

Temporal and along-shelf distribution of the larval fish assemblage at Gran Canaria, Canary Islands

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SUMMARY: 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, as the latter was not significant on a long time scale. Results suggest that there are 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 this relationship may be extended to certain neritic families. The most abundant neritic larvae (Sparidae) showed this lunar pattern, which partially supports 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.

RESUMEN: VARIACIONES ESTACIONALES Y ESPACIALES DE LA COMUNIDAD DE LARVAS DE PECES DE GRAN CANARIA, ISLAS CANARIAS. – Se estudiaron las variaciones temporales y espaciales en la comunidad de larvas de peces de la isla de Gran Canaria (Islas Canarias) a partir de muestreos semanales desde octubre 2005 a junio 2006. Se identificaron un total de 156 taxones, pertenecientes a 51 familias y 15 órdenes. La familia Myctophidae fue la más abundante (30%), seguida por Sparidae (11%), Clupeidae (9%) y Gonostomatidae (7%). Como es de esperar en una isla oceánica, los taxones neríticos y oceánicos contribuyeron en proporciones similares. Se encontraron dos zonas de retención para huevos y larvas de especies neríticas, a sotavento y barlovento de la isla. Sin embargo, la estacionalidad mostró una mayor influencia en la estructura de la comunidad larvaria que la zona de muestreo, siendo ésta no significativa a largo plazo. Se observaron dos asociaciones estacionales de larvas correspondiendo con los dos períodos más característicos en la columna de agua: período de mezcla (invierno) y de estratificación (verano). Además, se encontró una relación significativa entre la iluminación lunar y la biomasa del zooplancton de pequeño tamaño, que podría ser extensible a las larvas neríticas. Las larvas neríticas más abundantes (Sparidae) mostraron una relación con el ciclo lunar, apoyando parcialmente una hipótesis reciente sobre el efecto de la iluminación lunar en la supervivencia larvaria y su desarrollo en aguas subtropicales.

Palabras clave: ictioplancton, asociaciones de larvas, mesozooplancton, variaciones estacionales, iluminación lunar.

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 these populations (Cowen *et al.*, 2006).

Gran Canaria is one of the major islands of the Canary Archipelago, and is located in the NE Atlantic at latitude 28°N. 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, and 2) downstream (south-southwest) where a warm lee is generated. This pattern has also been recently proposed for neritic decapod larvae (Landeira *et al.*, 2009). High values of mesozooplankton biomass have also been recorded in this warm lee (Rodríguez *et al.*, 2001; Hernández-León, 1988).

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 influ-

ence 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). Furthermore, most of these studies consisted in 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 biophysical environment were studied. The use of these data for determining species spawning periods and grounds was examined.

MATERIAL AND METHODS

Weekly sampling was carried out from October 2005 to June 2006 during daylight hours onboard 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). 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 fluorimetric 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 to 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

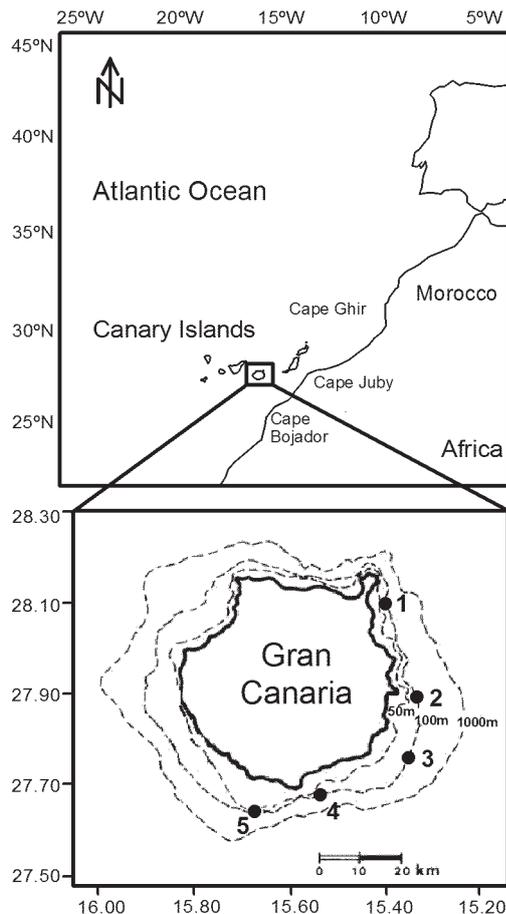


Fig. 1. – Map of the study area showing the location of the five sampling stations over the Gran Canaria shelf, Canary Islands (northeast subtropical Atlantic).

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. Following Rodríguez *et al.* (1999), these larvae were divided into three categories (Neritic, Oceanic and Other) in relation to adult behaviour.

In order to analyze the relationships between 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 the standardized variables to analyze differences among the four lunar phases centred in the 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 species composition among months (averaged across sites), as well as differences in the species composition among sites (averaged across months). Only species contributing at least 5% to the 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°C (Fig. 2a). In December, surface waters cooled, and the mixing period started. In January, when the mixed layer temperatures dropped below 19°C (Fig. 3a), nutrients were pumped to the surface, promoting a progressive increase in chlorophyll *a* (Figs. 2, 3a). After the bloom, in April-May, the thermocline started to reform, leading to a surface euphotic zone depleted of inorganic nutrients. Environmental parameters on the eastern flank (Stations 2 and 3) were significantly different from those in the island wake (Stations 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.

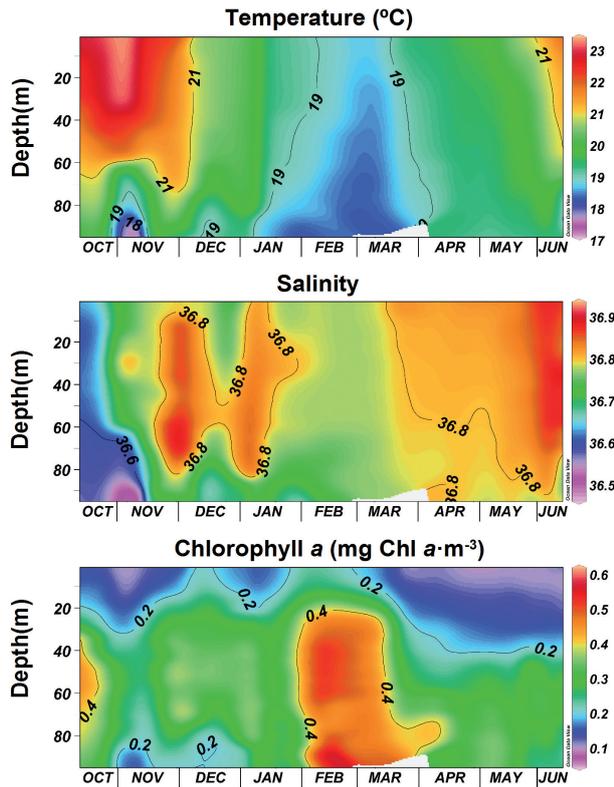


FIG. 2. – Temporal variation of a) temperature (°C), b) salinity and c) chlorophyll *a* (mg Chl *a*·m⁻³) during the sampling period in the warm lee area (Station 5).

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. The ichthyoplankton distribution was highly variable during the whole study period (Fig. 3c). Average concentrations were 1.05 ± 1.4 SD eggs·m⁻³ and 1.2 ± 0.8 SD larvae·m⁻³. Neritic larvae 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.

The ichthyoplankton abundance and mesozooplankton biomass values suggested a monthly periodicity (Fig. 3b,c), and therefore 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 significantly lower values were found during the new moon and higher values were found during the crescent and full moon (KW-ANOVA, $p < 0.005$). However, lower abundance of neritic larvae also appeared during the new moon, although this pattern was not

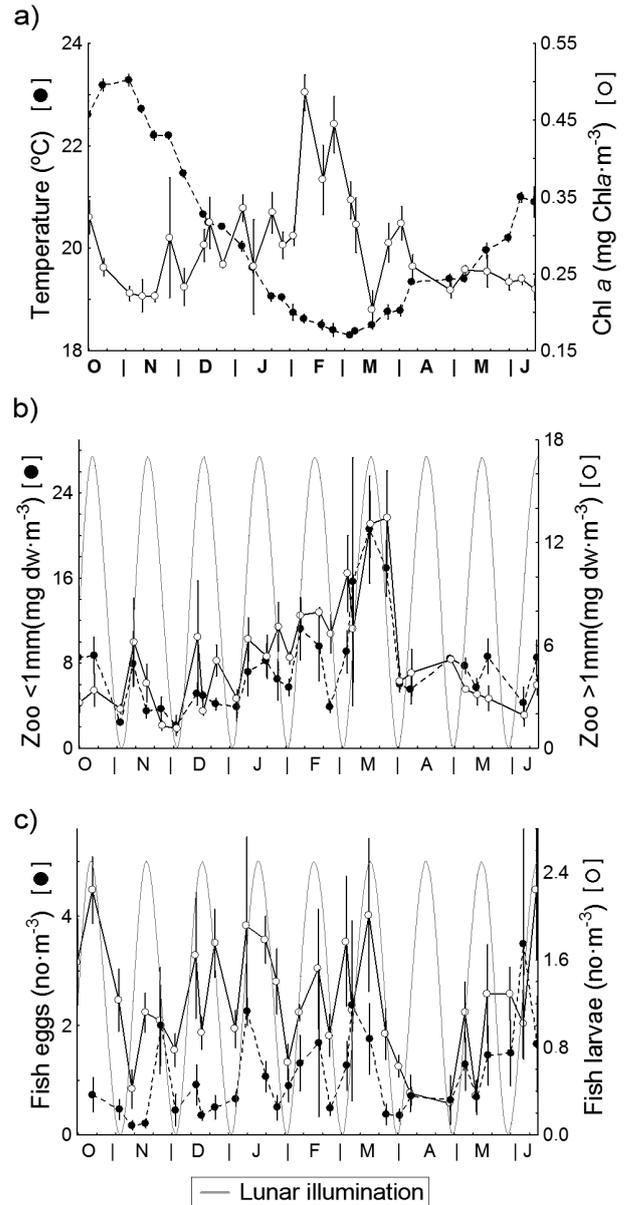


FIG. 3. – Temporal distribution of a) average temperature in the mixed layer (°C) and average chlorophyll *a* (mg chl *a*·m⁻³), b) Size fractionated mesozooplankton biomass (mg dry weight·m⁻³), c) concentration of fish eggs (no.eggs·m⁻³) and fish larvae (no.larvae·m⁻³). Average values for the five sampling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

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 had 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. 5; Friedman ANOVA,

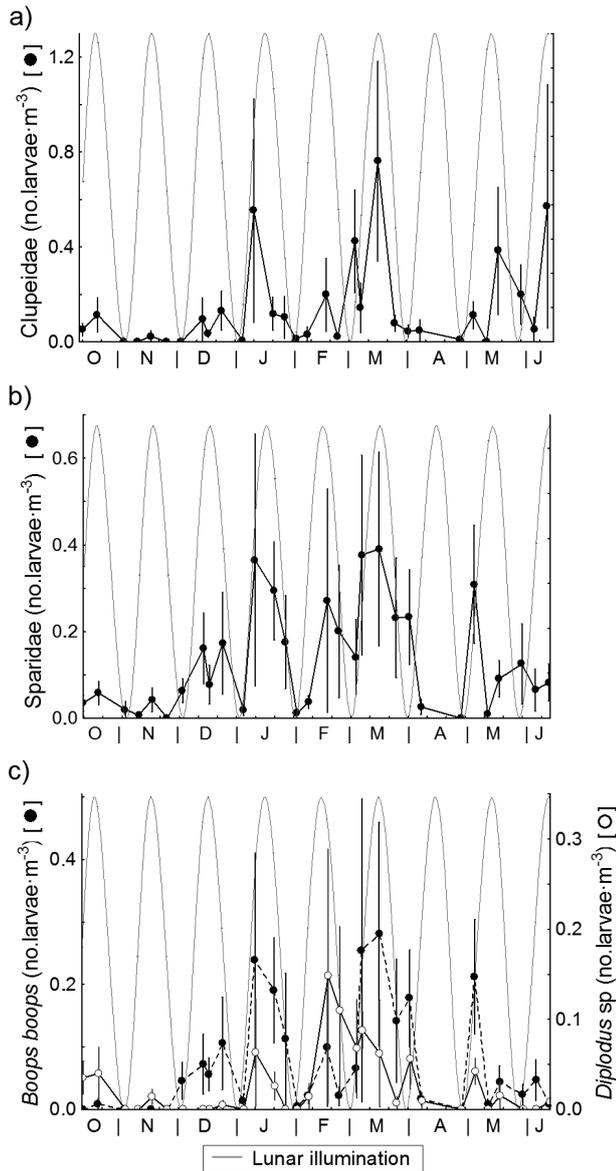


FIG. 4. – Temporal variation of average abundance (no. larvae·m⁻³) of a) Clupeidae larvae, b) Sparidae larvae and c) *Boops boops* and *Diplodus* sp larvae. Note that lunar illumination is plotted in all graphs as a fine grey line.

p<0.001). However, 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 trend than fish eggs and neritic larvae, and therefore they were only correlated with salinity in the mixed layer (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), and was mainly represented by *Ceratoscopelus warmingii*, *Hygophum 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), with *Cyclothone braueri* being the most frequent.

Sparidae, Clupeidae and Gobiidae were the families that contributed most to the 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, a seasonal analysis could lead to biased conclusions.

TABLE 1. – Matrix showing the Spearman correlation coefficients for environmental and biotic variables. Abbreviations: Temp (Average temperature in the mixed layer, °C), Salinity (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), 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 <i>a</i>	Sm Zoop	Lg Zoop	F Eggs	F Larvae	Neritic L
Salinity	0.37*							
Chl <i>a</i>	-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	0.37*	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)

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										
<i>Sardina pilchardus</i> (Walbaum, 1972)			0.28	0.16		0.17				0.10
<i>Sardinella aurita</i> (Valenciennes, 1847)	1.21	0.76	4.50	6.57	4.46	17.08	6.85	6.13	14.01	6.93
<i>Sardinella maderensis</i> (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										
<i>Cyclothone acclinidens</i> (Garman, 1899)	0.48		0.14							0.08
<i>Cyclothone braueri</i> (Jespersen & Täning, 1926)	9.93	5.81	5.63	8.17	7.64	4.98	2.74	6.13	8.17	6.75
<i>Cyclothone pallida</i> (Brauer, 1902)			0.14							0.03
<i>Cyclothone pseudopalida</i> (Mukhacheva, 1964)	0.73	0.25								0.10
<i>Cyclothone</i> sp.	2.18	1.26	0.28	0.32						0.46
<i>Gonostoma atlanticus</i> (Norman, 1930)						0.17				0.03
<i>Gonostoma</i> spp	0.24									0.03
Unidentified spp		1.01	0.14	0.16	0.32		5.48	0.20		0.31
FAMILY STERNOPTYCHIDAE										
<i>Argyropelecus hemigymnus</i> (Cocco, 1829)	0.24	0.25		0.16	0.96	0.33				0.21
FAMILY STOMIIDAE										
<i>Idiacanthus fasciola</i> (Peters, 1877)			0.14							0.03
<i>Stomias boa</i> (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										
<i>Ichthyococcus ovatus</i> (Cocco, 1938)					0.64	0.17				0.08
<i>Vinciguerria attenuata</i> (Cocco, 1938)	0.24									0.03
<i>Vinciguerria nimbaria</i> (Jordan & Williams, 1896)	0.97	0.51		0.32	0.32	0.17		0.59		0.33
<i>Vinciguerria poweriae</i> (Cocco, 1938)	0.48	0.25	0.70	0.80	0.96	0.17	1.37	0.59	0.39	0.56
<i>Vinciguerria</i> 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										
<i>Chlorophthalmus</i> sp.1								0.20		0.03
FAMILY NOTOSUDIDAE										
<i>Scopelosaurus lepidus</i> (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										
<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	0.24	1.01	0.84			0.17	2.74	0.40	0.39	0.44
<i>Ceratoscopelus warmingii</i> (Lütken, 1892)	7.75	4.29	4.36	1.76		0.17	5.48	10.67	5.45	4.21
<i>Diaphus brachycephalus</i> (Taning, 1928)									0.39	0.03
<i>Diaphus holti</i> (Taning, 1918)	0.73									0.08
<i>Diaphus metopoclampum</i> (Cocco, 1829)	0.24							0.20		0.05
<i>Diaphus mollis</i> (Taning, 1928)		0.25		0.16				0.40	0.78	0.15
<i>Diaphus rafinesquii</i> (Cocco, 1838)	0.48	0.51	0.56	0.32		0.17		0.20	0.78	0.31
<i>Diaphus</i> spp	2.18	0.76	0.98	0.96	0.32			1.58	0.78	0.92
<i>Diogenichthys atlanticus</i> (Täning, 1918)	0.97	0.76	0.42	0.16	1.91	1.16		0.20		0.64
<i>Hygophum benoiti</i> (Cocco, 1838)	1.21	0.25		0.48	1.27	0.17				0.36
<i>Hygophum hygomi</i> (Lütken, 1892)	3.87	7.07	8.72	3.04	0.32	0.50		0.20		3.34
<i>Hygophum macrochir</i> (Günther, 1864)	1.45	0.76	1.55	0.80	0.32			0.20	0.39	0.72
<i>Hygophum reinhardtii</i> (Lütken, 1892)	1.45	4.04	1.13	0.32		0.17		0.20	0.39	0.90
<i>Hygophum taaningi</i> (Becker, 1965)	0.97	0.76	0.98	1.12	0.32	0.33		0.20	0.78	0.69
<i>Hygophum</i> spp	1.94	0.76	0.84	1.28	0.64	0.50		0.40		0.82
<i>Lampadena</i> sp.1				0.48						0.10
<i>Lampadena</i> spp	2.66	1.26	0.28	0.16	0.32		1.37	1.38		0.72
<i>Lampanyctus</i> sp.1	0.97	0.25								0.13
<i>Lampanyctus</i> spp	4.84	4.04	2.53	2.88	4.14	2.49	8.22	1.58	2.33	3.08
<i>Lepidophanes guentheri</i> (Goode & Bean, 1896)		0.25	0.14		0.64					0.10
<i>Lobianchia dofleini</i> (Zugmayer, 1911)			2.11	4.65	1.27	1.82	1.37		0.39	1.57
<i>Lobianchia gemellarii</i> (Cocco, 1938)			1.69	1.44	0.32	0.50				0.64
<i>Lobianchia</i> spp	0.48	2.27	3.09	2.72	1.59	1.66		0.40		1.72
Myctophidae sp.1	0.24							0.20		0.05
Myctophidae sp.2	2.91	1.77	0.70						0.39	0.64
Myctophidae sp.3	1.94	0.25		0.48						0.31
Myctophidae sp.4				0.32	0.32	1.00	4.11	0.20	0.39	0.36
<i>Myctophum nitidulum</i> (Garman, 1899)	2.18	0.51	0.70	0.32	0.64	0.17				0.54
<i>Myctophum selenops</i> (Täning, 1928)			0.28		0.64					0.10
<i>Nannobranchium lineatum</i> (Täning, 1928)									0.78	0.05
<i>Notolychnus valdiviae</i> (Brauer, 1904)		0.76								0.08
<i>Notoscopelus resplendens</i> (Richardson, 1845)	0.24		0.28	0.80	0.64	0.50		0.40		0.38
<i>Notoscopelus</i> spp	0.97	0.51	2.39	5.77	6.37	3.98	2.74	1.19	3.89	3.10
<i>Symbolophorus</i> 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										
<i>Lestidiops jakari pseudospyraenoides</i> (Ege, 1918)		0.25		0.32						0.08
<i>Sudis hyalina</i> (Rafinesque, 1810)				0.16						0.03
Unidentified spp			0.14					0.20	0.39	0.08

	O	N	D	J	F	M	A	M	J	%
FAMILY MACRORHAMPHOSIDAE										
<i>Macroramphosus scolopax</i> (Linnaeus, 1758)	0.48	0.51	0.14		1.27	0.50				0.31
FAMILY SYGNATHIDAE										
<i>Hippocampus hippocampus</i> (Linnaeus, 1758)									0.39	0.03
FAMILY MELAMPHAIDAE										
<i>Melamphaes simus</i> (Ebeling, 1962)		0.25	0.42	0.16						0.13
FAMILY GADIDAE										
<i>Phycis</i> spp					0.32					0.03
FAMILY HEMIRHAMPHIDAE										
<i>Hemirhamphus balao</i> (Le Sueur, 1823)	0.58					0.17				0.03
FAMILY CAPROIDAE										
<i>Capros aper</i> (Linnaeus, 1758)			0.14	1.28	0.64					0.28
FAMILY SERRANIDAE										
<i>Anthias anthias</i> (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
<i>Serranus cabrilla</i> (Linnaeus, 1758)			0.14					0.59	0.39	0.13
<i>Serranus</i> 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										
<i>Trachurus picturatus</i> (Bowdich, 1825)				0.32	0.64	0.33		0.20		0.18
Unidentified spp						0.17				0.03
FAMILY CORYPHAENIDAE										
<i>Coryphaena hippurus</i> (Linnaeus, 1758)			0.28		0.32	0.83	1.37		0.39	0.26
FAMILY MULLIDAE										
<i>Mullus barbatus</i> (Linnaeus, 1758)								0.59		0.08
FAMILY BRAMIDAE	0.48		0.14			0.66				0.18
FAMILY SPARIDAE										
<i>Boops boops</i> (Linnaeus, 1758)	0.24		5.91	6.89	3.18	12.94	2.74	9.49	1.56	5.85
<i>Diplodus</i> spp	1.94	0.51	0.14	0.80	8.92	4.31	1.37	1.78	0.39	2.08
<i>Oblada melanura</i> (Linnaeus, 1758)		0.25			3.82	1.49		2.17		0.85
<i>Pagellus acarne?</i> (Risso, 1826)		0.76	1.27	0.32		0.50				0.44
<i>Pagellus bogaraveo</i> (Brünnich, 1768)			0.98		0.32					0.21
<i>Pagellus</i> spp					0.32					0.03
<i>Pagrus pagrus</i> (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										
<i>Centracanthus cirrus</i> (Rafinesque, 1810)	0.24		0.28	0.32	0.64					0.18
Unidentified spp			0.14	0.16						0.05
FAMILY LABRIDAE										
<i>Coris julis</i> (Linnaeus, 1758)	0.48					0.17			0.39	0.10
<i>Symphodus</i> spp					0.32	0.50		0.20		0.13
<i>Thalassoma pavo</i> (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										
<i>Chiasmodon niger</i>			0.14	0.16						0.05
FAMILY TRACHINIDAE										
<i>Trachinus draco</i> (Linnaeus, 1758)	0.97	0.25								0.13
FAMILY GEMPYLIDAE										
<i>Diplospinus multistriatus</i> (Maul, 1948)			0.70	0.96		0.33				0.33
<i>Nealotus tripes</i> (Jonhson, 1865)			0.14							0.03
Unidentified spp		0.51	0.14						0.78	0.13
FAMILY TRICHIURIDAE										
<i>Benthodesmus elongatus</i> (Clarke, 1879)		0.25	0.98	0.32	0.64					0.31
FAMILY SCOMBRIDAE										
<i>Sarda sarda</i> (Bloch, 1793)					0.32					0.03
<i>Scomber colias</i> (Houttuyn, 1792)				2.72	0.96	0.66				0.69
Unidentified spp									1.17	
FAMILY GOBIIDAE										
<i>Lebetus guilletii</i> (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										
<i>Ophioblennius atlanticus</i> (Valenciennes, 1836)	0.73			0.16	0.32	0.17		1.38	1.17	0.41
FAMILY OPHIDIIDAE								0.40	0.78	0.10
FAMILY TETRAGONURIDAE										
<i>Tetragonurus atlanticus</i> (Lowe, 1839)			0.42	0.80		0.17				0.23
FAMILY SCORPAENIDAE										
<i>Scorpaena porcus</i> (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										
<i>Arnoglossus imperialis</i> (Rafinesque, 1819)				0.16						0.03
<i>Arnoglossus thori</i> (Kyle, 1913)	0.48	0.51	0.14	0.16						0.15
<i>Arnoglossus</i> spp		0.25	0.28							0.08
<i>Bothus podas</i> (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

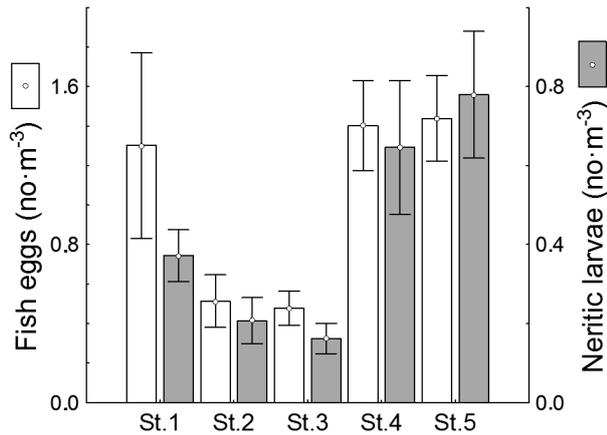


FIG. 5. – Average abundance (no. m⁻³) and standard error (SE) along the five sampling stations of total fish eggs (white bars) and neritic larvae (grey bars).

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 autumn and late spring. Pomacentridae sp2 and *Trachinus draco* are probably summer spawners in the region, as they were only found during the stratified period.

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. 4). Both families displayed a monthly trend similar to that shown by mesozooplankton biomass (Fig. 4a,b). Sparidae larvae exhibited significantly 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. 4). Larvae of the genus *Diplodus* also showed lower values during the new moon, although these differences were not significant (KW-ANOVA, $p > 0.005$) (Fig. 4c).

ANOSIM results indicated that there was a significant difference 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 $R = 0.055$, $p < 0.05$ respectively). Although sampling site did not significantly affect the composition

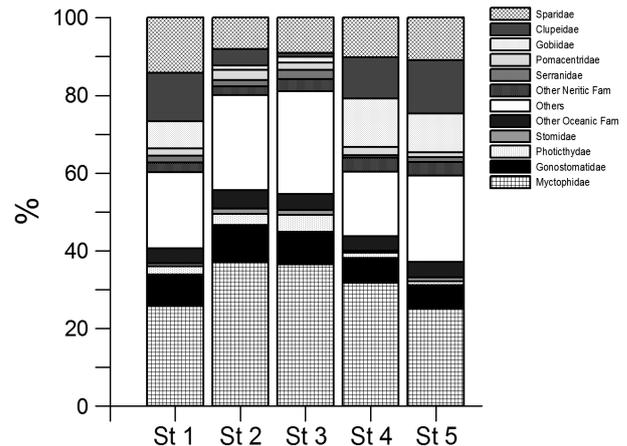


FIG. 6. – Percentage contribution of the nine most abundant families (contributing >0.9% of total collected larvae) to the total larval fish catches at each sampling station.

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 $p < 0.01$). However, mesopelagic families (e.g. Myctophidae, Gonostomatidae, and Phosichthyidae) 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 (Aristegui *et al.*, 2001). These authors attributed the first chlorophyll peak to an abrupt increase in phytoplankton cells $< 2 \mu\text{m}$ (mostly diatoms), whereas in the second peak, there were higher densities of cells $> 2 \mu\text{m}$. 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, which is 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 a temporal peak during the late winter bloom period. This temporal pattern of 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*, *Cyathothone braueri*).

Nevertheless, the larval concentrations of some species 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. *Scomber colias* and *Trachurus picturatus* larvae appeared during the mixing period of the water column (i.e., January to March), which coincides 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 compared to temperate Mediterranean Sea waters. Both ecosystems have 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 the limited representation of the summer months during this study precludes any conclusion.

In relation to local hydrography, mesozooplankton biomass and fish eggs and neritic larval abundances 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 has already been 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 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 found clear evidence of the mesozooplankton biomass increasing during the illuminated phase of the lunar cycle: low values during the new moon that increase through the crescent and full moon, and then decrease again during the waning moon. This pattern was explained by Hernández-León (1998), for zooplankton, to be a result of predator pressure. During the 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. However, 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 the 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, and argued 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 for the trend to be noticed. 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 ichthyoplankton 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 in 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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