo suficientemente fuerte para que el frente de afloramiento y el jet asociado se desplacen hacia el océano y sean atrapados por este remolino. El caso más claro de este tipo de génesis de filamentos se ilustra en Barton *et al.* (1998). Sin embargo, estudios posteriores citan la presencia de un filamento con estructura dual (Barton *et al.*, 2000; Barton *et al.*, 2004). Según estos trabajos parece que el origen del filamento localizado más al norte está relacionado con la presencia de un remolino antici-ciclónico situado al sur de Fuerteventura, mientras que el filamento más cercano a Cabo Bojador se origina por la interacción del frente de afloramiento con el remolino cuasi-permanente citado anteriormente. Una vez se adentran en el océano, ambos filamentos convergen en una estructura única mucho más débil.

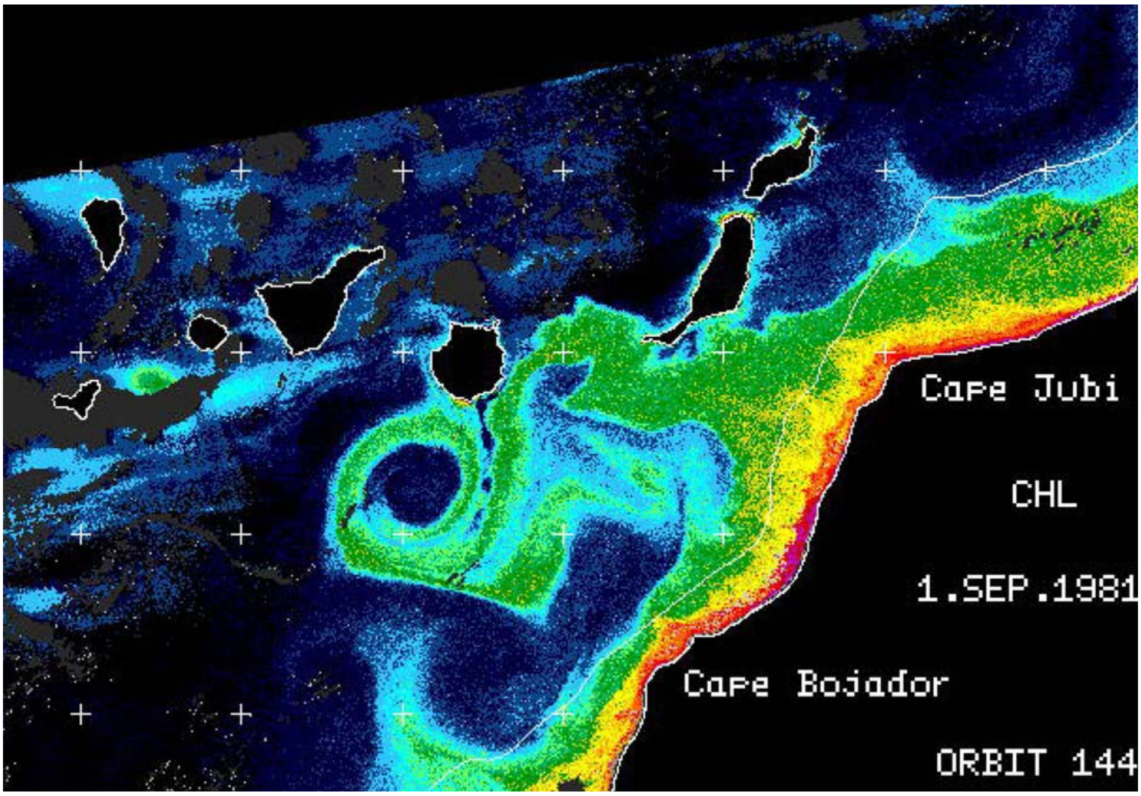


Figura 8 – Imagen SeaWiFS de septiembre de 1981 mostrando la distribución de la clorofila en un gran filamento desprendido de la zona de Cabo Jubi que interacciona con un remolino al sur de Gran Canaria.

El transporte de agua costera aflorada hacia el océano conlleva importantes efectos biológicos, debido al transporte asociado de elementos pasivos, como el plancton. Así, en California se encontraron evidencias de mayores concentraciones de nutrientes y fitoplancton (Chavez *et al.*, 1991) y de zooplancton (Mackas *et al.*, 1991) en el interior de estas estructuras respecto al entorno oceánico que las circundaba. Este transporte de material biogénico en los filamentos también ha sido confirmado en la ZTC Canario-Africana para nutrientes (García-Muñoz *et al.*, 2004), fitoplancton (Arístegui *et al.*, 1997), zooplancton (Hernández-León, 2001, 2002) y larvas de peces (Rodríguez *et al.*, 1999; Rodríguez *et al.*, 2004)

En el caso de larvas de peces neríticos, su desplazamiento desde las productivas costas africanas hacia océano abierto, puede tener consecuencias dramáticas para su supervivencia, que dependerá del destino final de los filamentos. Los estudios disponibles en la zona hasta el momento permiten identificar tres tipos de evolución de los filamentos (Rodríguez *et al*., 1999, 2004; Bécognée *et al*., 2006): (1) *Retención:* el filamento interacciona con el remolino ciclónico cuasi-permanente, de tal manera que las larvas serían devueltas a la región nerítica africana donde se reclutarían a las poblaciones de peces de esa región; (2) *Dispersión I*: El filamento se pierde en el océano abierto, de tal manera que las larvas morirían de inanición, por falta de alimento, o por predación; (3) *Dispersión II:* El filamento se dirige hacia el océano pero llega a las costas de las islas, permitiendo a las larvas ser reclutadas a las poblaciones de peces locales.

Si bien es cierto que la presencia de filamentos procedentes del afloramiento africano, alcanzando las islas más orientales del Archipiélago, ha sido confirmada en numerosas ocasiones en imágenes de satélite, la influencia de los afloramientos sobre las poblaciones locales de peces está aún por determinar. Esto es válido incluso para especies como la sardina (*Sardina pilchardus*) y la anchoa (*Engraulis encrasicolus*), en las que se han centrado todos los estudios anteriores (Rodríguez *et al.*, 1999; Rodríguez *et al.*, 2004; Bécognée *et al.*, 2006).

OBJETIVOS DE LA INVESTIGACIÓN

El objetivo de esta tesis es dar respuesta a las siguientes cuestiones:

1. ¿Qué sabemos sobre el ictioplancton de la Zona de Transición Costera Canario-Africana?
2. ¿Cuál es la composición y estructura de la comunidad de larvas de peces en aguas de la isla de Gran Canaria?
3. ¿Existen variaciones en la composición y abundancia de la comunidad larvaria a lo largo del año o en diferentes puntos en la plataforma de la isla de Gran Canaria?
4. ¿Cuál es el destino de las larvas transportadas por los filamentos de afloramiento procedentes de las costas africanas? Si alcanzan las costas de las Islas Canarias, ¿se puede detectar su influencia sobre las poblaciones de peces locales?

En primer lugar, para responder a la primera pregunta, se llevó a cabo una revisión bibliográfica sobre los trabajos previos realizados en la ZTC Canario-Africana (**Capítulo I**). La mayoría de estos estudios se centran en la dispersión de sardina y anchoa en filamentos de afloramiento o describen la influencia de la hidrografía sobre la comunidad larvaria en la isla de Gran Canaria.

En referencia a la segunda y tercera cuestión, se realizó una serie temporal de ictioplancton por primera vez en la zona. Durante esta serie temporal se llevaron a cabo muestreos semanales, durante más de dos años, en una serie de estaciones localizadas en el borde de la plataforma continental de la isla de Gran Canaria (**Capítulos II, III y IV**). De este muestreo intensivo se obtuvieron una importante cantidad de datos que nos han permitido describir con bastante precisión la composición y estructura de la comunidad de larvas de peces de la isla de Gran Canaria y sus variaciones temporales y espaciales.

En relación a la cuarta cuestión, evaluamos el papel dispersivo de los filamentos de afloramiento empleando dos tipos de métodos. Por un lado, se combinó (1) el muestreo del ictioplancton en estaciones fijas situadas en la plataforma de la isla de Gran Canaria con (2) el análisis de imágenes de satélite para determinar el transporte de larvas hacia la isla (**Capítulo II**). Por otro lado, se emplearon datos de una campaña en la ZTC Canario-Africana que se llevó a cabo en presencia de un filamento, en la que pudimos estudiar las larvas transportadas *in situ* y los cambios metabólicos de las mismas a lo largo del filamento (**Capítulo V**).

PLANTEAMIENTO Y METODOLOGÍA

Los estudios sobre ecología ictioplanctónica en zonas subtropicales resultan un desafío ya que las condiciones son todo menos ideales, como bien explicaba Leis (1991) para los trópicos. La mayor parte de estudios sobre ictioplancton se han centrado en zonas templadas, que poco tienen en común con nuestra zona de estudio, donde hay unas complicaciones adicionales que afectarán al proceso de identificación taxonómica:

- El número de especies de peces en la región canaria es elevado: 606 especies (Brito *et al.*, 2002).
- Los períodos de puesta de la mayoría de estas especies son largos, a diferencia de las zonas templadas donde son cortos y bien marcados.
- Los estadíos pelágicos de larvas y juveniles son difíciles de identificar, y para muchas especies están aún por describir.
- Las densidades larvarias son muy bajas, de hecho, no es inusual que incluso larvas de especies comunes estén ausentes en la mayoría de las muestras (Leis and Goldman, 1987; Leis and Trnski, 1989).

Toma de muestras

Toda la metodología llevada a cabo en cada trabajo de esta tesis se describe en cada capítulo correspondiente. Aún así, todos ellos constan de:

- Caracterización de las variables físicas de la columna de agua, para lo que se utilizó un CTD (bien SBE25 o Neil Brown Mark-III).
- Recopilación de imágenes de satélite de temperatura (SST) y clorofila (SeaWiFS) procedentes del Grupo de Investigación en Oceanografía Física y Oceanografía por Satélite (ULPGC) y del Centro de Recepción, Proceso, Archivo y Distribución de imágenes de observación de la Tierra (CREPAD) del Instituto Nacional de Técnica Aeroespacial (INTA).

- Estimación de la concentración de clorofila *a* por el método fluorimétrico (Yentsch and Menzel, 1963) a partir de muestras de agua obtenidas con una botella Niskin.
- Pescas oblícuas de mesozooplancton e ictioplancton con red bongo (40 cm de diámetro y malla de 200 µm) o red LHPR (Longhurst-Hardy Plankton Recorder, malla de 200 µm).

La biomasa del mesozooplancton se estimó como peso seco, siguiendo el método propuesto por Lovegrove (1966), o a partir del contenido en proteínas siguiendo el procedimiento de Lowry *et al.* (1951) modificado por Rutter (1967).

Las larvas de peces se triaron en su totalidad bajo un microscopio estereoscópico y se conservaron en una solución de agua de mar y formaldehido tamponado al 4%. Debido al empleo de la red Bongo en pescas diurnas, se capturaron sobre todo los primeros estadios larvarios y apenas se encontraron ejemplares avanzados. Sin embargo, estos ejemplares más avanzados junto con juveniles de especies mesopelágicas, se capturaron en las pescas nocturnas con la LHPR. En el caso de los huevos de peces, éstos sólo fueron considerados en algunos trabajos, debido a su escasez y a la dificultad para su identificación.

En relación a los parámetros fisiológicos, la actividad de transporte del sistema de electrones (ETS del inglés *Electron Transfer System*) se midió de acuerdo a Kenner and Ahmed (1975) siguiendo las modificaciones de Gómez *et al.* (1996), mientras que para la actividad AminoAcil tRNA sintetasa (AARS del inglés *AminoAcyl tRNA Synthetase*) se empleó el método colorimétrico de Chang *et al.* (1984), modificado por Yebra and Hernández-León (2004). La fluorescencia del tracto digestivo (GF del inglés *Gut Fluorescence*) se midió a partir de los homogenados crudos, siguiendo el método de Yebra *et al*. (2004).

Identificación, Terminología y Sistemática

Antes de comenzar las identificaciones fue necesario recopilar información sobre zonas y tiempos de puesta de los adultos. En el caso de las Islas Canarias, la lista de especies empleada fue la presente en Brito *et al.* (2002), complementada con la lista de especies para el Atlántico Norte del CLOFETA (Check List of the Fishes of the Eastern Tropical Atlantic, Queró *et al.*, 1990) y CLOFNAM (Check List of the fishes of the north-eastern Atlantic and of the Mediterranean, Whitehead *et al.*, 1984). Por otro lado, se empleó Franquet and Brito (1995) como referencia de los períodos de puesta de algunas especies. Para el resto de especies, en caso de existir, se buscó bibliografía específica (ej., Lorenzo-Nespereira and Pajuelo, 1993; Méndez-Villamil *et al.*, 1997; Wienerroither, 2005). Debido a la ausencia de una guía de ictioplancton local, se tuvo que recurrir a las de otras zonas: Mediterráneo (Ancona *et al.*, 1931-1956; Sabatés, 1988; Alemany, 1997), Atlántico Noroeste (Fahay, 1983; Richards, 2006), Atlático Noreste (Russell, 1976), Benguela (Olivar and Fortuño, 1991), Corriente de California (Moser *et al.*, 1984), Indo-Pacífico (Leis and Carson-Ewart, 2004).

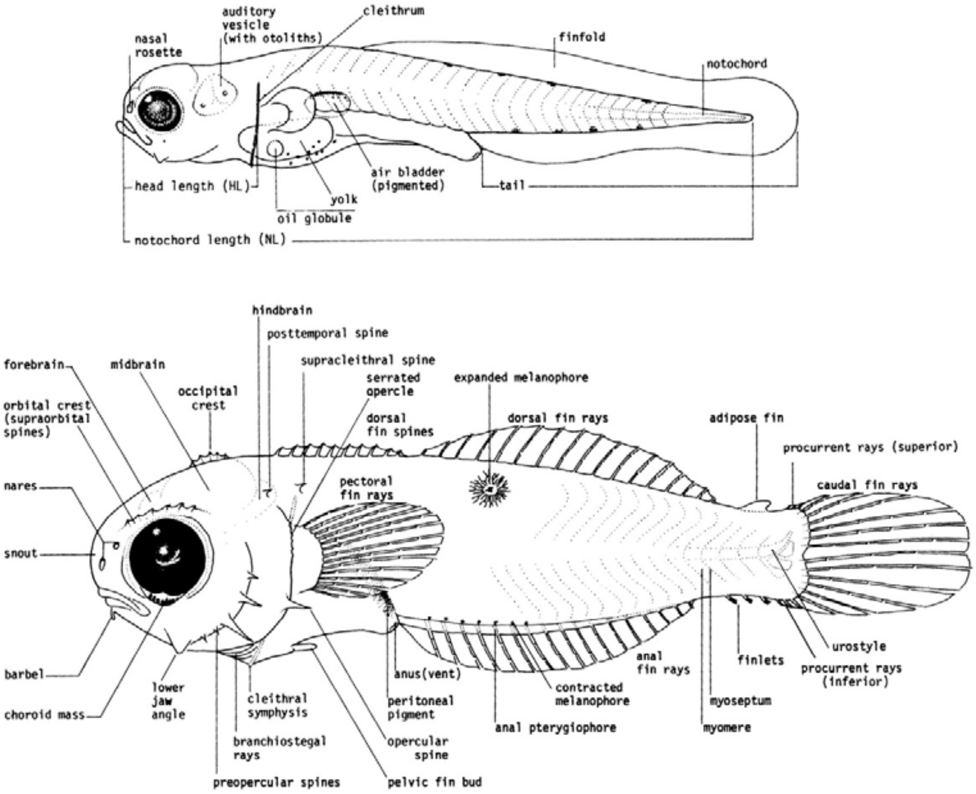


Figura 1. Esquema mostrando las características morfológicas de una larva de pez en estado de preflexión (superior) y postflexión (inferior), con las aletas desarolladas y la presencia de estructuras especializadas (espinas, barbillón…). De Fahay (1983).

A la hora de la identificación y clasificación de las larvas de peces (Fig. 1), se emplearon caracteres: morfológicos (forma y longitud de cuerpo, cabeza, digestivo, ojo; secuencia de aparición y posición de aletas; caracteres larvarios especializados…), merísticos (número de miómeros, radios…) y los patrones de pigmentación (melanóforos).

La identificación de las larvas se realizó al nivel taxonómico más bajo posible, aunque el pequeño tamaño o deterioro de algunos ejemplares dificultó en numerosas ocasiones alcanzar el nivel específico.

La terminología empleada para los estadíos de desarrollo de las larvas es la correspondiente al sistema de Ahlstrom y colaboradores (Kendall *et al.*, 1984). Por otro lado, la clasificación sistemática empleada ha sido la de Queró *et al.* (1990), complementada con la de Whitehead *et al.* (1984) y los nuevos nombres específicos aceptados recientemente (ej., *Scomber colias*).

En los diferentes capítulos se emplea con frecuencia, una clasificación artificial que separa las especies de larvas en tres grupos, según la ecología de sus estados adultos (Rodríguez *et al.*, 1999): (1) *Neríticas*, aquellas especies cuyos adultos normalmente viven y se reproducen sobre la plataforma, hasta los 200 m de profundidad; (2) *Oceánicas,* aquellas especies cuyos adultos viven y se reproducen en aguas más profundas (>200 m); y (3) *Otras,* este grupo incluye a todas las larvas no identificadas o aquellas identificadas al nivel de familia, en aquellas familias que poseen especies neríticas y oceánicas.

RESULTADOS

CAPÍTULO I. La comunidad ictioplanctónica de la Zona de Transición Canario-Africana: una síntesis

La Corriente de Canarias es la extensión natural de la Corriente de Azores que circula en dirección al Ecuador, entre las latitudes 33ºN-20ºN (Barton *et al.*, 1998). Como otros ecosistemas de afloramiento, el sistema de la Corriente de Canarias está caracterizado por una gran actividad de mesoscala en la zona transición entre las aguas frías y productivas de las costas africanas y las aguas más cálidas y oligotróficas de océano abierto. Pero la particularidad de este sistema radica en la presencia del Archipiélago Canario, que interrumpe el flujo principal de la Corriente de Canarias y de los vientos alisios. Esto generará una serie de estructuras de mesoscala, como estelas cálidas y remolinos ciclónicos y anticiclónicos, al sur de las islas en la denominada Zona de Transición Costera Canario-Africana (ZTC Canario-Africana).

La comunidad de larvas de peces en la ZTC Canario-Africana se caracteriza por: (2) una alta diversidad típica de sistemas subtropicales (Longhurst and Pauly, 1987); (2) la mayoría de las especies pertenecen a la región oceánica-mesopelágica, siendo los Mictófidos la familia más diversa y *Cyclothone braueri* la especie más abundante; (3) presencia de larvas de especies tropicales (p.e,. *Hygophum macrochir, Vinciguerria nimbaría*), que podría ser el resultado del proceso de *tropicalización* que, según Brito *et al.* (2005), está sufriendo la ictiofauna de las Islas Canarias.

Pero quizás, la conclusión más importante de esta revisión es la estrecha relación entre la distribución larvaria y los fenómenos de mesoscala. Así, podemos identificar dos tipos de procesos:

- *Transporte por corrientes y estructuras mesoscalares generadas por las islas.* La Corriente de Canarias y los remolinos generados en las islas dispersan los huevos y larvas de especies neríticas hacia el océano abierto (Fig. 2a, Cap. I) (ej., *Anthias anthias* Rodríguez, 2000; Rodríguez *et al.*, 2001). Sin embargo, también las estelas cálidas y algunos remolinos pueden retener larvas neríticas cerca de la isla, como se observó en un modelo hidrodinámico de la distribución ictioplanctónica alrededor de la isla de Gran Canaria (Rodríguez *et al.*, 2001).

- *Transporte en filamentos de afloramiento*. Las especies más abundantemente transportadas en estos filamentos son *Sardina pilchardus* y *Engraulis encrasicolus,* muy comunes en la región nerítica africana. Ambas especies parecen haber encontrado una forma de retención en el complejo remolino-filamento, en la zona de Cabo Juby-Cabo Bojador (Figs. 1-2, Cap. I) (Rodríguez *et al.*, 1999). Por otro lado, también, estos filamentos pueden desplazarse hacia el océano, pudiendo, en este caso, alcanzar las costas canarias y transportar larvas neríticas de África hasta éstas. Esto ya se ha demostrado para *Sardina pilchardus,* cuyas larvas fueron transportadas hasta las costas de Gran Canaria, tanto en invierno como en verano (Bécognée *et al.*, 2006; Moyano *et al.*, 2009). Estos filamentos pueden interaccionar a su vez con remolinos generados por las islas, intercambiando agua y material biogénico, incluyendo larvas de peces.

La presencia de *Sardina pilchardus* y *Engraulis encrasicolus* en filamentos de afloramiento es lógica, considerando su abundancia y su distribución superficial, lo que las sitúa en la capa de Ekman y, por tanto, en la masa de agua transportada por los filamentos. La presencia de una u otra especie durante el verano parece depender de la temperatura del agua en la región del afloramiento (Rodríguez *et al.*, 1999; Rodríguez *et al.*, 2004), mientras que en invierno, coincidiendo con el pico de puesta de *Sardina pilchardus*, las larvas de esta especie predominarán.

En cuanto a las migraciones verticales, sólo *Engraulis encrasicolus* mostró un patrón claro en el que las larvas más grandes se encuentran en capas más superficiales durante la noche (Fig. 3, Cap. I). La comunidad larvaria al completo, no parece mostrar una variación diaria en su distribución vertical, ya que los diferentes patrones de migración vertical de las diferentes especies parecen compensarse (Rodríguez, 2006).

En conclusión, esta revisión da una idea bastante precisa sobre la estructura, composición y abundancia de la comunidad larvaria en la ZTC Canario-Africana. También muestra una clara relación entre la distribución larvaria y los procesos de mesoscala. Así, estos procesos, principalmente los filamentos, afectan a la composición, estructura y abundancia de la comunidad larvaria en la zona de transición entre la costa Africana y las Islas Canarias.

CAPÍTULO II. Abundancia y distribución de larvas de peces durante el bloom de finales de invierno en la isla de Gran Canaria, Islas Canarias

Los procesos que actúan durante las primeras fases de la vida de un pez van a tener consecuencias muy importantes para el posterior éxito del reclutamiento. Es por esto que el conocimiento de la ecología de estos primeros estados es tan relevante en términos de gestión pesquera y diseño de reservas marinas (Fuiman, 2002).

A pesar de que el ictioplancton de muchas zonas ha sido ampliamente estudiado (ej., California, Golfo de México, Mar Báltico), éste no es el caso de las Islas Canarias, donde apenas se han llevado a cabo unas pocas campañas puntuales, a partir de las cuales, se ha descrito la composición de esta comunidad. Sin embargo, los cambios fenológicos de la misma son totalmente desconocidos. Para resolver estos problemas, se planteó un estudio temporal en la isla de Gran Canaria que consistió en muestrear seis estaciones localizadas en la isóbata de los 100m (Fig. 1, Cap. II), muestreadas semanalmente durante ocho meses. El objetivo principal era estudiar la evolución de la comunidad de larvas de peces durante el período del bloom de finales de invierno, a la vez que intentar analizar en un plazo relativamente amplio, el efecto real de los filamentos sobre la comunidad local de peces de la isla (Bécognée *et al.*, 2006).

Los resultados muestran una comunidad de larvas muy diversa compuesta a partes iguales por especies neríticas y oceánicas, como era de esperar en una isla oceánica (Miller, 1979; Leis, 1986), en una zona subtropical (Longhurst and Pauly, 1987). Esta alta contribución de especies oceánicas se explica claramente por la batimetría y las condiciones hidrográficas de la isla, aunque su abundancia es menor que la encontrada en otros trabajos más centrados en la región oceánica (Rodríguez *et al.*, 1999; Rodríguez, 2000). Tres familias, Myctophidae, Gonostomatidae y Photichthydae, suponen casi el total de larvas de este grupo, con porcentajes de 26.6%, 7.3%, 3.2%, respectivamente del total de larvas capturadas. Por otro lado, las familias neríticas más importantes fueron Sparidae, Clupeidae y Gobiidae (12.7, 11.9 y 8.7% del total de larvas capturadas).

Durante el bloom, se observó claramente el patrón característico de temperatura y clorofila previamente descrito por Arístegui *et al.* (2001) y de zooplancton (Hernández-León *et al.*, 2004). Las larvas de peces parecen seguir una tendencia similar al zooplancton durante este período, básicamente debido a las especies neríticas. Esto nos hace pensar que podrían estar sometidas al mismo ciclo de predación por los migradores verticales que el mesozooplancton (ver Hernández-León *et al.*, 2004). A este respecto, cabe destacar que las distribuciones temporales de familias, tan ecológicamente diferentes en su etapa adulta, como Mictófidos, Espáridos y Clupéidos fueron similares durante todo el período de muestreo, con una cierta tendencia a mostrar máximos coincidiendo con los mínimos de salinidad (Figs. 3-4, Cap. II).

Otro aspecto importante de este estudio era comprobar el modelo hidrodinámico de la distribución del plancton alrededor de la isla de Gran Canaria propuesto por Rodríguez *et al.* (2001) con una mayor resolución espacial y temporal. Así, los resultados obtenidos confirman el efecto de retención de mesozooplancton de pequeño tamaño y larvas neríticas que se produce en la zona a barlovento y sotavento (estela cálida) de la isla (Fig. 6, Cap. II). Los valores máximos para ambos grupos fueron encontrados en la estación 5, que se encuentra en la zona de convergencia del margen este de la estela cálida. A pesar de encontrarse una cantidad de larvas neríticas significativamente mayor en las zonas de retención, este patrón espacial no fue significativo para las diferentes familias (Fig. 7, Cap. II). Así, sólo la familia Gobiidae mostró diferencias significativas en cuanto a su distribución espacial, con valores menores en las estaciones del flanco este de la isla.

La familia clave en este estudio son los Clupeidos, por su importancia comercial en las Islas. *Sardinella aurita* fue la especie más abundante, mientras que *Sardina pilchardus* apenas apareció en cuatro ocasiones, coincidiendo siempre con la llegada de filamentos de afloramiento a la isla (Fig. 4-5, Cap. II). El transporte de esta especie en filamentos procendentes del afloramiento norafricano y su llegada a las costas orientales de algunas islas ya había sido propuesto anteriormente (Rodríguez *et al.*, 1999; Bécognée *et al.*, 2006), pero durante este trabajo se pudo comprobar cómo el aporte de larvas de sardina ocurre durante todo el año. Debido a la disminución de los stocks de sardina en las islas y a los resultados del estudio biométrico en adultos realizado paralelamente, en el que no fue posible encontrar ningún individuo en estado grávido o postpuesta, se plantea el hecho de que ésta pueda ser la única fuente de reclutamiento para las poblaciones de sardina de la isla de Gran Canaria.

En resumen, podríamos decir que la importancia de este estudio radica en que es el primero que describe la composición de la comunidad costera de larvas de peces en aguas de la isla de Gran Canaria y su variación temporal y espacial. Este trabajo muestra, por lo tanto, cómo las familias neríticas (principalmente lideradas por Espáridos, Clupéidos y Góbidos) predominan en dos zonas de retención al nor-este y sur-oeste de la isla, zonas en las que también se registran valores más altos de zooplancton. La coincidencia de máximos de abundancia de Clupéidos y mínimos de salinidad sugiere que el transporte de larvas desde el afloramiento a las islas puede ser recurrente. De todos modos, la importancia de esas contribuciones para la población local de clupéidos aún necesita un estudio más profundo.

CAPÍTULO III. Variaciones temporales y espaciales del conjunto de larvas de peces en Gran Canaria, Islas Canarias

En el particular entorno de las islas oceánicas, conocer los procesos que regulan el auto-reclutamiento y la ecología de las larvas de peces será vital a la hora de analizar el mantenimiento de las poblaciones en la isla. Basándose en muestreos semanales a lo largo de nueves meses en cinco estaciones costeras de la isla de Gran Canaria (Fig.1, Cap. III), se analizaron las variaciones estacionales y espaciales de la comunidad de larvas de peces y su relación con los parámetros hidrológicos.

Respecto a la variación temporal de los factores variables ambientales, se observó la típica evolución en aguas canarias: una fuerte estratificación en otoño, que se rompe en diciembre cuando comienza la mezcla vertical, que determina el principio del bloom de finales de invierno (Fig. 2, Cap. III). Después, en abril-mayo, la estratificación vuelve a aparecer. A pesar de que la abundancia de larvas de peces no parece seguir un patrón general en su distribución temporal, como lo hace el zooplancton con valores máximos durante el bloom (Fig. 3, Cap. III), sí que parecen presentar cierta estacionalidad.

La composición y densidad media de larvas está en el rango esperado respecto a otros estudios en la zona (Rodríguez, 2000; Rodríguez *et al.*, 2001) y en otras partes del mundo (ej., Smith and Suthers, 1999; Alemany *et al.*, 2006). Aunque este estudio no muestrea un año completo, los resultados sugieren que existen dos asociaciones de larvas estacionales (invierno y verano). Estas asociaciones coincidirían básicamente con las dos posibles situaciones de la columna de agua, mezcla y estratificación, respectivamente. La asociación de larvas de invierno estaría dominada por *Boops boops*, *Sardinella aurita* y *Cyclothone braueri*, además de la presencia de típicas especies de puesta invernal como *Trachurus pictoratus* y *Scomber colias*. En la asociación de verano, por otro lado, parecen dominar dos especies mesopelágicas *Ceratoscopelus warmingii* e *Hygophum hygomii*, junto con varias especies de puesta estival: *Trachinus draco*, Pomacentridae sp2 y una especie de Tetraodóntidos.

En cuanto a la variación espacial, las estaciones del flanco este de la isla mostraron valores significativamente más bajos de temperatura mínima y salinidad que las estaciones situadas en la estela cálida. Estas variaciones hidrográficas parecen no ser suficientes para que haya diferencias significativas en la comunidad de larvas de peces. Sin embargo, sí que se comprobó la retención de huevos y larvas de especies neríticas en la zona de la estela cálida de la isla (Fig. 4, Cap. III), previamente descrita por Rodríguez *et al.* (2001). Sólo Clupéidos y Góbidos mostraron abundancias significativamente mayores en esta estela, con respecto a las estaciones del flanco este de la isla, mientras que la familia Photichthyidae siguió una distribución inversa.

Los resultados de este estudio, respecto a la relación entre el zooplancton e ictioplancton y el ciclo lunar, resultan muy interesantes. El mesozooplancton de pequeña talla mostró una periodicidad significativamente ligada al ciclo lunar, mostrando máximos de biomasa durante la luna llena. Este comportamiento fue explicado por Hernández-León *et al.* (2004), como un resultado de la presión predadora que ejercen los migradores verticales. Durante los períodos de poca iluminación (luna nueva) estos organismos son capaces de alcanzar zonas más someras en la columna de agua, mientras que cuando hay mucha iluminación (luna llena), no son capaces de ascender tanto, liberando de la presión depredadora al epizooplancton. Por lo tanto, dado que se encontró una relación significativa entre el mesozooplancton de pequeño tamaño y las larvas neríticas, se podría esperar una relación también de éstas con el ciclo lunar, apoyando una reciente teoría de Hernández-León (2008). Este autor encontró evidencia de un acoplamiento entre la reproducción de los peces y los máximos de biomasa del epizooplancton durante los períodos de mayor iluminación lunar, argumentando que este patrón puede constituir una versión a corto plazo de la teoría del match-mismatch de Cushing (1990). Por lo tanto, los resultados de este estudio parcialmente corroboran esta teoría fundamentalmente para las familias de Clupéidos y Espáridos, principales representantes de las larvas neríticas (Fig. 5, Cap. III). Máximas abundancias para estas dos familias se registraron durante las fases iluminadas de la luna, lo que apoya la idea de que la puesta está regulada para potenciar la supervivencia larvaria en un momento de baja predación y alta cantidad de alimento.

Como resumen, podríamos decir que la comunidad larvaria de la isla de Gran Canaria parece mostrar dos asociaciones estacionales que se corresponden con las épocas de mezcla o estratificación de la columna de agua. A pesar de la presencia de algunas especies durante todo el año, son las que tienen puesta invernal o estival las que parecen definir estas asociaciones estacionales. En este sentido, las variaciones temporales parecen tener más peso a la hora de estructurar la comunidad larvaria que la situación en la isla a lo largo del tiempo. La alta variabilidad de la abundancia larvaria durante el período de muestreo y su estrecha periodicidad junto al pequeño mesozooplancton cuestionan los factores que en último término controlan la dinámica larvaria en esta zona oceánica subtropical. Por último, la influencia del ciclo de predación de los migradores verticales, unido al ciclo lunar, sobre el zooplancton e ictioplancton parece controlar su variabilidad temporal. Por lo tanto, un mayor conocimiento de la dinámica larvaria en la zona mejoraría enormemente los aspectos de la gestión de pesquerías y reservas marinas en el archipiélago.

CAPÍTULO IV. Variaciones interanuales y estacionales de las asociaciones de larvas de peces en Gran Canaria, una isla oceánica en el Atlántico NE

Las asociaciones de larvas de peces son temporales y su estudio ha tratado de comprender por qué ocurren en los lugares y momentos que lo hacen y cómo se pueden traducir esas distribuciones espaciales y temporales en patrones de reclutamiento (Miller, 2002). El estudio de la composición de estas asociaciones de larvas y la manera en que éstas reflejan los procesos oceanográficos tanto perpendiculares como parelelos a costa ha sido explicado en numerosos ecosistemas (ej., Sabatés, 1990; Gray and Miskiewicz, 2000; Hare *et al.*, 2001; Muhling *et al.*, 2008). Sin embargo, en la isla de Gran Canaria, nunca se habían estudiado estas asociaciones en una serie temporal larga. Empleando datos semanales de una estación situada enfrente de Las Palmas de Gran Canaria, en el borde de la plataforma continental (100 m de profundidad) (Fig. 1, Cap. IV), se estudiaron las variaciones estacionales e interanuales de las larvas de peces y del ambiente que las rodea.

La alta diversidad típica de aguas subtropicales (Longhurst and Pauly, 1987) se reflejó en el número de taxones encontrados en este estudio: 49 familias, 69 géneros y 100 especies. El análisis de la estructura y composición de la comunidad larvaria (Primer, Clarke and Warwick, 2005) mostró diferencias significativa entre meses, pero no entre años. De este modo, los meses de invierno por un lado, y de verano, por otro, eran más parecidos, que los meses de primavera y otoño. Entonces, tras comprobar estadísticamente la existencia de diferencias estacionales, se pudieron identificar dos asociaciones estacionales de larvas: invierno-primavera y verano-otoño (Fig. 5, Cap. IV).

La estructura de las asociaciones de larvas en aguas canarias está determinada por la alta diversidad. Así, aunque algunas especies estén presentes en determinadas asociaciones, la mayoría tendrán una presencia dinámica, como ya se ha observado en las costas del suroeste australiano (Gray and Miskiewicz, 2000) o en el norte de Chile (Rodríguez-Graña and Castro, 2003). Estos estudios encontraron un patrón estacional con la presencia de larvas de determinadas especies durante una estación precisa, mientras que otros taxones dominantes aparecían durante todo el año (pudiendo o no presentar picos de puesta). Este es el caso para Gran Canaria donde unos pocos taxones relativamente abundantes dominan la comunidad larvaria durante todo el año: *Cyclothone braueri, Sardinella aurita, Ceratoscopelus* spp y Góbidos.

La asociación de invierno-primavera está dominada por *S. aurita*, *C. braueri* and *B. Boops.* Además, la presencia de Pomacentridae sp1 y *Lobianchia dofleini*, así como de species con puesta típicamente invernal como *Pagellus bogaraveo* (Bauchot and Hureau, 1986; Stockley *et al.*, 2005), caracterizan este grupo. *Stomias* sp y *Bathylagus* sp también identifican este grupo.

La asociación de verano-otoño está dominada por Góbidos y *Cyclothone braueri*, pero lo que realmente identifica a este grupo son las abundancias de *Ceratoscopelus warmingii*, Pomacentridae sp2, *Lampanyctus* spp and *Anthias anthias.* Otras especies como *Trachinus draco*, *Arnoglossus thori* o Tetraodontidae sp1 únicamente aparecen en estos meses cálidos, con lo que parecen presentar puesta estival, similar al Mediterraneo (Sabatés, 1990).

Al analizar las variables ambientales para estudiar su efecto estructural sobre la variabilidad de la comunidad larvaria (Bio-Env), se comprobó que las asociaciones estacionales de larvas eran básicamente dependientes de la temperatura ($R=0,355$, $p<0.01$) y, en menor medida, de la salinidad (temperatura+salinidad, $R=0.402$, $p<0.01$). Además, se determinaron las características ambientales de las dos asociaciones (Fig. 6, Cap. IV). Así, la asociación de invierno aparece en aguas frías, con menores salinidades y más productivas (mayor concentración de clorofila y biomasa mesozooplanctónica). Por el contrario, la asociación de verano se caracteriza por temperaturas y salinidades más altas y menores concentraciones de clorofila y mesozooplancton.

Durante el verano de 2005 se registró la llegada de filamentos de afloramiento a la isla de Gran Canaria (Moyano *et al.*, 2009). A pesar de que otro filamento se detectó en febrero de 2007, sólo se detectaron variaciones en la comunidad larvaria en agosto de 2005. Durante este mes, se encontraron mayores concentraciones de especies mesopelágicas, así como la presencia de larvas de *Sardina pilchardus* y *Engraulis encrasicolus.* A pesar de que la contribución de estos clupeidos trasportados en filamentos de afloramiento hacia las Islas Canarias se ha debatido en varios trabajos (Rodríguez *et al.*, 1999; Rodríguez *et al.*, 2004; Bécognée *et al.*, 2006; Moyano *et al.*, 2009), esta es la primera vez en que realmente la llegada del filamento sugiere un cambio real en la comunidad larvaria local. De cualquier manera, mayor cantidad de muestreos son necesarios para poder confirmar este efecto sobre las comunidades locales.

Además de la clara estructuración de la comunidad larvaria, este trabajo reveló variaciones interanuales bastante interesantes durante el período del bloom de finales de invierno (Figs. 3-4, Cap. IV). La temperatura mínima y la salinidad claramente aumentaron en 2007, mientras que la concentración de clorofila y la biomasa total del mesozooplancton mostraron una tendencia decreciente. Así, parece que la magnitud de este bloom depende de la temperatura (un buen indicador son <19ºC en la capa de mezcla); así durante los años fríos, el bloom tendrá lugar antes y se alcanzarán unas mayores concentraciones de clorofila y biomasa de mesozooplankton, mientras que en los años cálidos, al retrasarse el comienzo del bloom, los valores de ambas variables serán menores. Además de todo esto, parece que el índice mensual de la Oscilación del Atlántico Norte (*del inglés* NAO, North Atlantic Oscillation) podría estar relacionado con los valores mensuales de biomasa mesozooplanctónica, aunque son necesarias series temporales más largas para poder confirmar este hecho.

En conclusión, este trabajo ha revelado que las asociaciones de larvas de Gran Canaria exhiben un claro patrón estacional de acuerdo con las variaciones de las variables físicas y biológicas. En nuestra región, estas asociaciones de larvas están caracterizadas por la alta diversidad de especies y la extensión de los períodos de puesta de la mayoría de las especies que habitan estas aguas subtropicales. Este estudio ha mostrado patrones temporales muy útiles para comprender las variaciones de la comunidad larvaria en la isla de Gran Canaria y supone la base para futuros estudios en esta área, enfatizando la importancia de estos primeros estadíos de los peces como estudio adicional para la gestión de pesquerías y diseño de reservas marinas.

CAPÍTULO V. Distribución mesoscalar de larvas de clupeoides en un filamento de afloramiento atrapado por un remolino ciclónico casi-permanente en el NO África

La gran actividad de mesoscala en la Zona de Transición Canaria (ZTC) (Barton *et al.*, 1998), la convierte en una región muy adecuada para los estudios de dispersión larvaria. Así, el transporte de larvas peces en filamentos de afloramiento del NO África ha sido estudiado únicamente en dos ocasiones (Rodríguez *et al.*, 1999; Rodríguez *et al.*, 2004) y resulta la base de este capítulo también. Durante el invierno de 2001, se llevaron a cabo cuatro transectos en esta región que muestrearon un remolino ciclónico y un filamento de afloramiento asociado al mismo (Figs. 1-2, Cap. V). Se analizó la distribución vertical de larvas de tres especies de Clupéidos (*Sardina pilchardus*, *Sardinella aurita* y *Engraulis encrasicolus*) y el metabolismo de las mismas (GF, ETS y AARS, como proxies de pastaje, respiración y crecimiento, respectivamente).

Los parámetros hidrográficos mostraron claramente la presencia de un remolino (Figs. 4-6, Cap. V) cuyo origen se debe a la conservación de la vorticidad potencial, a diferencia de los generados en el sur de Gran Canaria que derivan en la formación de una calle de remolinos *von Karman vortex stret* (Arístegui *et al.*, 1994). También a diferencia de éstos producidos por el efecto de la isla, el remolino ciclónico presentaba mayores dimensiones, pero menor intensidad.

La distribución horizontal de larvas totales no se vio alterada por la presencia de las estructuras mesoscalares (Fig. 7, Cap. V). Sin embargo, su distribución vertical coincide con la del zooplancton (Fig. 8, Cap. V), cuyos valores máximos de densidad se presentaban más someros en la costa africana, mientras que iban profundizando en dirección a mar abierto.

En cuanto a las larvas de Clupéidos, la mayoría de éstos fueron *Sardina pilchardus* (73.9% del total de larvas de este grupo), aunque también estaban presentes *Engraulis encrasicolus* y *Sardinella aurita* (20.7 y 5.4%, respectivamente). La baja abundancia de las dos últimas especies se debe a su puesta estival (Ettahiri, 1996; Ettahiri *et al.*, 2003). Los Clupeoides presentaron una distribución, tanto horizontal como vertical, muy ligada al filamento de afloramiento (Figs. 7-9, Cap. V). Así, se encontraron fundamentalmente entre los 0-120m, zona de aguas frías y con altos niveles de clorofila.

En cuanto a la actividad metabólica de este grupo de Clupéidos, los valores de respiración (ETS) y pastaje (GF) mostraron un gradiente inverso en sus distribuciones tanto verticalmente (Fig. 10, Cap. V) como horizontalmente (Fig. 11, Cap. V). Así, el GF presentaba valores mayores en superficie en la zona del afloramiento, mientras que la actividad ETS aumentaba con la profundidad y hacia mar abierto. El crecimiento (AARS) mostró valores mayores cerca de la estructura del filamento y menores en el centro del remolino.

La evolución del filamento de afloramiento, en este caso, es diferente a trabajos anteriores (Rodríguez *et al.*, 1999; Rodríguez *et al.*, 2004; Bécognée *et al.*, 2006). Durante este estudio, el filamento, y las larvas que transporta, se mantendrían en mar abierto, de tal modo que el futuro de estas larvas sería incierto. Aunque la posibilidad de crecer hasta alcanzar el estado juvenil sigue presente, la ausencia de transporte hacia zonas costeras conllevaría una gran presión predadora (Hopkins and Gartner, 1992; Hernández-León, 1998) y una gradual desaparición de las larvas.

En resumen, este trabajo confirma que hay un transporte de *Sardina pilchardus* desde las costas africanas hacia mar abierto y que otras especies, como *Engraulis encrasicolus* y *Sardinella aurita* pueden ser también transportados por estas estructuras. Las condiciones de alimento, temperatura y salinidad que presentan el filamento y el remolino ciclónico podrán ser favorables para el transporte de estas larvas neríticas, pero su supervivencia dependerá de si la dispersión se produce hacia un área favorable para el reclutamiento (Rodríguez *et al.*, 1999) o hacia océano abierto (como en este trabajo). Además de todo esto, los resultados preliminares obtenidos sobre alimentación y metabolismo sugieren que estos organismos podrían estar afectados por la transición de la comunidad planctónica desde la zona costera eutrófica al régimen oligotrófico de mar abierto.

DISCUSIÓN GENERAL

El propósito de esta tesis es analizar la ecología de la comunidad de larvas de peces de la zona oriental de las Islas Canarias. En primer lugar, se llevó a cabo una revisión de los conocimientos de la comunidad de larvas de peces en la zona de transición Canario-Africana (Capítulo I). En vista de la ausencia de estudios de larga duración, se empleó una serie temporal de más de dos años para estudiar esta comunidad en diferentes puntos de la plataforma de Gran Canaria (Capítulos III y IV). Se identificaron asociaciones de larvas estacionales (Capítulo IV), al mismo tiempo que se confirmaron dos zonas de retención para determinadas familias neríticas alrededor de la isla (Capítulo III).

Un componente importante de esta tesis se centra en el análisis del transporte larvario de determinadas especies (principalmente los Clupeoides, sardina y anchoa) dentro de filamentos de afloramiento originados en las costas africanas. La combinación de muestreo en estaciones fijas en la plataforma de Gran Canaria y el análisis de imágenes de satélite revelaron un transporte real de larvas de sardina (*Sardina pilchardus)* hacia la isla (Capítulo II). Por otro lado, el estudio del desarrollo de un filamento en la zona de transición Canario-Africana mostró un ejemplo en el cual las larvas de peces eran probablemente retenidas en la zona oceánica con pocas posibilidades de ser reclutadas en las costas africanas o canarias (Capítulo V).

La comunidad de larvas de peces de Gran Canaria

Estacionalidad y composición de la comunidad larvaria

Las comunidades de larvas de peces en islas tropicales y subtropicales están compuestas por un elevado número de especies de peces (Leis, 1991a) con diferentes papeles ecológicos en su fase adulta (ej., mesopelágicos, costero-pelágicos). En el caso de las Islas Canarias, pocos estudios han analizado la comunidad larvaria (Rodríguez *et al.*, 1999; Rodríguez, 2000; Rodríguez *et al.*, 2000; Rodríguez *et al.*, 2001; Rodríguez *et* *al.*, 2004; Rodríguez, 2006) y todos ellos fueron el resultado campañas de corta duración. Por lo tanto, la evolución temporal del ictioplancton en Canarias permanece prácticamente desconocida. En los estudios comprendidos en esta tesis (Capítulos II, III y IV), la descripción de la comunidad larvaria de peces de Gran Canaria ha revelado patrones temporales bastante interesantes.

La comunidad de larvas de peces de Gran Canaria muestra una alta diversidad (más de 150 taxones identificados) y está compuesta casi a partes iguales por especies neríticas y oceánicas (ver Anexo II). Estos resultados son consistentes con los encontrados en estudios previos en la zona (Rodríguez *et al.*, 2001) y en otras islas oceánicas (Leis and Miller, 1976; Leis, 1991b; Boehlert *et al.*, 1992). Clupeidos, Espáridos y Góbidos fueron las familias neríticas más abundantes, mientras que Mictófidos, Gonostomátidos y Photíctidos prevalecieron dentro de las familias oceánicas. Los patrones temporales de estas familias no mostraron diferencias significativas entre los meses, probablemente debido a la estacionalidad poco marcada en las variables de la columna de agua (temperatura, salinidad, clorofila). En zonas tropicales y subtropicales, la ausencia de cambios dramáticos en los factores ambientales se traduce en la extensión de los períodos de puesta de los peces (Lowe-McConnell, 1987). Esto es patente también en aguas de las Islas Canarias, donde un alto porcentaje de las especies de peces poseen unos períodos de puesta que se alargan durante bastantes meses o incluso durante todo el año. Las densidades larvarias también son similares a las encontradas en otras zonas oligotróficas (Alemany *et al.*, 2006; Muhling *et al.*, 2008).

A pesar de esta extensión de los períodos de puesta, se encontraron dos asociaciones estacionales de larvas de peces en Gran Canaria: invierno-primavera y verano-otoño (Capítulos III y IV). La temperatura fue la variable ambiental más importante a la hora de estructurar ambas asociaciones, aunque la salinidad y el mesozooplancton de pequeña talla también influyeron (Capítulo IV). Sin embargo, abundancia total de larvas no parece presentar ningún pico estacional, como sí sucede en aguas templadas (hipótesis del match-mismatch, Cushing, 1975). Por lo tanto, no parece que ninguna especie se beneficie de los valores más altos de zooplankton durante el bloom de finales de invierno (Capítulo III). Así, estas asociaciones parecen reflejar las dos situaciones típicas durante el año en la columna de agua: mezcla y estratificación, respectivamente:

- *Asociación de invierno.* Está presente durante el período de mezcla de la columna de agua y, por lo tanto, durante el bloom de finales de invierno. Esta etapa se caracteriza por, bajas temperaturas, valores medios de salinidad y valores medio-altos de clorofila y biomasa mesozooplanctónica. Las larvas de *Sardinella aurita*, *Boops boops* y *Cyclothone braueri* dominan en este grupo. La presencia de Pomacentridae sp1, *Lobianchia dofleini* y algunas especies con puesta típicamente invernal como *Pagellus bogaraveo*, *Trachurus pictoratus* o *Scomber colias*, ayudan también a caracterizar esta asociación.

- *Asociación de verano.* En los meses más cálidos, la columna de agua está estratificada, las temperaturas y salinidades son altas y los valores de clorofila y mesozooplancton son bajos. Durante este periodo, la comunidad de larvas de peces está dominada por góbidos y *Cyclothone braueri.* Sin embargo, las especies que identifican esta asociación son *Ceratoscopelus warmingii*, Pomacentridae sp2, *Lampanyctus* spp y *Anthias anthias.* Otras especies como *Trachinus draco* and Tetraodontidae sp1 sólo se encontraron durante estos meses con temperaturas cálidas.

Empleando todos los datos disponibles de la serie temporal de la costa de Gran Canaria (Capítulos II, III y IV), se creó una tabla con las especies más importantes, ya fuese por sus elevadas abundancias relativas (ej., *Cyclothone braueri, Vinciguerria poweriae*) o por su interés comercial (ej., *Scomber colias, Sarda sarda, Trachurus pictoratus*) (Tabla 1). En esta tabla, se muestran los períodos de puesta conocidos para la región canaria o, en su defecto, para el Mediterráneo o Atlántico Norte. En los casos en que no había datos para la región canaria (ej., *Arnoglossus thori, Trachinus draco*), se ve claramente la extensión de los mismos con respecto al Mediterráneo. *Arnoglossus thori* prolonga su período de puesta hasta principios de invierno en Canarias. Por otro lado, *Trachinus draco* pone en verano en el Mediterráneo, mientras que en Canarias sus larvas aparecieron en verano y otoño. Además, se debe mencionar que larvas de especies con puesta estival en el Mediterráneo, frezan en invierno (*Scomber colias, Trachurus picturatus*) o durante todo el año (*Sardinella aurita*, *Hygophum hygomii*) en Canarias.

Tabla 1. Presencia de larvas de las especies más importantes a lo largo del año y sus períodos de puesta propuestos para Canarias o regiones cercanas o similares ecológicamente. Realizada a partir de las capturas de la serie temporal de Gran Canaria (Enero 2005 – Junio 2007).

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	**References**
Anthias anthias	X	X	X	X	X	X	X	X	X	X	X	X	Fage (1918)[a]
Apogon imberbis							X	X					Tortonese (1986)[a]
Arnoglossus thori	X						X		X	X	X	X	Sabatés (1990)[a]; Macpherson & Raventos (2007)[a]
Bathylagidae sp1	X	X	X									X	
Boops boops	X	X	X	X	X	X	X				X	X	Franquet & Brito (1995)
Bothus podas							X	X		X			Nash *et al.* (19991)[b]
Ceratoscopelus warmingi	X	X	X	X	X	X	X	X	X	X	X	X	Loeb (1980)[c]
Cyclothone braueri	X	X	X	X	X	X	X	X	X	X	X	X	Jespersen & Taning (1926)[a]
Engraulis encrasicolus					X			X			X	X	Frunestin & Furnestin (1959)[a]
Lampanyctus spp	X	X	X	X	X	X	X	X	X	X	X	X	
Lobianchia dofleini	X	X	X	X	X	X	X					X	Taning (1918)[a]
Mullus barbatus					X	X							Hureau (1986)[a]
Mullus surmuletus					X		X						Pajuelo *et al* (1997)
Pagellus bogaraveo	X	X	X	X							X	X	Bauchot & Hureau (1986)[d]
Pagrus pagrus	X		X		X	X							Pajuelo & Lorenzo (1996)
Pomacentridae sp1	X	X	X	X	X					X		X	
Pomacentridae sp2					X	X	X	X	X	X	X		
Sarda sarda		X	X									X	Collete & Nauer (1983)[e]
Sardina pilchardus	X		X	X	X			X				X	Méndez-Villamil *et al.* (1997)
Sardinella aurita	X	X	X	X	X	X	X	X	X	X	X	X	Bécognée et al. (2006)
Sardinella maderensis	X				X	X		X	X	X	X	X	Whitehead (1985)
Scomber colias	X	X	X	X		X							Franquet & Brito (1995)
Stomias boa ferox	X	X	X		X					X		X	Ege (1934)[a]
TETRAODONTIDAE						X	X	X		X		X	
Trachinus draco						X		X		X	X		Sabatés (1990)[a]; Hoşusu & Ak (2002)[a]
Trachurus pictoratus	X	X	X		X								Franquet & Brito (1995)
Vinciguerria poweriae	X	X	X	X	X	X	X	X		X	X	X	Franquet & Brito (1995)

[a] Mediterranean Sea, [b] Azores, [c] Central North Pacific, [d] Morocco, [e] Eastern Atlantic, [f] Western Central North Atlantic

Algunas larvas de *Sardina pilchardus* se encontraron fuera del período de puesta descrito para el área (Tabla 1). La presencia de estas larvas en aguas de la isla sugiere una advección desde las costas del noroeste africano que se discute en profundidad más adelante. Por otro lado, la relación entre el tamaño de las poblaciones larvarias de *Sardinella aurita* (alacha)*, Sardina pilchardus* (sardina) y *Engraulis encrasicolus* (anchoa) parece estar cambiando a lo largo de los últimos 15 años (Tabla 2). Los resultados de 2005 y 2006 sugieren que la población de alacha puede estar incrementando, mientras que las de sardina y anchoa estarían decreciendo.

Tabla 2. Comparación de la contribución larvaria de tres especies de Clupeoides en tres estudios en la isla de Gran Canaria.

	Sardinella aurita	*Sardina pilchardus*	*Engraulis encrasicolus*
October 1991 [a]	83.9%	8.1%	8.1%
July 2000-June 2001 [b]	92.9%	4.7%	2.4%
January -December 2005 [c]	95.4%	2.7%	1.93%

[a] Rodríguez *et al.* (2001) [b] Bécognée *et al.* (2006) [c] Data from Chapters II and III

La alacha es una especie termofílica que aparece en aguas tropicales y subtropicales al este y oeste del Atlántico, en el Pacífico y en el Mediterráneo (Bauchot, 1987). Esta especie es muy móvil, se alimenta de pequeño plancton, tiene una alta fecundidad, siendo muy plástica en cuanto a su crecimiento, supervivencia y otros caracteres vitales (Alheit *et al.*, 1997). Además, estos autores afirman que la abundancia de este pequeño pelágico puede responder de manera rápida y dramática a variaciones climáticas, lo que normalmente viene acompañado de cambios en su distribución. Ésta es la situación de la alacha en el Mediterráneo, donde se está reproduciendo con éxito en zonas más al norte que hace 20 años (Sabatés *et al.*, 2006). Además, las capturas de sardina y anchoa en el Mediterráneo han descendido en los últimos 15 años. Así, estos autores encontraron una clara relación entre este cambio de distribución y un aumento de la temperatura del agua (~1.1ºC en aguas superficiales y 0.7ºC a 80 m de profundad, desde 1970).

Observaciones recientes indican que durante los últimos 23 años, la tendencia al calentamiento en la región de la Corriente de Canarias (al norte de Cabo Blanco, 20ºN) ha sido la más intensa de todos los principales sistemas de afloramiento (Arístegui *et al.*, 2009). Este calentamiento puede explicar, por tanto, el dramático incremento de la alacha en las aguas canarias y el descenso de la sardina. De cualquier modo, los factores que realmente causan este cambio, si es que éste existe de verdad, se desconocen. La ausencia de datos históricos de las capturas pesqueras impide reconocer un agotamiento del stock de sardina en las Islas Canarias, más aún teniendo en cuenta que el stock en las costas africanas está en buena forma (FAO, 2009).

Por otro lado, dos species de Pomacéntridos (Pomacentridae sp1 y Pomacentridae sp2) fueron relativamente abundantes en las muestras. Parece existir una segregación temporal entre ambas especies, ya que Pomacentridae sp1 abunda en invierno y primavera, mientras que Pomacentridae sp2 lo hace en verano (Tabla 1). Esta distribución temporal se relaciona con los períodos de puesta de *Chromis limbata* (invierno-primavera) y *Abudefduf luridus* (verano) (A. Brito, *comm. pers.*). Sólo existen tres especies de Pomacéntridos en aguas de Gran Canaria (Brito *et al.*, 2002): *Chromis limbata*, *Abudefduf luridus* y *Abudefduf saxatilis*. Considerando que las dos primeras están consideradas como abundantes, mientras que la última es muy rara (Brito *et al.*, 2002), es muy probable que Pomacentridae sp1 sea *Chromis limbata* y Pomacentridae sp2 sea *Abudefduf luridus*. Sin embargo, se necesita profundizar en los análisis morfológicos de las larvas para poder describir los estadíos larvarios de ambas especies, ya que solamente las larvas recién eclosionadas de *Abudefduf luridus* han sido descritas por Ré (1980).

Distribución espacial de las larvas de peces en Gran Canaria

La acumulación de larvas de peces en las zonas a sotavento de las islas oceánicas es un hecho bien conocido (Leis, 1991b; Boehlert *et al.*, 1992; Boehlert and Mundy, 1993). En la isla de Gran Canaria, los huevos y larvas de especies neríticas de peces aparecen en mayores abundancias en dos puntos de retención a barlovento y sotavento de la isla (Rodríguez *et al.*, 2001). Durante la serie temporal llevada a cabo en la isla, confirmamos esta retención para las densidades totales de huevos y larvas neríticas durante todo el año (Capítulos II y III).

Por otro lado, analizando este efecto de acumulación a nivel estructural de la comunidad larvaria, se observó que sólo dos familias, Clupéidos y Góbidos fueron capturados en mayores densidades en las zonas a sotavento y barlovento de la isla, básicamente en la estela cálida. Así, durante un estudio de 8 meses observamos que esta retención no supone un cambio en la composición de la comunidad larvaria a lo largo del tiempo (Capítulo III).

¿Influye la iluminación lunar en la variación temporal de la abundancia de larvas?

Parece existir una relación entre la abundancia de larvas neríticas y el mesozooplancton de pequeño tamaño (<1000 μm), que podría estar acoplada al ciclo lunar (Capítulo III). El mesozooplancton de pequeña talla mostró una periodicidad mensual que ya había sido explicada por Hernández-León (1998), como resultado de la presión depredadora de los migradores verticales de las capas de reflexión profunda. Este autor hipotetizó que durante los períodos con menor iluminación (luna nueva), los migradores verticales son capaces de alcanzar capas más superficiales de la columna de agua y depredar sobre el epi-mesozooplancton. Por otro lado, durante los períodos de mayor iluminación (luna llena), estos migradores verticales están ausentes de estas capas, permitiendo a la población de epizooplancton crecer.

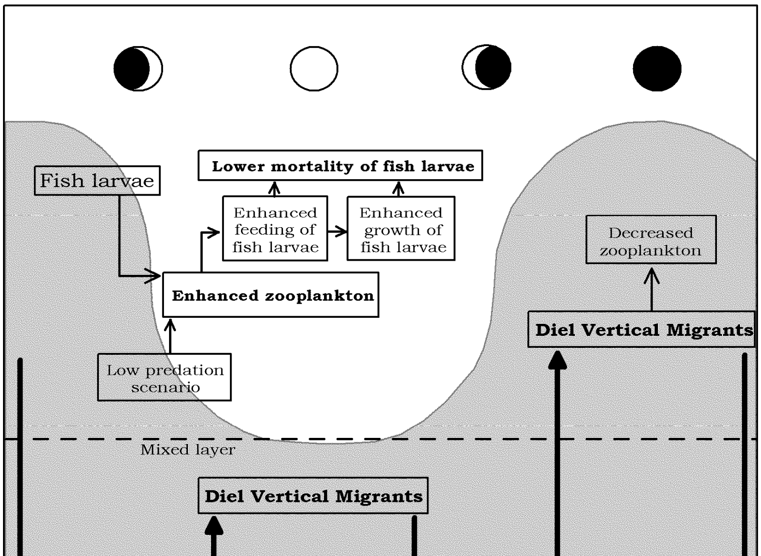


Figura 1. Ilustración esquemática de la mortalidad y crecimiento de las larvas de peces bajo la influencia del ciclo lunar. Redibujado de Hernández-León (2008).

Nuestros resultados muestran que la abundancia de larvas neríticas podría estar también influenciada por este ciclo de predación, mostrando valores menores durante la luna nueva. En este sentido, Hernández-León (2008) apuntó que las larvas de peces pueden verse afectadas por este ciclo lunar, no sólo por la presión depredadora de los migradores verticales (como el zooplancton), sino también por (1) la mejora en la alimentación de los peces adultos gracias al incremento de zooplancton durante el ciclo lunar, cuya entrada de energía se traduciría en productos para la reproducción; y (2) la mejora en la alimentación zooplanctónica de las larvas de peces durante el ciclo lunar. Un mayor énfasis en esta línea de trabajo es necesario para evaluar las causas últimas de esta variabilidad: ¿influye el ciclo lunar en la abundancia de larvas neríticas en aguas subtropicales? Si esto es así, ¿esta influencia sólo se traduce en mortalidades mayores durante la luna nueva o realmente hay una estrategia reproductiva para evitar la presión depredadora durante la luna nueva?

La Zona de Transición Canario-Africana

El Sistema de la Corriente de Canarias es uno de los 49 grandes ecosistemas marinos del mundo (Sherman, 1993). Al igual que otras corrientes de frontera este, este sistema está caracterizado por una intensa actividad oceanográfica de mesoscala en la zona de transición entre las frías y productivas aguas costeras y las más cálidas y oligotróficas aguas del océano abierto. En la zona del NO de África (al norte de 25 ºN), la época de mayor intensidad del afloramiento tiene lugar de Julio a Septiembre, aunque eventos de menor escala pueden ocurrir en cualquier momento (Mittelstaedt, 1991; Van Camp *et al.*, 1991). El sistema de la Corriente de Canarias es singular debido a la presencia de las Islas Canarias que interrumpen el flujo de la Corriente de Canarias y los vientos alisios, generando estructuras mesoscalares al sur de las islas (i.e., estelas cálidas y remolinos ciclónicos y anticiclónicos).

Gracias a la revisión bibliográfica realizada con todos los datos disponibles para la ZTC Canario-Africana (Capítulo I), se pudieron definir una serie de características de la comunidad larvaria, como que presenta una alta diversidad, típica de zonas subtropicales (Longhurst and Pauly, 1987). Esta diversidad conlleva una alta contribución de especies mesopelágicas, siendo los Mictófidos la familia más diversa.

Además, *Cyclothone braueri* es la especie más abundante. Adultos de esta especie se encontraron en densidades relativamente altas en una zona oceánica cercana (Badcock, 1970; Badcock and Merret, 1976).

Durante el verano, la comunidad larvaria de la ZTC Canario-Africana está dominada por clupeoides transportados en filamentos de afloramiento (*Sardina pilchardus, Engraulis encrasicolus*). Sin embargo, durante invierno y primavera, otras especies neríticas procedentes de las islas (ej., *Boops boops, Sardinella aurita*) son más importantes.

La presencia de larvas de especies tropicales (ej., *Hygophum macrochir*, and *Vinciguerria nimbaria*) podría soportar la hipótesis de tropicalización de la ictiofauna del archipiélago canario sugerida por Brito *et al*. (2005). Esta tropicalización estaría potenciada por el incremento de temperatura en la zona (Arístegui *et al*., 2009). De cualquier manera, es necesario un mayor número de estudios para poder evidencia este proceso.

Dinámica larvaria en la Zona de Transición Canario-Africana

Las estructuras oceanográficas mesoscalares generadas al sur de las Islas Canarias ejercen un profundo efecto sobre la dinámica de las larva de peces, tanto por su efecto dispersivo como de retención. El funcionamiento de las estelas cálidas como zonas de retención para huevos de peces y larvas neríticas es bien conocida (Capítulos II y III). También los remolinos ciclónicos pueden jugar el mismo papel retentivo al sur de las islas (Rodríguez *et al*., 2001). Sin embargo, el efecto de esta deriva larvaria, bien en la Corriente de Canarias o en remolinos generados en islas, sobre la supervivencia de las mismas es desconocido (Capítulo I). Existen evidencias de que los remolinos generados en islas transportan larvas hacia océano abierto (ej., *Anthias anthias*) (Capítulo I). La evolución de estos remolinos determinará el destino de larvas, ya que si logra alcanzar otra isla, las larvas podrían sobrevivir, como se sugiere en Rodríguez *et al*. (2000).

El transporte larvario en filamentos procedentes del afloramiento del NO africano ha sido estudiado en pocas ocasiones (Rodríguez *et al*., 1999; Rodríguez *et al*., 2004; Bécognée *et al.*, 2006) y todos estos trabajos se han centrado en dos especies de clupeoides, *Sardina pilchardus* (sardina) y *Engraulis encrasicolus* (anchoa). Ambas especies están consideradas como buenos trazadores de estos filamentos de afloramiento (Rodríguez *et al.*, 1999; Rodríguez *et al.*, 2004). Estas especies ponen durante todo el año en la región del afloramiento NO africano, aunque *Sardina pilchardus* tiene el pico de puesta en invierno (Ettahiri *et al.*, 2003), mientras que *Engraulis encrasicolus* lo tiene en verano (Furnestin and Furnestin, 1959; Berraho, 2007). Durante el verano, la dominancia de una especie sobre la otra en los filamentos de afloramiento parece depender de la temperatura superficial en la zona del afloramiento (Capítulo I). Sin embargo, durante el invierno, *Sardina pilchardus* parece predominar (Capítulo V), aunque más datos son necesarios para confirmar estas observaciones.

El desarrollo de estos filamentos de afloramiento puede resultar en retención en las costas africanas, dispersión hacia las costas orientales de las Islas Canarias o dispersión hacia océano abierto (Rodríguez *et al.*, 1999; Rodríguez *et al.*, 2004; Bécognée *et al.*, 2006). En nuestros resultados mostramos un claro caso en el que el destino del complejo remolino-filamento, y de las larvas de peces en él, es permanecer en la región oceánica (Capítulo V). En este caso, las larvas no podrían reclutarse debido a la fuerte presión depredadora ejercida por los migradores verticales en el océano abierto (Hopkins and Gartner, 1992; Hernández-León, 1998). A pesar de que existe la posibilidad de que estas larvas se transformen en juveniles dentro del complejo remolino-filamento y sean reclutadas, es bastante improbable.

Para complementar estos estudios, evaluamos por primera vez la actividad metabólica de las larvas de Clupeoides en la ZTC Canario-Africana en presencia de un filamento de afloramiento (Capítulo V). La actividad del Sistema de Transporte de Electrones (ETS, del inglés *Electron Transfer System*) y la Fluorescencia del Tracto Digestivo (GF, del inglés *Gut Fluorescence*) se tomaron como representantes de la respiración y del pastaje, respectivamente. La actividad ETS y el GF mostraron un gradiente inverso en su distribución espacial, ya que el GF era mayor cerca de la costa africana, mientras que la actividad ETS aumenta hacia mar abierto. El crecimiento (medido como la actividad de la AminoAcyl-tRNA Sintetasa, AARS) presentó valores mayores cerca de la estructura del filamento y menor en el centro del remolino. Estos resultados sugieren que las larvas de peces pueden verse afectadas por la transición entre la comunidad planctónica del régimen eutrófico al oligotrófico.

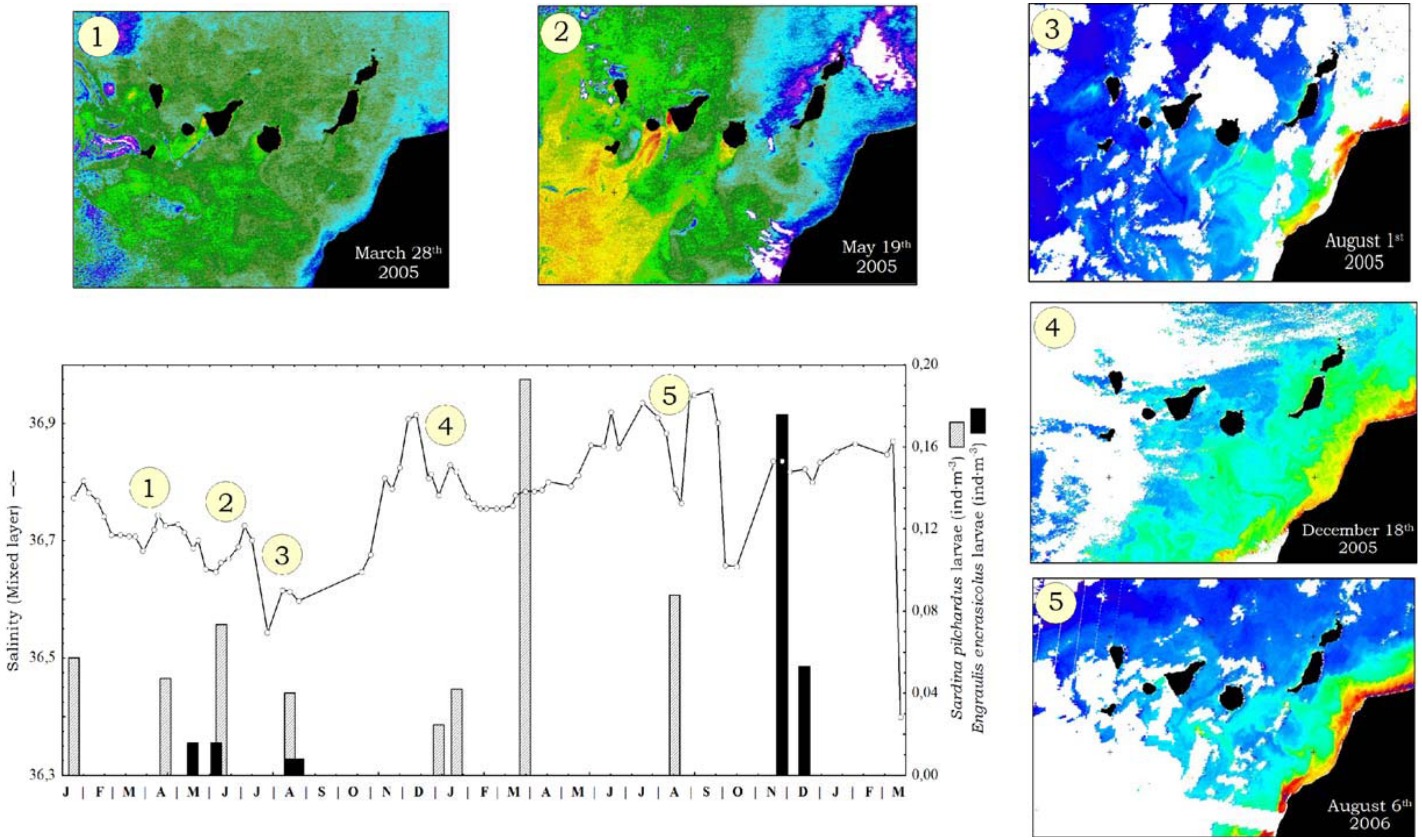
Transporte larvario de sardina y anchoa hacia la isla de Gran Canaria

El transporte de larvas de *Sardina pilchardus* en filamentos de afloramiento procedentes de las costas africanas hacia las costas de Gran Canaria fue confirmado por Bécognée *et al.* (2006). Este mecanismo dispersivo fue analizado considerando la serie temporal de larvas de peces capturadas durante los estudios incluidos en esta tesis (datos de los capítulos II, III y IV, recopilados en la Fig. 2).

Las larvas de *Sardina pilchardus* fueron muy escasas, contribuyendo menos de 0.5% del total de larvas capturadas durante este período de más de dos años. La presencia de estas larvas en Mayo y Agosto (Fig. 2), fuera de su período de puesta en aguas de Gran Canaria (Diciembre-Marzo, Méndez-Villamil *et al.*, 1997), indica claramente que existe un transporte desde otra zona (Capítulo II). De cualquier manera, la presencia de estas larvas coincidiendo con la llegada de los filamentos de afloramiento durante el invierno, sugiere también la adveción de estas larvas durante esta estación también (Fig. 2). La llegada de estos filamentos de afloramiento hacia la isla se detectó en las imágenes de satélite y confirmado por los bajos valores de salinidad en la capa de mezcla.

Engraulis encrasicolus está considerada como una especie ocasional en el archipiélago canario (Brito *et al.*, 2002). Aunque su período de puesta en las costas africanas se prolonga durante todo el año, con un pico de puesta en verano (Furnestin and Furnestin, 1959), su estrategia reproductiva en las Islas Canarias es desconocida. Cantidades relativamente grandes de huevos de esta especie fueron registradas en Mayo y Junio al sur de Gran Canaria (Moyano, unpublished data), lo que sugiere que el pico de puesta puede localizarse al final de la primavera y durante el verano. Pero es probable que esta especie se reproduzca durante todo el año en aguas canarias ya que sus larvas fueron capturadas durante el invierno (Noviembre-Diciembre 2007, Tabla 1) y también en un estudio previo en 2001 (Bécognée *et al.*, 2006).

Figura 2. Evolución temporal de la salinidad en la capa de mezcla y la abundancia de larvas de *Sardina pilchardus* y *Engraulis encrasicolus* en la isla de Gran Canaria. La presencia de larvas de *S. pilchardus* coincide con la llegada de filamentos del afloramiento del NO Africano hacia Gran Canaria



Además, las aguas de Gran Canaria oscilan todo el año dentro del rango termal de puesta registrado para esta especie en las costas marroquís (Berraho, 2007). Aún así, tendremos que tener en cuenta la coincidencia en las muestras de larvas de anchoa junto con larvas de sardina y la llegada de filamentos de afloramiento (Fig. 2, Mayo y Agosto 2005) y, por lo tanto, la contribución que el transporte larvario de anchoa puede tener sobre las poblaciones locales.

Recientemente, se han realizado una serie de simulaciones para modelar este transporte larvario de *Sardina pilchardus* y *Engraulis encrasicolus* (Brochier *et al.*, *in prep.*; Brochier *et al.*, 2008). Dos características principales surgen del modelo desarrollado en Brochier *et al.* (2008): (1) la mayoría de las partículas que alcanzan las costas orientales de Canarias proceden principalmente de la región localizada entre Cabo Draa y Cabo Juby, que resulta ser una zona de puesta muy importante para ambas especies (especialmente para anchoa en verano); (2) la llegada de estas partículas a Gran Canaria presenta dos picos: uno mayor en Marzo-Abril y un segundo en Julio-Agosto. Estos datos se asemejan a nuestras observaciones de la llegada de larvas de *Sardina pilchardus* a Gran Canaria que fueron mayores en el período de Marzo-Mayo y en Agosto (Fig. 2). Sin embargo, la zona de liberación de la mayor parte de las partículas fue Cabo Juby-Cabo Draa, mientras que se pensaba que las larvas transportadas provenían mayormente de la zona Cabo Juby-Cabo Bojador. Por lo tanto, es necesario profundizar en estos estudios para poder evaluar la magnitud real de esta conectividad y mejorar así la gestión pesquera en la zona. En este sentido, se debería considerar la creación de modelos hidrodinámicos de alta resolución que incluyan otros factores clave para el hábitat, zonas de puesta o de alevinaje (temperatura, alimento, homing).

CONCLUSIONES

Las conclusiones obtenidas en esta tesis son las siguientes:

- La comunidad de larvas de peces de la isla de Gran Canaria es altamente diversa, como es típico en islas oceánicas de regiones subtropicales. Especies neríticas y oceánicas contribuyen en porcentajes similares al conjunto de larvas. Clupeidos, Espáridos y Góbidos son las familias neríticas más abundantes, mientras que Mictófidos, Gonostomátidos y Phosíctidos lo son dentro de las oceánicas.
- Se encontraron dos asociaciones temporales de larvas de peces, dependientes de la temperatura, en la isla de Gran Canaria:
    - La asociación de invierno-primavera que aparece durante el período de mezcla de la columna de agua, cuando se produce el bloom de finales de invierno. Durante este período, la temperaturas del agua es fría, la salinidad presenta valores medios y la concentración de clorofila y la biomasa de mesozooplancton son medio-altas. Esta asociación está caracterizada por relativamente altas abundancias de *Sardinella aurita*, *Boops boops* y *Cyclothone braueri,* así como por la presencia de Pomacentridae sp1, *Lobianchia dofleini, Pagellus bogaraveo, Trachurus pictoratus* y *Scomber colias*.
    - La asociación de larvas de verano-otoño aparece cuando la columna de agua se encuentra bien estratificada, presentando altas temperaturas y salinidades, bajos valores de clorofila y mesozooplancton. Esta asociación está caracterizada por la dominancia de Góbidos, *Cyclothone braueri*, *Ceratoscopelus warmingii*, Pomacentridae sp2, *Lampanyctus* spp y *Anthias anthias*, así como la presencia de *Trachinus draco* y Tetraodontidae sp1.
- Se ha encontrado una clara influencia lunar sobre la distribución temporal de la biomasa mesozooplanctónica de pequeño tamaño, apoyando las hipótesis de Hernández-León *et al.* (2004). Parece existir también una influencia de este ciclo

lunar sobre la distribución de larvas neríticas (principalmente Espáridos), que presentan valores menores durante la luna llena.

- Se ha confirmado con una mayor definición temporal la retención de huevos y larvas neríticas en las zonas de calma situadas a sotavento y barlovento de Gran Canaria descritas en Rodríguez *et al.* (2001). Sin embargo, estas áreas no suponen un cambio significativo en la composición del conjunto de larvas de peces a lo largo del tiempo. De hecho, sólo dos familias (Clupeidae y Gobidae) presentaron valores significativamente mayores en estas zonas.

- Existe una fuerte relación entre los procesos oceanográficos de mesoscala y la distribución de larvas de peces, especialmente para los filamentos de afloramiento y dos especies de clupeoides (*Sardina pilchardus* y *Engraulis encrasicolus*).

    - Este transporte larvario en filamentos de afloramiento es la causa de las altas abundancias de larvas neríticas registradas en la zona oceánica durante el verano.

    - Las larvas de Clupeoides transportadas hacia Gran Canaria suponen un aporte para las poblaciones locales. A pesar de las implicaciones para las poblaciones locales de estas especies, la importancia para las pesquerías a nivel local necesita ser evaluada en mayor profundidad para mejorar la gestión pesquera de la zona.

    - Los filamentos de afloramiento pueden ser atrapados por el remolino ciclónico quasi-permanente que se encuentra entre la costa africana y el Archipiélago Canario. Este sistema remolino ciclónico-filamento puede actuar bien como un sistema de retención para las especies neríticas africanas o como un sistema de dispersión si el remolino se dirige hacia la región oceánica.

- Una primera evaluación de la actividad metabólica de las larvas de Clupeidos en la región de transición Canario-Africana durante la presencia de un filamento de afloramiento reveló un patrón inverso entre respiración y pastaje. El pastaje decrece a medida que se incrementa la distancia de la costa, mientras que la respiración aumenta en esa dirección.

FUTURAS LINEAS DE INVESTIGACIÓN

Los resultados obtenidos a partir de esta tesis han aumentado considerablemente los conocimientos sobre la dinámica del ictioplancton en la región oriental de Canarias. Así, han sentado la base descriptiva sobre la ecología del conjunto de larvas de peces y sus variaciones anuales y con el entorno.

A pesar de esto, es necesario continuar con la investigación de este complejo grupo si pretendemos llevar a cabo una buena gestión pesquera y diseño de reservas marinas. El conocimiento del intercambio larvario entre poblaciones es vital para este tipo de estudios (Cowen *et al*., 2000). Así, sería muy interesante una mayor interacción con oceanógrafos físicos y modeladores para la creación de modelos hidrodinámicos complejos que analicen la distribución por estrato de las larvas de especies clave tanto alrededor de Gran Canaria como en la zona del upwelling nor-africano. Para lograr unos modelos hidrodinámicos lo más reales posible, sería muy interesante experimentar con modelos individuales (IBMs, *del inglés* Individual Based Models) para estas especies (ej., *Sardina pilchardus*, *Sardinella aurita*, *Engraulis encrasicolus*, *Scomber colias*). Estos modelos integrarían estudios metabólicos, energéticos, tróficos y de crecimiento. En este sentido, se están realizando colaboraciones para realizar un modelo biofísico para estudiar el transporte larvario de *Sardina pilchardus* en la zona (Brochier *et al*., *in prep.*).

Por otro lado, resultaría muy interesante profundizar en la dinámica de las poblaciones de sardina de Canarias y las costas africanas. Análisis genéticos, con biomarcadores e incluso el estudio de los elementos traza de los otolitos pueden ayudar en la comprensión de este clásico ejemplo de metapoblaciones. Es de destacar se han realizado unos análisis experimentales de la microquímica de otolitos realizados con sardinas procedentes de la isla de Tenerife y de la costa marroquí. Si bien aún no han obtenido resultados concluyentes para encontrar elementos que separen ambas poblaciones, sí que parece haber una periodicidad muy clara en los otolitos de las sardinas marroquís, que podría estar ligado al índice de upwelling.

Por último, sería muy beneficioso el empleo de muestreos subacuáticos, así como el uso de trampas de luz. Esto permitiría obtener larvas y postlarvas de diferentes especies en buen estado para poder plantearse diferentes tipos de experimentos. Quizá se deberían observar las diferentes técnicas empleadas en otras islas oceánicas del Pacífico o en arrefices coralinos y se encontraría toda una gama de prácticas y efectivas que podrían ser aplicadas en la isla de Gran Canaria.

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ANNEXES

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ANNEX I

Species composition of the larval fish community (LFC) and seasonal (Spring, Summer, Autumn and Winter) larval fish populations, origin of the species (N, neritic species; Oc, oceanic species; O, other) and their percentage contribution to the LFC and seasonal populations. Upper indices indicate the rank order of the species that most contributed (≥0.5% of larval fish catches) to the LFC and seasonal populations. (Prepared from Rodríguez *et al.*, 1999; Rodríguez, 2000; John *et al.*, 2004; Rodríguez *et al.*, 2004; Moyano *et al.*, 2009; Moyano and Hernández-León, unpublished data)[*]

Species	Origin	LFC	Spring	Summer	Autumn	Winter
Family ARGENTINIDAE						
Microstoma microstoma	Oc	0.01	-	0.02	-	-
Nansenia oblita	Oc	0.02	-	0.02	0.02	-
Unidentified spp		0.01	-	0.02	-	-
Family ALEPISAURIDAE						
Alepisaurus ferox	Oc	0.01	-	-	0.02	-
Family ASTRONESTHIDAE						
Astronesthes gemmifer	Oc	0.01	-	-	-	0.04
Astronesthidae sp 1	Oc	0.02	-	-	0.04	-
Astronesthidae sp 2	Oc	0.01	-	-	0.02	-
Unidentified spp	Oc	0.02	-	-	0.02	0.04
Family AULOPIDAE						
Aulopus filamentosus?	Oc	0.01	-	0.02	-	-
Aulopus sp	Oc	0.01	-	0.02	0.01	-
Family BATHYLAGIDAE						
Bathylagus bericoides	Oc	0.01	-	-	-	0.04
Bathylagus euriops	Oc	0.01	-	0.02	-	-
Bathylagus greyae	Oc	0.03	-	-	-	0.19
Bathylagus longirostris	Oc	0.03	-	-	0.06	-
Unidentified spp	Oc	0.23	-	0.10	0.12	1.03
Family BELONIDAE						
Platybelone argalus	N	0.02	-	-	0.03	-
Family BLENNIIDAE						
Ophioblennius atlanticus	N	0.12	1.04^{11}	0.06	0.03	0.11
Unidentified spp	N	0.29	0.22	0.99	-	-
Family BOTHIDAE						
Arnoglossus imperialis	N	0.06	-	0.17	-	0.08
Arnoglossus thori	N	0.16	-	0.21	0.16	0.11
Arnoglossus spp	N	0.16	-	0.58	-	-
Bothus podas maderensis	N	0.32	-	0.46^{21}	0.37	-
Lepidorhombus boscii	N	0.01	-	-	-	0.04
Family BRAMIDAE						
Unidentified spp	Oc	0.09	-	-	0.02	0.53
Family CALLIONYMIDAE						
Callionymus reticulatus	N	0.01	-	0.02	-	-
Callionymus spp	O	0.03	-	0.04	0.02	0.04
Family CAPROIDAE						
Antigonia capros	N	0.01	-	-	0.01	-
Capros aper	N	0.62^{23}	-	-	1.19^{13}	0.08

Annex I. Continued

Species	Origin	Yearly	Spring	Summer	Autumn	Winter
Family CARANGIDAE						
Trachurus trachurus	N	0.01	-	-	-	0.04
Trachurus picturatus	N	0.04	0.15	-	-	0.23
Trachurus sp	O	0.07	-	0.27	-	-
Carangidae sp 1	O	0.01	-	-	0.02	-
Unidentified spp	O	0.09	0.07	0.23	0.04	-
Family CARAPIDAE						
Carapus acus	N	0.01	-	-	0.02	-
Family CENTRACANTHIDAE						
Centracanthus cirrus	N	0.04	-	-	0.01	0.23
Unidentified spp	N	0.02	-	-	-	0.11
Family CEPOLIDAE						
Cepola macrophthalma	N	0.01	-	0.02	-	-
Family CHAULIODONTIDAE						
Chauliodus dana	Oc	0.06	0.07	0.06	-	0.27
Chauliodus sloani	Oc	0.10	-	0.04	0.18	-
Family CHIASMODONTIDAE						
Chiasmodon niger	Oc	0.02	-	-	-	0.11
Unidentified spp	Oc	0.01	-	0.02	-	-
Family CHLOROPHTHALMIDAE						
Chlorophthamus agassizii	Oc	0.11	-	0.08	0.18	-
Chlorophthalmus sp1	Oc	0.01	0.07	-	-	-
Family CLUPEIDAE						
Sardina pilchardus	N	2.04^{9}	0.15	7.20^{3}	0.01	0.23
Sardinella aurita	N	2.46^{7}	11.70^{1}	0.41	0.46^{23}	9.04^{1}
Sardinella maderensis	N	0.21	0.67^{13}	0.06	0.27	0.04
Family CONGRIDAE						
Ariosoma balearicum	N	0.01	-	-	0.02	-
Gnathophis mystax	N	0.01	-	-		0.04
Unidentified spp	O	0.07	-	0.15	0.06	-
Family CORYPHAENIDAE						
Coryphaena hippurus		0.06	0.15	-	-	0.34
Family CYNOGLOSSIDAE						
Symphurus nigrescens	O	0.08	-	0.21	0.04	-
Family DERICHTHYDAE						
Derichthys serpentinus	Oc	0.02	-	0.06	-	-
Family ENGRAULIDAE						
Engraulis encrasicolus	N	6.22^{2}	0.15	22.28^{1}	0.02	0.31
Family EPINEPHELINAE						
Unidentified spp		0.01	0.07	-	-	-
Family EVERMANNELLIDAE						
Evermannella balbo	Oc	0.04	-	0.02	0.06	-
Unidentified spp	Oc	0.04	-	-	-	0.27
Family GADIDAE						
Unidentified spp	N	0.01	-	-	-	0.04

Annex I. Continued

Species	Habitat	Yearly	Spring	Summer	Autumn	Winter
Family GEMPYLIDAE						
Diplospinus multistriatus	Oc	0.47^{32}	-	0.23	0.60^{22}	0.69^{20}
Gempylus serpens	Oc	0.02	0.07	0.02	-	0.04
Nealotus tripes		0.01	-	-	0.01	-
Nesiarchus nasutus	Oc	0.14	-	-	0.28	-
Unidentified spp	Oc	0.08	0.30	0.15	0.02	0.04
Family GIGANTACTINIDAE						
Gigantactis sp 1	Oc	0.01	-	-	0.02	-
Family GOBIIDAE						
Lebetus guilletii	N	0.03	0.22	0.06	-	-
Lebetus scorpiodes	N	0.01	0.15	-	-	-
Unidentified spp	N	3.35	10.22	1.06	3.71	3.05
Family GOBIESOCIDAE						
Unidentified spp	N	0.94	0.15	3.35	-	0.04
Family GONOSTOMATIDAE						
Bonapartia pedaliota	Oc	0.02	-	-	0.04	-
Cyclothone acclinidens	Oc	0.41	-	0.17	0.70^{20}	-
Cyclothone alba?	Oc	0.21	-	0.04	0.39	0.04
Cyclothone braueri	Oc	8.89^{1}	6.37^{4}	5.75^{4}	11.72^{1}	6.03^{3}
Cyclothone microdon	Oc	0.01	-	0.02	-	-
Cyclothone pallida	Oc	0.39	-	0.58^{16}	0.43	0.04
Cyclothone pseudopallida	Oc	0.16	-	0.04	0.29	-
Cyclothone spp	Oc	2.26	2.74	4.04	0.43	5.19
Diplophos maderensis?	Oc	0.01	-	-	0.02	-
Diplophos taenia	Oc	0.02	-	-	0.04	-
Gonostoma atlanticum	Oc	0.24	-	0.12	0.39	0.04
Gonostoma denudatum	Oc	0.25		0.10	0.43	-
Gonostoma elongatum	Oc	1.02^{16}	-	0.12	1.94^{8}	-
Gonostoma sp d	Oc	0.02	-	0.08	-	-
Gonostoma sp 1	Oc	0.02	-	0.06	0.01	-
Gonostoma sp 2	Oc	0.18	-	0.06	0.32	-
Gonosttoma spp	Oc	0.12	0.52	0.14	0.01	0.27
Margrethia obtusirostra	Oc	0.02	-	-	0.04	-
"*Maurolicine alpha*"	Oc	0.01	-	-	0.02	-
Pollichthys mauli	Oc	0.01	-	0.02	-	-
Unidentified spp	Oc	0.52	0.52	0.41	0.70	0.08
Family HEMIRHAMPHIDAE						
Hemirhamphus balao	N	0.02	0.07	-	0.02	-
Family IDIACANTHIDAE						
Idiacanthus fasciola	Oc	0.02	-	-	0.03	-
Family LABRIDAE						
Coris julis	N	0.16	0.67^{14}	0.23	0.08	0.04
Thalassoma pavo	N	0.13	0.15	0.19	0.13	0.04
Xyrichthys novacula	N	0.07	-	0.10	0.08	-
Labrus sp	N	0.01	-	0.02	-	-
Symphodus sp.	N	0.04	0.37	-	-	0.08
Unidentified spp	N	0.12	0.30	0.17	0.05	0.19
Family MACRORAMPHOSIDAE						
Macroramphosus scolopax	Oc	0.55^{27}	0.15	0.12	0.83^{16}	0.61^{22}

Annex I. Continued

Species	Origin	Yearly	Spring	Summer	Autumn	Winter
Family MACROURIDAE						
Unidentified spp	Oc	0.05	-	0.02	0.06	0.08
Family MALACOSTEIDAE						
Unidentified spp	Oc	0.01	0.07	-	-	-
Family MELAMPHAIDAE						
Melamphaes simus	Oc	0.07	-	0.06	0.06	0.15
Melamphaes thyplops?	Oc	0.02	-	0.02	0.02	-
Melamphaes sp 1	Oc	0.04	-	0.06	0.04	-
Unidentified spp	Oc	0.01	0.07	-	-	-
Family MELANOCETIDAE						
Melanocetus murrayi	Oc	0.03	-	0.02	0.04	-
Melanocetus spp	Oc	0.03	-	0.02	0.04	-
Family MELANOSTOMIIDAE						
Eustomias sp	Oc	0.01	-	-	0.02	-
Photonectes sp		0.01	-	-	-	0.08
Melanostomiidae sp 1	Oc	0.01	-	-	0.02	-
Melanostomiidae sp 2	Oc	0.03	-	-	0.06	-
Unidentified spp	Oc	0.21	-	0.14	0.32	0.04
Family MONACANTHIDAE						
Stephanolepis hispidus	N	0.02	-	0.04	0.02	-
Family MORIDAE						
Unidentified spp	Oc	0.01	-	0.02	-	0.04
Family MULLIDAE						
Mullus surmuletus	N	0.02	0.22	0.02	-	-
Mullus barbatus	N	0.03	0.37	-	-	-
Family MURAENIDAE						
Unidentified spp	N	0.01	-	0.02	-	-
Family MUGILIDAE						
Unidentified spp	N	0.14	-	0.02	0.26	-
Family MYCTOPHIDAE						
Benthosema glaciale	Oc	0.01	-	0.02	-	-
Benthosema suborbitale	Oc	0.96^{17}	0.15	0.60^{15}	1.40^{12}	0.46^{29}
Bolinichthys indicus	Oc	0.02	-	0.02	-	0.08
Ceratoscopelus maderensis	Oc	1.54^{12}	2.74^{7}	3.35^{5}	0.80^{17}	0.08
Ceratoscopelus warmingii	Oc	4.77^{3}	6.96^{3}	1.30^{9}	7.48^{2}	0.57^{24}
Diaphus bertelseni	Oc	0.01	-	-	-	0.04
Diaphus brachycephalus	Oc	0.01	0.07	-	-	-
Diaphus holti	Oc	2.59^{6}	0.07	1.20^{10}	4.39^{4}	0.11
Diaphus metopoclampus	Oc	0.25	0.07	0.31	0.31	-
Diaphus mollis	Oc	0.03	0.30	-	0.01	0.04
Diaphus rafinesquei	Oc	1.13^{15}	0.15	0.50^{19}	1.85^{9}	0.23
Diaphus taaningi	Oc	0.01	-	-	-	0.04
Diaphus thermophilus	Oc	0.01	-	-	-	0.04
Diaphus spp	Oc	2.24	-	1.59	3.51	0.04
Diogenichthys atlanticus	Oc	3.49^{4}	0.89^{12}	3.10^{6}	4.40^{3}	2.29^{8}
Electrona rissoi	Oc	0.03	0.07	-	0.04	0.04
Hygophum benoiti	Oc	2.35^{8}	-	0.02	4.38^{5}	0.76^{16}
Hygophum "bruni"	Oc	0.01	0.07	-	-	-
Hygophum hygomii	Oc	1.20^{14}	0.15	0.06	1.54^{11}	2.79^{6}
Hygophum macrochir	Oc	0.46^{33}	0.52^{20}	0.41	0.35	0.95^{11}

Annex I.Continued

Species	Origin	Yearly	Spring	Summer	Autumn	Winter
Hygophum reinhardtii	Oc	0.67^{21}	0.30	0.64^{12}	0.76^{18}	0.57^{25}
Hygophum taaningi	Oc	0.33	0.22	0.33	0.28	0.57^{25}
Hygophum sp	Oc	0.13	0.15	0.04	0.04	0.61^{23}
Lampadena sp	Oc	0.15	0.59	-	0.18	0.11
Lampadena sp1	Oc	0.03	0.07	-	-	0.15
Lampanyctus alatus	Oc	0.01	0.07	-	-	-
Lampanyctus ater	Oc	0.16	-	-	0.26	0.19
Lampanyctus crocodilus	Oc	0.06	-	0.14	0.04	-
Lampanyctus lineatus	Oc	0.01	-	-	-	0.04
Lampanyctus photonotus	Oc	0.01	-	0.02	-	-
Lampanyctus pusillus	Oc	0.48^{31}	-	0.21	0.75^{19}	0.27
Lampanyctus spp	Oc	6.31	4.44	4.26	8.21	4.43
Lepidophanes gaussi	Oc	0.87^{19}	-	0.15	1.61^{10}	0.04
Lepidophanes guentheri	Oc	0.02	-	-	0.01	0.11
Lobianchia dofleini	Oc	0.60^{24}	0.59^{18}	0.23	0.15	2.98^{5}
Lobianchia gemellarii	Oc	0.42	0.52^{21}	0.06	0.10	2.25^{9}
Loweina interrupta	Oc	0.01	-	0.02	-	-
Loweina rara	Oc	0.02	-	0.06	-	-
Myctophum nitidulum	Oc	0.39	-	0.23	0.43	0.72^{18}
Myctophum punctatum	Oc	0.78^{20}	-	2.03^{7}	0.37	0.19
Myctophum selenops	Oc	0.52^{28}	-	0.10	0.92^{15}	0.19
Nannobrachium lineatum	Oc	0.01	0.15	-	-	-
Notolychnus valdiviae	Oc	2.01^{10}	-	1.84^{8}	2.90^{6}	0.15
Notoscopelus (Not.) resplendens	Oc	0.25	0.15	0.15	0.19	0.69^{21}
Notoscopelus sp	Oc	0.91^{18}	2.07^{9}	0.06	0.31	4.16^{4}
Notoscopelus spp	Oc	0.40	1.19	0.33	-	1.60
Symbolophorus rufinus	Oc	0.32	-	0.02	0.62^{21}	-
Symbolophorus veranyi	Oc	0.06	-	0.14	0.04	-
Symbolophorus spp	Oc	0.27	0.22	0.70	-	0.42
Taaningichthys minimus	Oc	0.01	-	-	0.02	-
Myctophidae sp 1	Oc	0.05	-	-	0.10	-
Myctophidae sp 2	Oc	0.04	-	-	0.08	-
Unidentified spp	Oc	8.30	5.85	3.60	10.83	9.61
Family NEMICHTHYDAE						
Nemichthys scolopaceus	Oc	0.01	0.07	-	-	-
Family NETTASTOMATIDAE						
Nettastoma melanurum	Oc	0.05	0.07	0.14	-	0.08
Unidentified spp	Oc	0.11	-	0.04	0.20	-
Family NOMEIDAE						
Nomeidae sp 1	Oc	0.09	-	0.12	0.10	-
Unidentified spp	Oc	0.01	-	-	0.02	-
Family NOTOSUDIDAE						
Ahliesaurus berryi	Oc	0.03	-	-	0.06	-
Scopelosaurus argenteus	Oc	0.01	-	-	0.02	-
Scopelosaurus lepidus	Oc	0.07	-	-	0.13	0.08
Family OMUSUDIDAE						
Omosudis lowei	Oc	0.01	-	-	0.02	-
Family ONEIRODIDAE						
Chaenoprhyne draco	Oc	0.01	-	-	0.02	-
Dolopichthys sp	Oc	0.01	-	-	0.02	-

Annex I. Continued

Species	Origin	Yearly	Spring	Summer	Autumn	Winter
Family OPHICHTHIDAE						
Ophichthidae sp 2	Oc	0.01	-	-	0.02	-
Unidentified spp	Oc	0.03	-	0.04	0.02	0.04
Family OPHIDIIDAE						
Parophidion vassali	N	0.04	-	0.02	0.06	-
Ophidiidae sp 1	Oc	0.01	-	-	0.02	-
Ophidiidae sp 2	Oc	0.02	-	-	0.04	-
Unidentified spp	Oc	0.06	0.30	0.06	0.04	0.04
Family PARALEPIDIDAE						
Lestidiops affinis	Oc	0.03	-	-	0.06	-
Paralepis coregonoides	Oc	0.01	-	-	-	0.04
Lestidiops jayakari	Oc	0.20	-	0.43	0.14	0.08
Lestidiops sphyrenoides	Oc	0.01	-	-	0.02	-
Macroparalepis affinis	Oc	0.02	-	-	0.04	-
Paralepis atlántica atlántica	Oc	0.14	-	0.08	0.24	-
Sudis hyalina	Oc	0.06	-	0.08	0.04	0.11
Unidentified spp	Oc	0.18	0.30	0.43	0.07	0.04
Family PHOTICHTHYDAE						
Ichthyococcus ovatus	Oc	0.05	-	0.06	0.02	0.19
Vinciguerria attenuata	Oc	0.17	0.22	0.39	0.07	0.04
Vinciguerria nimbaria	Oc	0.59^{25}	1.56^{10}	0.52^{18}	0.45^{24}	0.76^{17}
Vinciguerria poweriae	Oc	0.56^{26}	0.59^{19}	0.64^{13}	0.40	0.95^{12}
Vinciguerria spp	Oc	1.55	1.48	0.41	2.05	2.02
Family PHYCIDAE						
Unidentified spp		0.01	-	-	-	0.08
Family POMACENTRIDAE						
Chromis chromis	N	0.14	0.22	0.31	0.04	0.11
Pomacentridae sp1	N	0.34	0.67^{15}	-	0.12	1.68^{10}
Pomacentridae sp2	N	0.49^{30}	2.52^{8}	1.08^{11}	0.01	-
Family SCARIDAE						
Sparisoma (Euscarus) cretense	N	0.14	-	0.04	0.26	-
Family SCIAENIDAE						
Unidentified spp		0.02	-	0.06	-	-
Family SCOMBEROSOCIDAE						
Nanichthys simulans	Oc	0.01	-	0.02	-	0.04
Scomberesox saurus	Oc	0.03	-	0.06	0.03	-
Unidentified spp		0.01	-	-	-	0.04
Family SCOMBRIDAE						
Auxis sp	O	0.07	-	0.25	-	-
Scomber colias	N	0.15	0.22	-	-	0.95^{13}
Sarda sarda		0.01	-	-	-	0.08
Unidentified spp	O	0.02	-	-	0.03	-
Family SCOPELARCHIDAE						
Benthalbella infans	Oc	0.22	-	0.31	0.26	-
Unidentified spp	Oc	0.05	-	0.06	0.02	0.15

Annex I. Continued

Species	Origin	Yearly	Spring	Summer	Autumn	Winter
Family SCORPAENIDAE						
Scorpaena porcus	N	0.02	0.07	-	0.01	0.08
Scorpaena scrofa?	N	0.01	-	-	0.02	-
Scorpaena sp	N	0.01	-	0.04	-	-
Scorpaenidae sp 1	O	0.01	-	-	0.02	-
Scorpaenidae sp 2	O	0.01	-	-	0.02	-
Scorpaenidae sp 3	O	0.03	-	-	0.06	-
Scorpaenidae sp 5	O	0.01	-	-	0.02	-
Unidentified spp	O	0.33	0.44	0.04	0.30	0.92
Family SERRANIDAE						
Anthias anthias	N	2.71^{5}	2.81^{6}	8.67^{2}	0.08	0.50^{28}
Serranus cabrilla	N	0.14	0.37	0.39	-	0.04
Epinephelus sp	N	0.02	-	0.02	0.02	-
Serranidae sp1	N	0.03	-			0.19
Unidentified spp	N	0.15	0.81	0.14	0.02	0.31
Family SOLEIDAE						
Buglossidium luteum	N	0.01	-	0.02	-	-
Microchirus ocellatus	N	0.11	-	0.41	-	-
Unidentified spp	N	0.02	-	0.02	0.02	-
Family SERRIVOMERIDAE						
Serrivomer beani	Oc	0.05	-	0.02	0.08	-
Family SPARIDAE						
Boops boops	N	1.89^{11}	10.96^{2}	-	0.23	7.02^{2}
Diplodus spp	N	0.68	2.37	0.08	0.10	3.13
Oblada melanura	N	0.33	3.11^{5}	-	0.01	0.72^{19}
Pagellus acarne?	N	0.64^{22}	0.07	0.12	1.02^{14}	0.57^{27}
Pagellus bogaraveo?	N	0.15	-	-	0.07	0.80^{14}
Pagellus sp	N	0.02	-	0.02	0.02	0.04
Pagrus pagrus	N	0.11	0.67^{16}	0.12	0.01	0.19
Pagrus spp	N	0.09	-	0.31	-	-
Unidentified spp	N	0.41	0.81	0.17	0.35	0.92
Family SPHYRAENIDAE						
Sphyraena viridensis	N	0.01	-	0.02	-	-
Family STERNOPTYCHIDAE						
Argyropelecus aculeatus	Oc	0.01	-	0.02	-	-
Argyropelecus hemigymnus	Oc	0.28	0.07	0.48^{20}	0.19	0.34
Argiropelecus sp 1	Oc	1.49^{13}	-	0.64^{14}	2.56^{7}	-
Argiropelecus *spp*	Oc	0.01	-	0.04	-	-
Maurolicus muelleri	Oc	0.51^{29}	-	0.54^{17}	-	2.59^{7}
Sternoptyx diphana	Oc	0.01	-	0.04	-	-
Sternoptix obscura	Oc	0.02	-	-	0.04	-
Sternoptyx pseudobscura	Oc	0.03	-	0.10	-	-
Sternoptyx spp	Oc	0.15	-	0.17	0.20	-
Valenciennellus tripunctulatus	Oc	0.11	-	0.10	0.10	0.19
Unidentified spp	Oc	0.50	0.81	0.95	-	1.30

Annex I. Continued

Species	Origin	Yearly	Spring	Summer	Autumn	Winter
Family STOMIIDAE						
Stomias atriventer	Oc	0.01	-	-	-	0.04
Stomias boa	Oc	0.20	0.15	0.06	0.13	0.80[15]
Eustomias sp	Oc	0.01	-	0.02	-	-
Stomiidae sp 1	Oc	0.01	-	-	0.02	-
Unidentified spp	Oc	0.22	0.37	0.04	0.07	1.07
Family SYNGNATHIDAE						
Hippocampus hippocampus	N	0.01	0.07	-	-	-
Family SYNODONTIDAE						
Synodus saurus	N	0.11	-	0.06	0.18	-
Synodus synodus	N	0.03	-	-	0.06	-
Unidentified spp	O	0.10	0.30	0.02	0.03	0.38
Family TETRAGONURIDAE						
Tetragonurus atlanticus	Oc	0.14	0.07	0.15	0.08	0.34
Tetragonurus cuvieri	Oc	0.09	-	0.02	0.17	-
Unidentified spp	Oc	0.04	-	0.14	-	-
Family TETRAODONTIDAE						
Sphoeroides spp	O	0.02	-	-	0.04	-
Tetraodontidae sp 1	O	0.01	-	-	0.02	-
Tetraodontidae sp 2	O	0.01	-	-	0.02	-
Unidentified spp	O	0.08	0.30	0.15	0.03	-
Family TRACHINIDAE						
Trachinus draco	N	0.13	-	0.25	0.12	-
Trachinus sp	N	0.03	0.07	0.08	-	0.04
Family TRICHIURIDAE						
Benthosdesmus elongatus simonyi	O	0.07	-	0.02	0.13	0.04
Lepidopus caudatus	O	0.12	-	0.12	0.06	0.42
Trichiuridae sp 1	O	0.01	-	-	0.02	-
Unidentified spp	O	0.02	-	0.04	0.02	-
Family TRIGLIDAE						
Unidentified spp	N	0.05	-	0.02	-	0.34

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[*] These papers show results of cruises carried out in the C-ACTZ: An autumn, the Mast 1 cruise (Rodriguez et al., 2000). Two cruises carried out in summer, the Hesperides and the Fax cruise (Rodriguez et al., 1999, 2004). Five transects (John et al, 2004), three crossing the C-ACTZ from the African shelf-break to the longitude of the westernmost Canary Island, one in winter, one in March and another one in summer. Two transects located a little bit north of the C-ACTZ, extending the African shelf-break towards the Madeira Islands, sampled once during winter and summer. A 21 month-study off the Gran Canaria coast, sampling weekly (Moyano et al., in pres and Moyano and Hernandez-Leon, submitted).

ANNEX II

Presence of the different species of fish larvae found during the time series off Gran Canaria (data from Chapters II-IV) and their percentage contribution to total larvae collected. For those species whose abundance was considered representative, proposed spawning periods are shaded. Note that September 2005 was not sampled.

	2005												2006												2007						
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	%
FAM. NETTASTOMIDAE																															
Anguiliforme sp.1						X	X	X			X																				0.067
Nettastoma melanurum (Rafinesque, 1810)	X						X																								0.04
FAM. CLUPEIDAE																															
Sardina pilchardus (Walbaum, 1972)	X			X	X			X				X	X		X					X								X			0.162
Sardinella aurita (Valenciennes, 1847)	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X		X			7.233
Sardinella maderensis (Lowe, 1838)					X					X		X	X				X	X		X	X	X	X	X						X	0.445
Unidentified spp	X	X		X		X	X	X					X		X	X	X	X		X		X			X		X		X	X	1.349
FAM. ENGRAULIDAE																															
Engraulis encrasicolus (Linnaeus, 1758)					X			X															X	X							0.135
FAM. BATHYLAGIDAE																															
Bathylagidae sp1	X	X										X	X		X											X					0.445
FAM. GONOSTOMATIDAE																															
Cyclothone acclinidens (Garman, 1899)							X	X		X		X							X		X		X								0.162
?*Cyclothone alba* (Brauer, 1906)	X						X												X												0.04
Cyclothone braueri (Jespersen & Tåning, 1926)	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X		5.277
Cyclothone microdon (Günther, 1878)																						X									0.013
Cyclothone pallida (Brauer, 1902)												X																			0.013
Cyclothone pseudopalida (Mukhacheva, 1964)								X		X	X																				0.081
Cyclothone spp										X	X	X	X						X	X		X				X			X		0.337
Gonostoma atlanticus (Norman, 1930)						X	X								X																0.04
Gonostoma spp	X	X	X			X	X	X		X																			X		0.162
Gonostomatidae sp.1					X																										0.013
Unidentified spp					X						X	X	X	X		X	X				X			X							0.202
FAM. STERNOPTYCHIDAE																															
Argyropelecus hemigymnus (Cocco,1829)			X			X	X			X	X		X	X	X																0.189
Maurolicus muelleri (Gmelin, 1789)																										X					0.027

	2005												2006												2007						
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	%
FAM. STOMIIDAE																															
Chauliodus spp	X	X																													0.054
Idiacanthus fasciola (Peters, 1877)												X																			0.013
Photonectes spp	X																														0.027
Stomias boa ferox (Risso, 1810)	X											X	X	X	X		X					X		X		X					0.405
Stomias sp.A	X		X	X																											0.067
Unidentified spp	X	X										X	X	X	X											X					0.202
FAM. PHOTICHTHYIDAE																															
Ichthyococcus ovatus (Cocco, 1838)	X					X								X	X																0.081
Vinciguerria attenuata (Cocco, 1938)		X	X	X						X																					0.054
*Vinciguerria nimbaría (*Jordan & Williams, 1896)	X		X			X				X	X		X	X	X		X											X			0.243
Vinciguerria poweriae (Cocco, 1938)	X	X	X	X	X			X		X	X	X	X	X	X	X	X	X	X										X		0.648
Vinciguerria spp	X	X	X	X	X	X		X		X	X	X	X	X	X		X	X					X	X		X			X		0.999
FAM. ALEPISAURIDAE																										X					0.013
FAM. CHLOROPHTHALMIDAE																															
Chlorophthalmus sp1																	X														0.013
FAM. EVERMANELLIDAE																															
Evermanella balbo (Risso, 1820)	X											X	X													X					0.094
FAM. NOTOSUDIDAE																															
Scopelosaurus lepidus (Krefft & Maul, 1955)														X	X																0.027
FAM. SCOPERLARCHIDAE																															
Benthalbella infans (Zugmayer, 1911)						X	X																								0.04
FAM. SYNODONTIDAE																															
Synodontidae sp.B			X	X	X	X					X	X	X	X		X		X		X											0.243
Unidentified spp		X	X			X																									0.081
FAM. MYCTOPHIDAE																															
Benthosema suborbitale (Gilbert, 1913)	X	X				X	X	X																					X		0.229
Ceratoscopelus maderensis (Lowe, 1839)				X	X	X	X	X		X	X	X			X	X	X	X										X	X		0.81
Ceratoscopelus warmingi (Lütken,1892)	X				X	X	X	X		X	X	X	X		X	X	X	X	X	X	X		X	X			X	X	X	X	2.874
Diaphus brachycephalus (Taning,1928)																		X						X							0.027
Diaphus holti (Taning, 1918)	X									X																					0.054

	2005												2006												2007						
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	%
Diaphus metopoclampum (Cocco, 1829)										X							X				X										0.04
Diaphus mollis (Taning, 1928)											X		X				X	X													0.081
Diaphus rafinesquii (Cocco, 1838)							X			X	X	X	X		X		X					X									0.216
Diaphus spp										X	X	X	X	X			X	X	X	X		X							X	X	0.607
Diogenichthys atlanticus (Tåning, 1918)	X	X	X	X		X	X	X		X	X	X	X	X	X		X		X		X					X	X		X		0.769
Gonichthys cocco (Cocco, 1829)																									X						0.013
Hygophum benoiti (Cocco, 1838)	X	X	X							X	X		X	X	X				X			X	X	X							0.378
Hygophum hygomii (Lütken, 1892)	X				X			X		X	X	X	X	X	X		X						X		X	X					1.835
Hygophum macrochir (Günther, 1864)	X	X	X		X		X	X		X	X	X	X	X			X	X		X											0.58
Hygophum reinhardtii (Lütken, 1892)	X	X	X	X			X	X		X	X	X	X		X		X	X			X			X					X		0.634
Hygophum taaningi (Becker*, 1965*)	X									X	X	X	X	X	X		X	X		X			X		X						0.445
Hygophum spp						X	X			X	X	X	X	X	X		X				X			X		X					0.54
Lampadena sp.1	X												X					X													0.067
Lampadena spp										X	X	X	X	X		X	X		X	X	X	X		X	X	X			X		0.648
Lampanyctus pusillus (Johnson, 1890)								X																							0.013
Lampanyctus sp.A	X									X	X																				0.094
Lampanyctus sp.B		X																													0.04
Lampanyctus spp	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X			X	X	3.32
Lepidophanes guentheri (Goode & Bean, 1896)											X	X		X					X		X										0.121
Lobianchia dofleini (Zugmayer, 1911)	X	X	X			X	X					X	X	X	X	X		X						X		X	X		X		1.161
Lobianchia gemellarii (Cocco, 1938)	X	X	X	X	X			X				X	X	X	X																0.58
Lobianchia spp	X	X	X	X						X	X	X	X	X	X		X						X	X		X					1.066
Myctophidae pte.1										X							X														0.027
Myctophidae pte.2										X	X	X						X													0.337
Myctophidae pte.3										X	X		X																		0.162
Myctophidae sp.B	X			X	X	X	X	X																							0.513
Myctophidae sp.C					X								X	X	X	X	X	X													0.216
Myctophidae sp.D					X	X															X							X	X		0.405
Myctophum nitidulum (Garman, 1899)	X	X						X		X	X	X	X	X	X								X			X					0.445
Myctophum selenops (Tåning, 1928)	X											X		X						X			X			X					0.135
Nannobrachium atrum (Tåning, 1928)																							X	X							0.027

	2005												2006												2007						
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	%
Nannobrachium lineatum (Tåning, 1928)																		X		X						X					0.054
Notolychnus valdiviae (Brauer, 1904)		X					X	X			X										X										0.175
Notoscopelus resplendens (Richardson, 1845)	X	X	X							X		X	X	X	X		X														0.283
Notoscopelus spp	X	X	X	X		X	X	X		X	X	X	X	X	X	X	X	X	X					X		X	X	X	X		1.903
Symbolophorus spp		X	X	X	X			X				X	X	X	X																0.202
Unidentified spp	X	X	X	X	X	X		X		X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	1	3.428
FAM. PARALEPIDAE																															
Lestidiops jakari pseudospyraenoides (Ege, 1918)								X			X		X																		0.054
Lestidiops spp																					X										0.027
Paralepis coregonoides (Risso, 1820)	X																														0.013
Sudis hyalina (Rafinesque, 1810)		X											X							X					X						0.067
Unidentified spp						X	X					X					X	X							X				X		0.108
FAM. LOPHIDAE																															
Lophius piscatorius (Linnaeus, 1758)																									X						0.013
FAM. SYGNATHIDAE																															
Hippocampus hippocampus (Linnaeus, 1758)																		X													0.013
FAM. CENTRISCIDAE																															
Macroramphosus scolopax (Linnaeus, 1758)	X	X	X		X	X		X		X	X	X		X	X						X					X					0.391
FAM. MELAMPHAIDAE																															
Melamphaes simus (Ebeling, 1962)		X									X	X	X								X										0.108
FAM. GADIDAE																															
Phycis spp	X													X										X							0.04
Unidentified spp	X																														0.013
FAM. HEMIRHAMPHIDAE																															
Hemiramphus balao (Lesueur, 1821)															X																0.013
FAM. SCOMBERESOCIDAE	X																														0.013
FAM. CAPROIDAE																															
Capros aper (Linnaeus, 1758)	X											X	X	X																	0.175
FAM. SERRANIDAE																															
Anthias anthias (Linnaeus, 1758)	X				X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X		X				X	X	X	1.417

	2005												2006												2007						
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	%
Serranus cabrilla (Linnaeus, 1758)					X	X						X					X	X		X				X							0.162
Serranus spp													X				X						X			X	X	X	X		0.148
Serranidae sp.1	X												X	X	X																0.067
Epinephelinae sp.1					X																										0.013
Unidentified spp		X				X				X		X	X		X		X	X	X					X			X		X		0.27
FAM. APOGONIDAE																															
Apogon imberbis (Linnaeus, 1758)																			X	X											0.027
FAM. CARANGIDAE																															
Trachurus pictoratus (Bowdich, 1825)					X								X	X	X		X										X				0.121
Unidentified spp															X																0.013
FAM. CORYPHAENIDAE																															
Coryphaena hippurus (Linnaeus, 1758)			X									X		X	X	X		X		X									X		0.216
FAM. MULLIDAE																															
Mullus barbatus (Linnaeus, 1758)					X	X											X														0.067
Mullus surmuletus (Linnaeus, 1758)					X		X																								0.054
FAM. BRAMIDAE																															
Brama brama (Bonnaterre, 1788)	X		X							X		X			X											X					0.229
FAM. SPARIDAE																															
Boops boops (Linnaeus, 1758)	X	X	X	X	X	X				X		X	X	X	X	X	X	X	X				X	X	X	X	X	X	X		4.71
Diplodus spp	X	X	X	X	X	X		X		X	X	X	X	X	X	X	X	X	X	X		X			X		X	X	X		1.997
Oblada melanura (Linnaeus, 1758)	X		X		X	X					X			X	X		X				X								X		0.958
?*Pagellus acarne* (Risso, 1826)	X										X	X	X		X										X			X			0.324
Pagellus bogaraveo (Brünnich, 1768)	X	X	X									X		X									X	X	X			X			0.459
Pagellus erythrynus (Linnaeus, 1758)																									X						0.013
Pagellus sp														X																	0.013
Pagrus pagrus (Linnaeus, 1758)			X		X	X				X			X				X	X											X	X	0.243
Unidentified spp		X	X	X	X	X					X	X	X		X		X	X	X		X					X	X			X	0.688
FAM. CENTRACANTHIDAE																															
Centracanthus cirrus (Rafinesque, 1810)	X									X		X	X	X																	0.135
FAM. MALACANTHIDAE																	X														0.013
FAM. SPHYRAENIDAE																															
Sphyraena sp.							X																								0.013

	2005												2006												2007						
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	%
FAM. LABRIDAE																															
Coris julis (Linnaeus, 1758)					X	X		X		X					X			X	X	X						X					0.283
Symphodus sp.				X	X									X	X		X														0.094
Thalassoma pavo (Linnaeus, 1758					X								X				X						X								0.054
Unidentified spp		X				X	X	X			X	X	X	X	X		X	X	X	X											0.297
FAM. SCARIDAE																															
Sparisoma cretense (Linnaeus, 1758)								X												X											0.04
FAM. POMACENTRIDAE																															
Pomacentridae sp.1	X		X	X	X					X		X	X	X	X	X	X								X						0.661
Pomacentridae sp.2						X	X	X		X							X	X	X	X	X	X	X						X	X	2.227
Unidentified spp		X				X							X																X		0.094
FAM. CHIASMODONTIDAE																															
Chiasmodon niger (Jonhson, 1864)			X									X	X																		0.04
FAM. TRACHINIDAE																															
Trachinus draco (Linnaeus, 1758)	X				X	X	X	X		X	X									X								X			0.216
FAM. GEMPYLIDAE																															
Diplospinus multistriatus (Maul, 1948)	X	X	X					X				X	X		X				X	X											0.364
Nealotus tripes (Jonhson, 1865)												X								X											0.027
Gempylus serpens (Cuvier, 1829)	X				X																										0.027
Unidentified spp				X	X		X	X			X	X						X											X		0.148
FAM. TRICHIURIDAE																															
Lepidopus caudatus (Euphrasen, 1788)	X																														0.027
Benthodesmus elongatus (Clarke, 1879)								X			X	X	X	X																	0.175
FAM. SCOMBRIDAE																															
Sarda sarda (Bloch, 1793)			X											X										X							0.04
Scomber colias (Houttuyn, 1792)	X												X	X	X			X										X			0.391
FAM. BLENNIDAE																															
Ophioblennius atlanticus (Valenciennes, 1836)			X		X	X				X			X	X	X		X	X	X	X								X	X		0.499
Scartella cristata (Linnaeus, 1758)																														X	0.013
Blennidae sp.A					X																										0.013

	2005												2006												2007						
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	%
FAM. GOBIIDAE																															
Lebetus guilletii (Le Danois, 1913)					X		X	X						X			X														0.108
Lebetus scorpiodes (Collet, 1874)	X	X		X	X																										0.054
Lebetus spp																				X				X	X			X			0.067
Unidentified spp	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	6.478
FAM. OPHIIDAE																															
Paraophidion vassali (Risso, 1810)																				X											0.013
Unidentified spp								X									X	X	X	X	X										0.135
FAM. NOMEIDAE																															
Nomeidae sp.1						X	X																								0.081
FAM. TETRAGONURIDAE																															
Tetragonurus atlanticus (Lowe, 1839)					X							X	X		X																0.135
FAM. SCORPAENIDAE																															
Scorpaena porcus (Linnaeus, 1758)												X	X		X					X				X							0.094
Scorpaena spp	X																														0.013
Scorpaenidae sp.1													X																		0.027
Unidentified spp	X		X			X	X					X	X	X	X			X		X				X					X		0.499
FAM. TRIGLIDAE	X					X						X	X		X																0.094
FAM. BOTHIDAE																															
Arnoglossus imperialis (Rafinesque, 1810)	X												X																		0.027
Arnoglossus spp						X		X			X	X								X											0.108
Arnoglossus thori (Kyle, 1913)							X			X	X	X	X								X										0.108
Bothus podas (Delaroche, 1809)							X	X		X									X												0.108
Bothus spp																				X		X									0.108
Unidentified spp					X							X	X					X													0.054
FAM. SCOPHTHALMIDAE																															
Lepidorhombus boscii (Risso, 1810)	X																														0.013
FAM. MONOACANTHIDAE																															
Stephanolepis hispidus (Linnaeus, 1766)																				X											0.013
FAM. TETRAODONTIDAE						X	X	X		X		X						X	X	X		X									0.405

Temporal and spatial distribution of the ichthyoplankton in the Canary Islands

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Despite the ongoing interest in the early life history of fishes, there still are a lot of regions in the world where this community is relatively unknown. This is the case of the Canary Islands. Thus, this thesis has precisely characterized the composition, structure and variability of the ichthyoplankton off Gran Canaria Islands, based on weekly surveys at the edge of the island shelf during more than two years. Clupeidae, Sparidae and Gobiidae were the most abundant neritic families, while Myctophidae, Gonostomatidae, and Photichthydae prevailed among the oceanic families. Temporal variability in the larval fish community seems to be more related to temperature and small-scale changes (hydrography, local productivity, and lunar cycle) than to enhanced annual productivity during the late winter bloom. Thus, two seasonal larval assemblages were identified: (1) a winter-spring assemblage, dominated by *Sardinella aurita*, *Boops boops* and *Cyclothone braueri*, and characterize by Pomacentridae sp1, *Trachurus picturatus* or *Scomber colias* species; and (2) summer-autumn assemblage when Gobids and *Cyclothone braueri* dominate and species such as *Ceratoscopelus warmingii*, Pomacentridae sp2 and *Anthias anthias* appeared. In relation to horizontal variability, two retention areas up- and downstream (warm lee) of the islands were confirmed for eggs and neritic larvae. Nevertheless, there were not significant differences in the composition of the larval assemblage between different sites on the island shelf during a relatively long-time scale.

The Canaries-African Coastal Transition Zone is characterized by a strong mesoscalar activity which influences the distribution of larvae of African neritic fish species. This interaction is particularly evident for those clupeoid larvae (sardine and anchovy) transported within upwelling filaments generated in the Cape Juby-Cape Bojador area. These filaments may be entrapped into cyclonic eddies normally formed south of Gran Canaria. This cyclonic eddy-filament system may act not only as a retention but also as a dispersal mechanism for larvae of African neritic species, depending on its evolution. During the summer some of these transported larvae may reach the eastern shores of Gran Canaria Island, contributing to the island's local larval fish community. Despite the information provided in this thesis, additional studies are necessary to assess the real importance of this larval transport and its applications to fisheries management.