

Relative influences of space, time and environment on coastal ichthyoplankton assemblages along a temperate rocky shore

ERWAN ROUSSEL¹, ROMAIN CREC'HRIOU^{1,2}, PHILIPPE LENFANT³, JULIEN MADER⁴ AND SERGE PLANES^{1*}

¹USR 3278 CNRS-EPHE, CRIOBE – CBETM UNIVERSITÉ DE PERPIGNAN, 52 AVENUE PAUL ALDUY, 66860 PERPIGNAN CEDEX, FRANCE, ²MUSEUM OF NEW ZEALAND, TE PAPA TONGAREWA, NATURAL ENVIRONMENT, FISH DIVISION, 169 TORY STREET, PO BOX 467, WELLINGTON, NEW ZEALAND, ³UMR 5244 CNRS UPVD, CBETM, UNIVERSITÉ DE PERPIGNAN, 52 AVENUE PAUL ALDUY, 66860 PERPIGNAN CEDEX, FRANCE AND ⁴DEPARTAMENTO OCEANOGRAFÍA Y MEDIO AMBIENTE, AZTI, HERRERA KAIA - PORTU ALDEA Z/G, 20110 PASAIA (GIPUZKOA), SPAIN

*CORRESPONDING AUTHOR: planes@univ-perp.fr

Received June 21, 2009; accepted in principle April 11, 2010; accepted for publication April 18, 2010

Corresponding editor: Roger Harris

Fish egg and larval assemblages, and the factors that drive them in the nearshore environment remain largely unknown. In this study, two sampling methods were used to assess the relative influences of space, time and environment on ichthyoplankton communities at nearshore stations, near the Cerbère-Banyuls Marine Protected Area (France), during spring and summer 2003. Resulting data sets were analysed by variation partitioning, with redundancy analysis to estimate variance fractions based on adjusted R^2 . A total of 42 environmental descriptors were considered for the analyses. The descriptors that best explained the variance of the data set were selected to build models. Analyses of the relative influences show that the environmental conditions drive egg and larval density variations, specifically depth, currents and wind directions. However, time and space combined with environmental factors also contribute substantially to ichthyoplankton variability. The combined effect of space and environment is likely to be generated by the influence of the coast profile on ichthyoplankton from shallower water. At deeper stations, wind and current fluctuations result in a combined effect of time and environment in relation to eggs. These results strongly suggest that the nearshore area influence is between 25 and 30 m depth and is separated from the inner continental shelf. We propose the hypothesis that the rocky shore ecosystem is favourable for coastal accumulation and/or retention of ichthyoplankton.

KEYWORDS: ichthyoplankton; nearshore; variation partitioning; environment; time; space; NW Mediterranean

INTRODUCTION

Survival of fish offspring and their subsequent addition to existing populations is the result of a complex life history (Sponaugle *et al.*, 2002). Spawning marine fishes release their gametes and progeny into a naturally

fluctuating environment. Therefore, survival depends on how the surrounding water mass characteristics meet their requirements for development and growth (Cushing, 1974). In addition, fishes in their early stages are passive drifters, and hence the probability of them

being placed in a favourable habitat is also linked to the local current circulation (Cushing, 1990).

Favourable conditions for young fish development are defined by biological and physical factors. Biological factors that have been identified include predation (Pepin, 2004) and food availability (Fortier *et al.*, 1992; Scalfani *et al.*, 1997). Several physical factors have also been reported as influencing ichthyoplankton abundance, such as temperature, salinity, winds and currents (e.g. Lee *et al.*, 1992; Grothues and Cowen, 1999; Bergenius *et al.*, 2005; Fossheim *et al.*, 2005; Alemany *et al.*, 2006; Knutsen *et al.*, 2007). These environmental factors also change according to the spatial and temporal scale considered (Sanvicente-Añorve *et al.*, 2000).

The surroundings in which ichthyoplankton evolve are the product of multiple influences of space, time and environment. Egg and larval densities change with the environment, and both ichthyoplankton and environmental factors change in time and in space. Space–time integration is the key to the understanding of many of the ecological processes driving population dynamics, since the underlying processes also vary in space and time (Koenig, 1999). Along rocky shores, one example of site-specific environmental characteristic changing with time is that of the topographically generated long-shore currents (hence space-dependant). These currents are also wind-driven and may vary with time. The dynamics of these currents has been shown to significantly alter the distribution of many planktonic organisms in coves, while they did not do so on an open coastline (Shanks and McCulloch, 2003).

The coastal or nearshore area is generally defined as extending from the shore to the 20 m isobath. At this depth, the surface and bottom Eckman layer are confounded (Werner *et al.*, 1997). These limits often correspond to the width of the long-shore current. In contrast to offshore areas such as the continental shelf or slope, ichthyoplankton in temperate nearshore areas has only been investigated more recently (Bordehore *et al.*, 2001; Sabatés *et al.*, 2003; Koutrakis *et al.*, 2004; Beldade *et al.*, 2006; Borges *et al.*, 2007). As a result, very little is known about the relationships between environmental factors and fish eggs and larval abundance (Hernandez-Miranda *et al.*, 2003; Azeiteiro *et al.*, 2006). The coastal habitat is thought to provide more suitable conditions for fish eggs and larval survival than the other open sea areas (Myers and Pepin, 1994), because of higher water mass stability and higher food availability (Laprise and Pepin, 1995). Published studies on eggs and larval distribution over the continental shelf that included the inner-shelf zone (above 20 or 30 m isobath) have shown distinct ichthyoplankton assemblages in this latter region that are interpreted as a consequence of the reproductive behaviour of the adults,

which is bottom type and depth related (Sabatés, 1990a; Sabatés and Maso, 1992; Espinosa-Fuentes and Flores-Coto, 2004; Munk *et al.*, 2004; Quattrini *et al.*, 2005; López-Sanz *et al.*, 2009).

In this paper, we investigate the relationships between ichthyoplankton and the environmental factors in a rocky nearshore area of the north-western Mediterranean. We specifically addressed two questions: (i) What are the relative influences of space, time and environment on ichthyoplankton structures? (ii) Considering the large number of potential environmental factors, which are the ones probably driving egg and larval distributions in the near-shore area?

METHOD

Study area

The study site is located in the south of France (Fig. 1), in the vicinity of the Cerbère-Banyuls Marine Protected Area, orientated north-south, mainly straight, with some

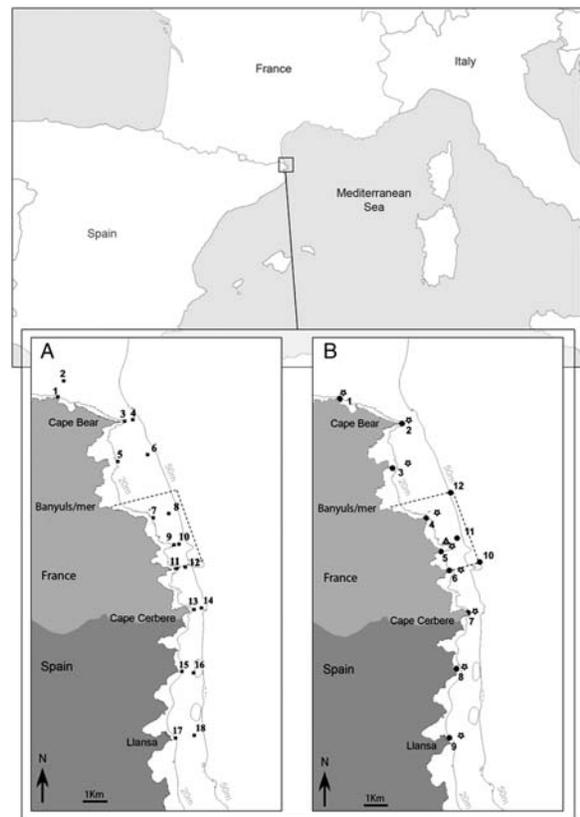


Fig. 1. Study area with Bongo net (A) and fixed net (B) stations. Asterisks indicate CTD sampling stations and the grey triangle is the position of the ADCP. Dotted line represents the MPA border.

bays and capes. Underwater slopes can be steep and fish habitats are diverse, including *Posidonia* meadows, coralligen, rocks and sand. Seasonality is well-marked with north-western winds blowing in January and July. South-eastern winds can be an important component in spring. The circulation is dominated by a southward long-shore current, which can reverse when strong south-eastern winds blow, limiting the cross-shelf transport (Rouault, 1971). Moreover, there is no upwelling and small-scale gyres can be observed in the bays that probably act as retention zones (Guizien *et al.*, 2006).

Sample collection

Sampling was conducted during spring and summer 2003. Two plankton sampling methods were used: Bongo nets and fixed nets, both mounted with 300 μ meshes and equipped with flowmeters (*General Oceanics* 2030R). The overall sampling framework consisted of nine radial transects coupling Bongo and fixed net collection sites. For the Bongo net collections, a grid of 18 stations (Fig. 1A) divided in 9 transects of 2 stations each from the coast (on the 20 m isobath) to offshore (on the 40 m isobath). This framework was surveyed 12 times from 7 May to 14 August. Bongo collections consisted of down and up oblique tows with a Bongo net, with a double 60 cm mouth opening, performed during daytime with the research vessel “NEREIS II” maintaining speed at 2 knots. The down tow was performed between the surface and a depth of 10 m above the ocean floor (i.e. the “max depth”) followed by an up tow performed between this maximum depth and the surface. During this up tow, 3 horizontal tows of 5 min were performed at 20, 10 and 2 m depths, respectively, with the aim of targeting larvae of coastal fish species, which have been reported to be more abundant in the upper 20 m of the water column (Sabatés, 1990a; Sabatés *et al.*, 2003). The GPS position of the vessel was recorded at the beginning and at the end of each tow, as well as at several intermediate points, in order to locate the exact position of the tow. Maximum depth of tows varied between 20 and 40 m within the sampling area. The catch of each tow (two replicas) was sieved and fixed directly on board with 4% formalin-seawater leading to a total of 186 samples (one of the two replicas) analysed from Bongo collections. The filtered volume was calculated by using flowmeters and the following formula:

$$\frac{3.14 \times (\text{Net Diameter})^2}{4} \times \frac{(\text{Arrival count} - \text{Start count}) \times (\text{Rotor const.})}{999.999}$$

The mean volume filtered was $268 \pm 70 \text{ m}^3$ (mean \pm SD).

At the same time as the Bongo net collections, fixed plankton nets (300 μ m mesh size and 60 cm mouth diameter) were deployed at 12 inshore stations regularly spaced along the coast (Fig. 1B). These nets, which are passive devices filtering and following ambient currents, were moored 10–20 m from the shore, on anchor lines fixed at depths ranging from 20 to 40 m and maintained at 2 m depth in the water column with floats. This sampling technique, adapted from Bordehore *et al.* (Bordehore *et al.*, 2001), is described in Crec’hriou (Crec’hriou *et al.*, 2010). This method provided collection of fish eggs and larvae from very shallow waters in locations that could not be sampled with research vessels. Sampling with fixed nets was conducted twice a week from 22 July to 20 August. This passive sampling was performed between dusk and dawn, as nets were deployed late in the afternoon and recovered the following morning with a total of 12–15 h of sampling daily. As currents were often low, nets were deployed with a low-speed rotor on the flowmeters. During the collection of the samples, every morning, the plankton from each net was maintained alive, separately, in seawater in 5 L plastic containers. These were sieved and fixed with 4% formalin once back at the harbour, leading to a total of 76 samples analysed from Bongo collections. Before sieving, a random sub-sample was taken from the surface of the containers for live egg identification.

Due to a technical limitation in the flowmeters’ sensitivity to low currents, even with a low-speed rotor, all samples with average nightly current speed lower than 2 cm s^{-1} were removed from further analysis. The mean volume filtered was $1185 \pm 1392 \text{ m}^3$. The filtered volume was very variable depending on the current speed at each location (min = 199 m^3 , max = 5984 m^3).

Oceanographic data

Vertical profiles of temperature, conductivity, fluorescence and pressure from 2 m above the bottom to the surface were obtained with a SB19 CTD (Fig. 1B). A moored ADCP (DCM 12, Teledyne RDI), located in the centre of the area (Fig. 1B), recorded current strength and directions for the whole water column every 30 min. Wind data were kindly provided by Meteo-France. Strength and direction were recorded at 3-h intervals at Cap Bear (Fig. 1). Bathymetric data were collected at a $1 \times 1 \text{ m}$ resolution using multi-beam sonar, along the French coast up to the 30 m isobath. Complementary bathymetric data were extracted from a SHOM marine map (No. 6843) which covers the study area.

Ichthyoplankton recovery

Fish larvae were sorted in the laboratory under a stereomicroscope and identified to the lowest taxonomic level possible (following Moser *et al.*, 1983; Sabatés, 1988; Alemany, 1997; Glamuzina *et al.*, 2001). Fish eggs were sorted in the laboratory under a stereomicroscope and identified to the lowest taxonomic level possible (Marinaro, 1971; Jug-Dujakovic and Kraljevic, 1995; Glamuzina *et al.*, 1998). Based on this identification, eggs were classified into 12 categories (Table I). When samples had less than 200 eggs, all eggs were identified. When eggs were more abundant, a sub-sample of at least 200 eggs was identified. Samples including more than 500 eggs were sub-sampled using a Motoda box.

Data analysis

Egg and larval abundances were divided by the volume filtered to obtain densities per 1000 m³. Rare species (i.e. present in less than 10% of the samples) were excluded. In addition, for the larvae, a second selection by abundance sorting was performed to reduce the number of taxa (Ibanez *et al.*, 1993). This method uses an index mixing abundance and frequency of species to retain the frequent and the locally abundant taxa, and removes the others. In the first step, we used multivariate regression tree (De'ath (2002)) at the community level to see if spatio-temporal variations are essential factors which explain an important part of the overall variability of the data set. Results (Fig. 2) show that the variations between spring and summer lead to marked discontinuities in eggs and larvae. Both Bongo net data sets were split according to the season. The week has been also demonstrated to be the major temporal scale in density variations and was considered the relevant

time descriptor. As a result, six data sets were analysed (Tables I and II). For eggs, 8 response variables (Taxa) were kept for spring for Bongo nets (*n* = 84 samples), 11 for summer for Bongo (*n* = 100 samples) and 10 for fixed nets (*n* = 76 samples). A total of 14 larvae taxa were kept for Bongo nets for spring (*n* = 70 samples), 20 for Bongo nets in summer (*n* = 116 samples) and 13 for fixed nets (*n* = 76 samples).

Spatial distances were calculated as the metric distance given by the UTM coordinates and were centred on the origin to reduce collinearity between terms following Legendre and Legendre (Legendre and Legendre, 1998). Nine terms of a cubic surface trend analysis were included (X, Y, X², Y², XY, X³, Y³, X²Y and Y²X) (Borcard *et al.*, 1992).

To account for the environmental variation, 42 descriptors for Bongo nets and 38 for fixed nets were considered in the analyses (Tables III and IV). These cover four categories:

- (1) *Topography* (Table III): six descriptors were built for each station with the GIS (Map info Pro©) after Natural Neighbor interpolation of the bathymetric data: the *distance* to the coast and the *depth* were measured directly on the map. the *average slope of the bottom*, and the *bottom complexity* defined as the total length of the isobaths divided by the number of isobaths, to account for slope artefacts. Both derived from data taken in a 200 m radius circle from the station. This radius was found to yield a greater variability of highest coefficient of variation (around 0.30) of the three distances tried (100, 150 and 200 m) and found to be homogeneous between Bongo and Fixed nets.

Table I: Species and mean densities (\pm SD) of egg categories in number of egg per 1000 m³

Category	Species or taxa identified	Bongo net densities (mean \pm SD)	Fixed net densities (mean \pm SD)	Bongo spring spatial structures			Bongo summer spatial structures			Fixed net spatial structures		
Cat 1	<i>Engraulis encrasicolus</i>	936 \pm 2304	2 \pm 10	S	+	✓	Co/Sh	-	✓	-	-	✓
Cat 2	-	5 \pm 26	-	-	-	-	-	-	-	-	-	-
Cat 2 A	<i>Scorpaena</i> sp.	35 \pm 81	94 \pm 298	-	-	-	N	+	✓	?	-	✓
Cat 3	<i>Centracanthus cirrus</i>	38 \pm 92	76 \pm 220	N/S	-	✓	Co/Sh	-	✓	Co/Sh	-	✓
Cat 4	<i>Sardinella aurita</i>	30 \pm 70	4 \pm 10	Co/Sh	-	✓	Co/Sh	-	✓	-	-	✓
Cat 5	Anguilliforms	7 \pm 23	27 \pm 62	-	-	-	-	-	-	C	+	✓
Cat 6	-	70 \pm 191	-	N/S	-	✓	?	-	✓	-	-	-
Cat 7	-	269 \pm 323	28 \pm 41	Co/Sh	-	✓	N	+	✓	?	-	-
Cat 8	<i>Coris julis</i>	2065 \pm 2593	1352 \pm 1426	Co/Sh	-	✓	Co/Sh	-	✓	Co/Sh	-	✓
Cat 9	-	2426 \pm 3057	450 \pm 624	N/S	-	✓	C	+	✓	C	+	✓
Cat 9 A	<i>Epinephelus marginatus</i>	26 \pm 76	178 \pm 993	-	-	-	C	+	✓	C	+	✓
Cat 9 B	<i>Sciaena umbra</i>	92 \pm 387	9 \pm 18	C	+	✓	C	+	✓	C	+	✓

Spatial structures of eggs have been identified with spatial models. Code: N, north; S, south; C, centre; N/S, north-south gradient; Co/Sh, coast-shelf structure. "+", zone of high density and "?", unidentified structures. "✓", variable used in the data set.

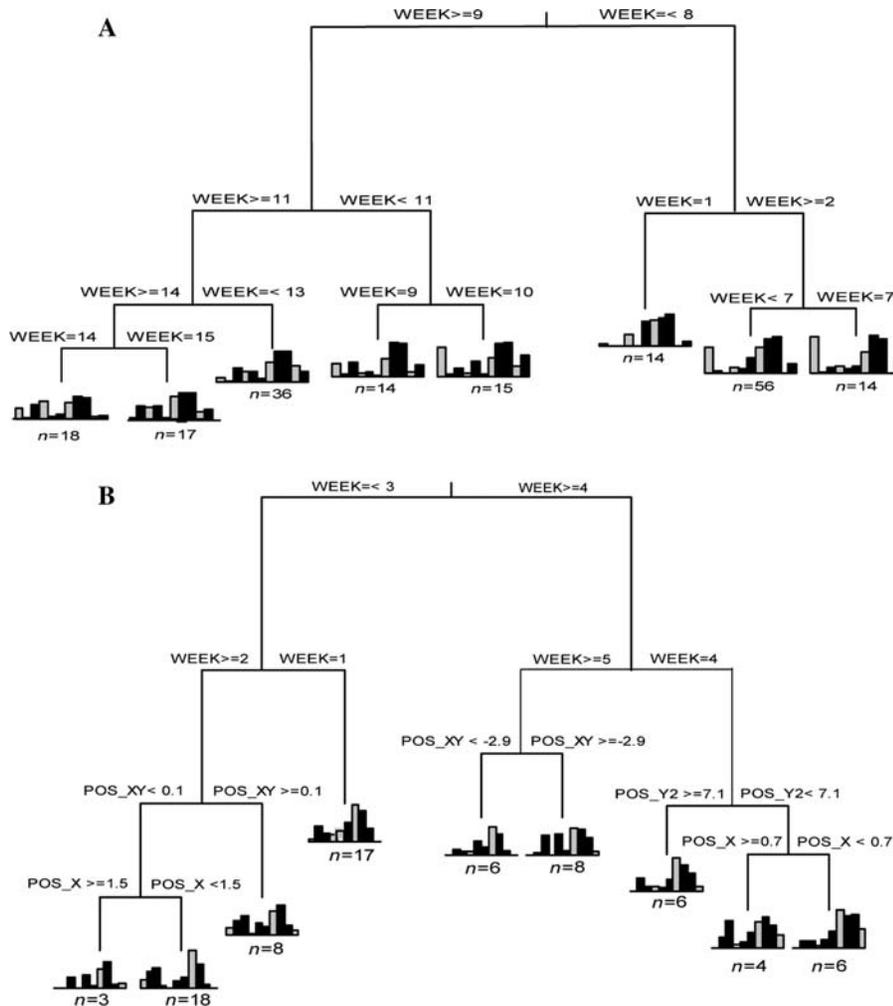


Fig. 2. Multivariate Regression Trees with spatio-temporal factors of Bongo nets (A) and fixed nets (B). Values of factors splitting the trees are given near the corresponding node. Histograms represent the contribution of egg categories in each final leaf and n is the number of samples of these leaves.

the *coast profiles* at *small and large scale* were used to characterize the topographic features of the coast-line (bays, capes and straight lines). They were calculated as the percentage of land in a circle around the station, multiplied by the ratio shore length/circle perimeter to account for shore complexity artefacts. A 600 and 2500 m radius circle was used for small and large scale, respectively, centred on the perpendicular intersection between the shore orientation and the distance from the station to the coast. The small-scale distance corresponded to the maximum distance from the near-shore stations to the coast, the large-scale distance to the radius of the biggest topographic feature of the area (Banyuls Bay).

(2) *Hydrology* (Table IV): *Temperature, salinity, density* and *fluorescence* were measured with the CTD. For each

parameter, six descriptors were considered: values at 1, 10 and 20 m depth, the average of the whole water column, the average in the subsurface layer (0.5–2 m depth) and the average above the pycnocline. The latter was determined visually from the CTD profiles for each transects and each sampling date. A total of 25 descriptors were collected in this category.

(3) *Winds* (Table III) and (4) *Currents* (Table III): as wind and current directions could not be included in community analyses because of their circular nature, they have been transformed into five categories: *NE* for directions 10–90°, *SE* for directions 90–180°, *SW* for directions 180–270°, *NW* for directions 270–360° and *variable*. Two time scales were taken into account for each of the four descriptors of wind, current strength and direction:

Table II: Frequent and locally abundant larval taxa selected for the two sampling methods

Taxa	Bongo net densities (mean + SD)	Fixed net densities (mean + SD)	Bongo net Spring spatial structures			Bongo net Summer spatial structures			Fixed net spatial structures		
Blennidae	93 ± 115	28 ± 46	C	+	✓	Co/Sh	-	✓	C	+	✓
<i>Callyonimus</i> sp.	16 ± 18	1 ± 2	N	+	✓	Co/Sh	-	✓	N/S	-	✓
<i>Trachurus</i> sp.	20 ± 35	1 ± 2	C	+	✓	S	+	✓	Co/Sh	-	✓
			S	-							
Clupeiforms	345 ± 407	123 ± 230	?	-	✓	Co/Sh	-	✓	Co/Sh	-	✓
Gobiidae	48 ± 57	3 ± 8	N/S	-	✓	N/S	-	✓	N/S	-	✓
									Co/Sh	-	
Labridae	29 ± 85	2 ± 3	Co/Sh	-	✓	Co/Sh	-	✓	S	+	✓
<i>Scomber japonicus</i>	13 ± 21	-	N/S	-	✓	Co/Sh	-	✓	-	-	-
Soleidae	11 ± 31	1 ± 3	N/S	-	✓	Co/Sh	-	✓	C	+	✓
Sparidae	89 ± 160	4 ± 7	N/S	-	✓	C	+	✓	C	+	✓
Anguilliforms	10 ± 36	-	-	-	-	Co/Sh	-	✓	-	-	-
<i>Arnoglossus</i> sp.	3 ± 8	-	N/S	-	✓	?	-	✓	-	-	-
<i>Spicara</i> sp.	5 ± 11	-	C	+	✓	C	+	✓	-	-	-
<i>Cepola macrophthalmia</i>	8 ± 22	-	N/S	-	✓	Co/Sh	-	✓	-	-	-
Gobiesocidae	26 ± 121	5 ± 16	N/S	-	✓	Co/Sh	-	✓	N/S	-	✓
			Co/Sh	-					Co/Sh	-	
Mugilidae	8 ± 15	1 ± 2	-	-	-	C	+	✓	Co/Sh	-	-
<i>Mullus</i> sp.	3 ± 10	-	-	-	-	Co/Sh	-	✓	-	-	-
Thunninae	5 ± 12	1 ± 3	-	-	-	Co/Sh	-	✓	Co/Sh	-	-
<i>Scorpaena</i> sp.	3 ± 9	2 ± 4	-	-	-	N/S	-	✓	N/S	-	-
<i>Serranus hepatus</i>	8 ± 20	-	N	+	✓	Co/Sh	-	✓	-	-	-
<i>Trypterion</i> sp.	9 ± 34	-	-	-	-	Co/Sh	-	✓	-	-	-
<i>Chromis chromis</i>	-	4 ± 22	-	-	-	-	-	-	?	-	-

Densities (±SD) are in number of larvae per 1000 m³. Spatial structures of larvae have been identified with spatial models. Code: N, north; S, south; C, centre; N/S, north-south gradient; Co/Sh, the coast-shelf structure. "+", zone of high density; "?", unidentified structures. "✓", variable used in the data set.

Table III: Topography, wind and currents descriptors used in analyses and corresponding abbreviations

Topography		Wind		Currents	
Abbreviation	Descriptor	Abb.	Descriptor	Abb.	Descriptor
Depth	Depth	WindDirD	Wind direction averaged on the sampling day	CurDirD1 m	Current direction at 1 m averaged on the sampling day
DistCoast	Distance to the coast	WindDirW	Wind direction averaged 3 days before sampling	CurDirD3 m	Current mean direction at 3 m averaged on the sampling day
Slope	Bottom slope	WindSpdD	Wind speed averaged on the sampling day	CurDirW1 m	Current direction at 1 m averaged 3 days before sampling
BottComp	Bottom complexity	WindSpdW	Wind speed averaged 3 days before sampling	CurDirW3 m	Current mean direction at 3 m averaged 3 days before sampling
CoastProfSmall	Coast profile at small scale	-	-	CurSpdD1 m	Current speed at 1 m averaged on the sampling day
CoastProfLarge	Coast profile at large scale	-	-	CurSpdD3 m	Current mean speed at 3 m averaged on the sampling day
-	-	-	-	CurSpdW1 m	Current speed at 1 m averaged 3 days before sampling
-	-	-	-	CurSpdW3 m	Current mean speed at 3 m averaged 3 days before sampling

the first was the average on the day when sampling occurred. The second is the average over 3 days before and during the sampling date. Current strength was measured at 1 m depth for both Bongo and fixed nets. As the whole water column was sampled with Bongo nets, with a longer sampling duration in the upper layer, another descriptor was added for these data sets by

compiling the mean of three depths (2, 3 and 4 m). Subsequently there were four descriptors for wind, while there are four currents descriptors for fixed nets and eight for Bongo nets.

Redundancy analyses (RDA) were used to analyse the partitioning of variance between spatial, temporal and environmental components, following Anderson and

Table IV: Hydrology descriptors used in analyses and corresponding abbreviations

Hydrology			
Abb.	Descriptor	Abb.	Descriptor
<i>Temp1m</i>	Temperature measured at 1 m	<i>TempAbPycn</i>	Temperature averaged above the pycnocline
<i>Sal1m</i>	Salinity measured at 1 m	<i>SalAbPycn</i>	Salinity averaged above the pycnocline
<i>Dens1m</i>	Density measured at 1 m	<i>DensAbPycn</i>	Density averaged above the pycnocline
<i>Fluo1m</i>	Fluorescence measured at 1 m	<i>FluoAbPycn</i>	Fluorescence averaged above the pycnocline
<i>Temp10m</i>	Temperature measured at 10 m	<i>TempSubSurf</i>	Temperature averaged in the subsurface
<i>Sal10m</i>	Salinity measured at 10 m	<i>SalSubSurf</i>	Salinity averaged in the subsurface
<i>Dens10m</i>	Density measured at 10 m	<i>DensSubSurf</i>	Density averaged in the subsurface
<i>Fluo10m</i>	Fluorescence measured at 10 m	<i>FluoSubSurf</i>	Fluorescence averaged in the subsurface
<i>Temp20m</i>	Temperature measured at 20 m	<i>TempWatCol</i>	Temperature averaged in the water column
<i>Sal20m</i>	Salinity measured at 20 m	<i>SalWatCol</i>	Salinity averaged in the water column
<i>Dens20m</i>	Density measured at 20 m	<i>DensWatCol</i>	Density averaged in the water column
<i>Fluo20m</i>	Fluorescence measured at 20 m	<i>FluoWatCol</i>	Fluorescence averaged in the water column
<i>DepthPycn</i>	Pycnocline depth	–	–

Gribble (Anderson and Gribble, 1998). This is an extension of Borcard *et al.* (Borcard *et al.*, 1992) to three matrices or more. Before running the analyses, all spatial and environmental descriptors were submitted to several stepwise procedures known as forward selection, which adds environmental variables one at a time, until no other variables “significantly” explain residual variation in species composition. We added the constraint that no more than six explicative variables per source of variation (i.e. environment and space) were included in the models, and selected ones producing models explaining the higher total variation. Following Legendre and Gallagher (Legendre and Gallagher, 2001), a Hellinger transformation was applied to the species as it ensures the applicability of RDA in data containing zero results (long environmental gradient). Finally, the estimation and comparison of variance fractions was based on the adjusted R^2 , since it is the only unbiased estimator of variance components in canonical analyses (Peres-Neto *et al.*, 2006).

Analyses were performed using the software Brodgar[®] (Highland Statistics Ltd), GeoDa[™] (Luc Anselin) and R software (R Development Core Team, 2007).

RESULTS

Environmental conditions

Topographic descriptors associated with each station are given in Table V for both sampling methods. Coast profiles (CP) quantitatively describe topographic features such as capes, bays and straight coastlines in front of nearshore stations. At the small scale, all CP (except the northern most station) corresponded to capes (CP < 0.30). At the large scale, coastal profiles indicate two

capes (Bongo stations 4 and 19 in Fig. 1) and two bays (CP > 0.60, Bongo stations 7 and 25). All other stations are located in front of straight CP (0.30 < CP < 0.60). At the Bongo stations, slopes were steeper for the coastal stations (mean = 6.85, SD = 1.98) than for the shelf stations (mean = 2.51, SD = 1.62) with a maximum in the north (slope = 10.83°). Results are very similar for the fixed net stations. Bottom complexity values for the Bongo stations (mean = 239, SD = 71, min = 147, max = 388) and for the fixed net stations (mean = 287, SD = 86, min = 148, max = 406) showed that the bottom was more complex in the north and around Cape Cerbère (Bongo station 19), and that there was no difference between coastal and shelf stations.

During May, temperature, salinity and density were stable ($T = 15\text{--}17^\circ\text{C}$, $S = 37.8$ psu and $\sigma_t < 28.5$) and homogenous in the water column with little subsurface variation (Fig. 3A). In early June (Fig. 3B), variations of temperature and salinity were marked and the upper layer (0–10 m depth) less saline. The stratification appeared first in the north, as shown by the pycnocline at 5–15 m depth. By late June, salinity variations decreased but temperature variations still persisted, and a second, deeper, pycnocline appeared at 20–25 m depth (Fig. 3C). The upper layer (0–10 m depth) was already homogenous. From July, the stratification was stable: the upper layer extended (0–20 m depth) and was homogenous above the pycnocline. Temperature variations were notable above the pycnocline but salinity changes occurred only at the pycnocline depth. During summer, surface temperature reached 25°C and salinity was stable at 38.4 psu, while the pycnocline depth only exhibit noticeable variations below 25 m depth in late July at the southern stations, rising to 5–15 m depth in August. Fluorescence levels were

Table V: Topography descriptors associated to each station for both sampling methods determined by GIS

Sampling method	Station	Depth (m)	Distance to the coast (m)	Slope degrees	Bottom complexity	CP small scale	CP large scale
Bongo nets	1	16	68	10.83	388	32.79	31.07
	2	33	808	0.51	334	–	–
	3	20	152	7.54	166	3.38	12.07
	4	35	497	3.59	194	–	–
	5	22	409	3.94	231	14.25	68.28
	6	39	1732	0.88	251	–	–
	7	23	270	6.08	200	20.15	36.80
	8	40	971	2.11	248	–	–
	9	26	600	7.85	147	19.90	31.21
	10	39	803	4.16	184	–	–
	11	25	286	5.31	163	10.44	45.50
	12	38	653	2.59	205	–	–
	13	27	189	7.98	173	14.18	25.02
	14	39	507	5.00	195	–	–
	15	16	148	5.83	328	16.65	46.02
	16	48	652	1.26	271	–	–
	17	20	168	6.25	335	18.37	77.93
	Fixed nets	18	44	963	0.00	293	–
1		6	24	10.72	400	32.79	31.07
2		7	38	9.24	238	3.38	12.07
3		8	120	4.86	149	14.25	68.28
4		8	84	6.58	241	20.15	36.80
5		7	73	6.10	232	19.90	31.21
6		7	49	7.73	174	10.44	45.50
7		8	47	10.88	406	14.18	25.02
8		7	53	6.46	391	16.65	46.02
9		9	78	6.94	350	18.37	77.93
10		58	1434	6.78	272	–	–
11		42	948	1.85	307	–	–
12	51	1654	1.01	278	–	–	

CP, coast profile, which is influential for nearshore stations.

generally low. Few variations in time or space were recorded. However, from the establishment of the pycnocline and during the following 2–3 weeks (late June–early July), high values of fluorescence were observed in the deeper layer. The gradient began exactly at the pycnocline depth and increased toward the bottom for almost all stations. Later in summer, this feature was observed again but much more sporadically.

Wind and current data during the study period are shown in Fig. 4. Most of the time, the study area experienced northern winds (Fig. 4A), with greater strength in spring than in summer. Southerly wind events were much less frequent, localized and had less intensity. Currents recorded at 3 m depth generally followed the wind patterns (Fig. 4C). However, two differences were noted: northward current speeds were similar to those of southward currents, and northward events lasted longer for current than wind. In addition, transitional currents between northward and southward flows were almost always westward, i.e. in the direction of the shore. Subsurface currents (1 m depth) were much more variable in direction (Fig. 4B). On average, they were also 2.5 times stronger than recorded at 3 m depth.

Eggs and larvae

Around 275 000 eggs were sorted, of which 42 000 were identified. Larvae were identified to the lowest possible taxa. Over 43 000 larvae were identified in Bongo net samples and over 23 000 in fixed net samples.

Egg and larval spatio-temporal assemblages are shown in Tables I and IV, respectively.

The two most abundant egg categories are *Coris julis* and category 9 in both Bongo and fixed nets. Anchovies (*Engraulis encrasicolus*) and category 7 are also found in abundance in the Bongo nets. Dusky grouper (*Epinephelus marginatus*) and *Scorpaena* sp. were frequently caught in the fixed nets. The most abundant larvae for both sampling methods were Clupeiforms (dominated by anchovies) and Blennidae. Sparidae, Gobidae, Labridae and Gobioidae were frequent in the Bongo nets as well.

The season and the week were identified as the dominant temporal scales influencing egg and larval densities (Fig. 2). Time had a greater influence than space for all data sets, although the influence of space was substantial, particularly in summer. The influence of space was also more obvious in fixed net data sets than in Bongo

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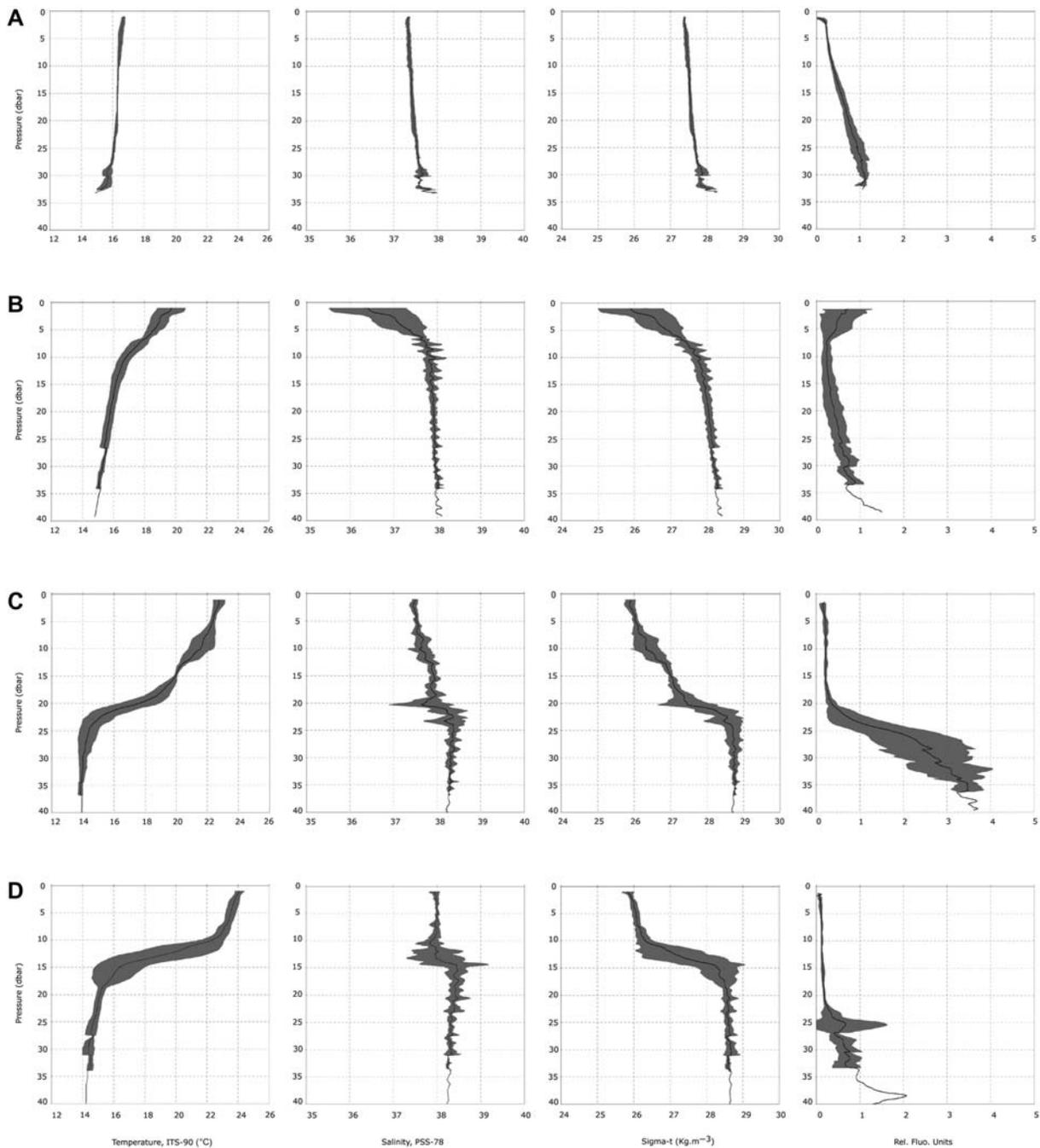


Fig. 3. Vertical profiles for temperature (**A**), salinity (**B**), density (**C**) and fluorescence (**D**), collected near Station 4 of fixed nets in the middle of the study area, at four characteristic dates. Turbidity not shown because of its homogeneity.

data sets. Moreover, models demonstrated the presence of spatio-temporal interactions.

Characteristic spatial homogenous clusters based on ichthyoplankton densities were defined for all data sets and closely matched topographic features. From these clusters, three spatial structures were determined to characterize eggs and larval distributions (Tables I and

II): (i) a north-south gradient, (ii) a coast-shelf separation and (iii) a zone with higher densities than its surroundings. Each larval taxon exhibited one, or in few cases a mix of two, of these spatial structures. Spatial structure presented no particular pattern. Globally, the main eggs spatial structure was a dense zone, particularly in the centre of the study area, while the larval distributions

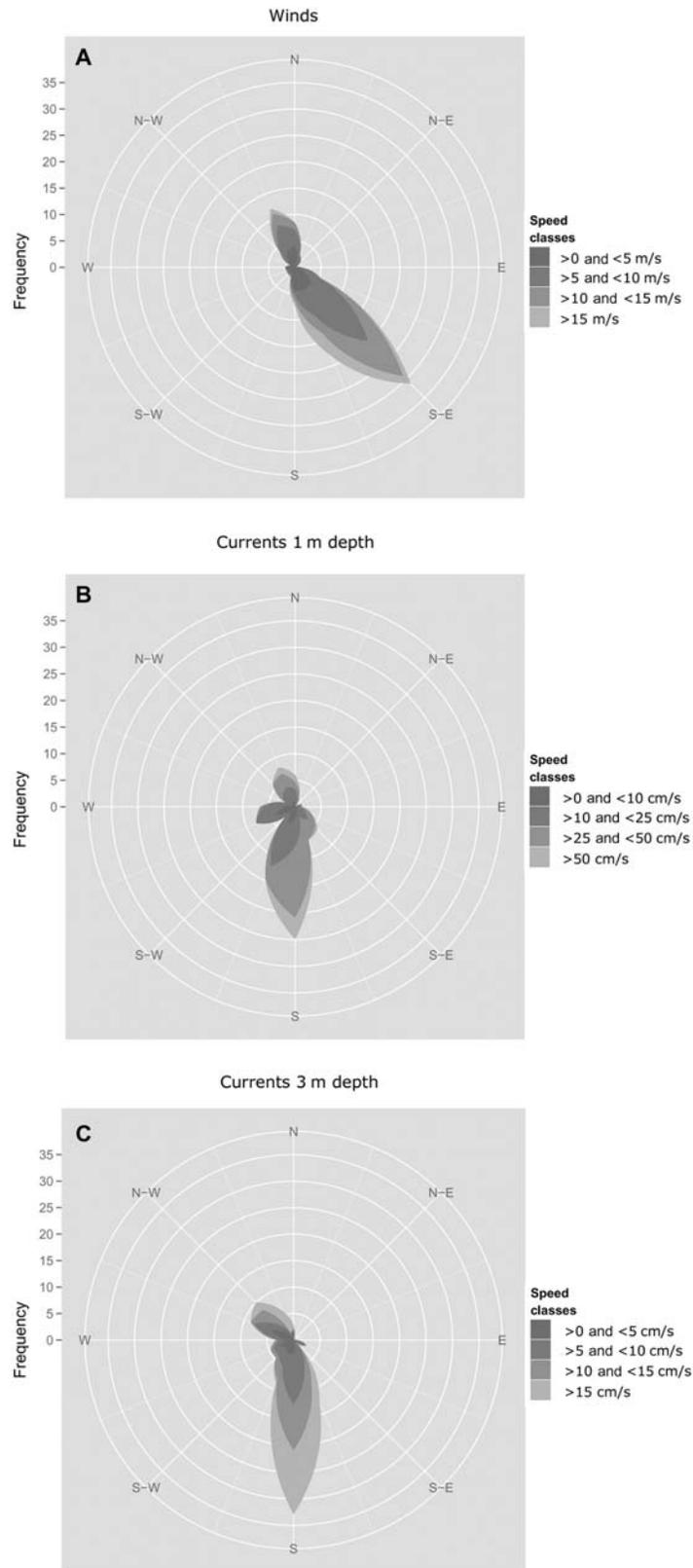


Fig. 4. Wind (A) and currents rose during the study period at 1 m depth (B) and 3 m depth (C). Direction follows wind and current direction. Currents at 3 m depth are the mean of currents at 2, 3 and 4 m depth.

were characterized by coast-shelf separation. In detail, this separation largely dominated in summer for both sampling methods and both developmental stages. For both sampling methods and both developmental stages, the gradient north-south appeared mostly in spring with very few cases in summer.

Relative influences of space, time and environment on ichthyoplankton

The relative contributions of the three explanatory matrices (space, time and environment) and their combined effects on the variability of eggs and larvae are shown in Table VI. Negative variances estimated by adjusted R^2 were due to sampling error around a true population value of 0 (P. Peres-Neto, personal communication), and corresponded to a null contribution of the fraction to the overall variability.

According to RDA, the total explained variability ranged from 40.26 to 67.26% in the six data sets. On average, this total explained variability was substantially higher for the eggs (54.47%, SD = 11.17) than for the larvae (41.43%, SD = 1.11). However, there were no differences between Bongo nets and fixed nets, or between spring and summer. The environment contributed to most of the variability, either in its pure form (Bongo data sets) or in combination with space (fixed net data sets). The combined effect of time and environment also significantly influences both Bongo egg data

sets. In total, the environmental contribution ranged between 33.57 and 61.95% of the ichthyoplankton variability. In contrast, there is no influence of the combined effect of the three matrices and the combined effect of space and time was always negligible. Pure time and space effects explained low fractions of the total variability as well (Table VI). However, because of their combined effect with the environment, time and space may have contributed to an important fraction of the variation in some data sets (from 3.45 to 32.81% and from 3.02 to 31.75%, respectively).

Table VII shows that two environmental factors prevailed, both in term of explained variation and/or occurrences in the models: the depth and the current direction (mostly when measured at 1 m depth averaged on the sampling day). Depth appears in all models, whereas current direction appeared in five out of six models and had the most explanatory power of all factors when used solely in the model. Current speed had little or no influence on ichthyoplankton densities. Fluorescence was also present in five out of six models, but had much less explanatory power. The best descriptor for this factor was the fluorescence averaged above the pycnocline. Density and temperature were the two other hydrological factors contributing to eggs and larval densities. Nevertheless, hydrological factors generally account for little of the explained variance. The contribution of winds is difficult to separate from that of currents, since many cases of collinearity between these

Table VI: Estimated percentages of variation in RDA explained by environmental (E), temporal (T) and spatial (S) fractions using adjusted R^2 for the six data sets

Data set	Environment (E)	Time (T)	Space (S)	E-T	S-T	E-S	E-S-T	Total explained variation	Residuals
Bongo net spring eggs	29.71	3.57	1.17	30.96	0.57	3.58	-2.29	67.26	32.74
Bongo net summer eggs	26.08	2.62	6.02	9.56	0.74	2.36	-0.74	46.65	53.35
Fixed net eggs	11.99	2.08	1.39	3.68	0.28	31.55	-1.46	49.50	50.50
Bongo net spring larvae	26.06	6.07	1.91	3.00	0.91	5.92	-1.42	42.46	57.54
Bongo net summer larvae	34.21	1.04	3.37	2.47	-0.18	0.53	0.14	41.57	58.43
Fixed net larvae	14.33	0.07	1.11	5.20	-0.26	20.15	-0.35	40.26	59.74

Explanations for negative variances are given in the text and correspond to a null contribution.

Table VII: Descriptors selected in RDA models with higher explanatory power for the six data sets according to each source of variation

Data set	Environment	Time	Space
Bongo net spring eggs	Depth+CurDirD3m+WindDirD+FluoAbPycn+Sal20m	Week	X+Y+XY+Y ²
Bongo net summer eggs	Depth+CurDirD1m+WindDirW+DensSubSurf+TempSubSurf+Fluo20 m	Week	Y ²
Fixed net eggs	Depth+CurDirD1m+CoastProfLarge+DensAbPycn	Week	X+Y ³
Bongo net spring larvae	Depth+CurDirD1m+BottComp+Temp20m+FluoWatCol	Week	XY ² +Y ³
Bongo net summer larvae	Depth+CurDirD1m+CurDirD3m+DensSubSurf+Temp10m+FluoAbPycn	Week	X+Y+XY+Y ²
Fixed net larvae	Depth+WindSpdW+WindDirD+CoastProfLarge+FluoAbPycn	Week	X+Y

Codes are given in Tables III and IV, X and Y correspond to longitude and latitude, respectively. The "total explained variation" is the sum of all previous parcels.

two factors were detected in the RDA. For all data sets, wind and current contributions were similar, but current explanatory power was generally slightly higher. This is why winds were less frequent in the models. The wind direction appeared to be more important than its speed. The combination of wind and current directions is characteristic of Bongo egg data sets. The coast profile at large scale influences both fixed net eggs and larvae highlighting the differences between the two sampling methods.

DISCUSSION

The purpose of this paper is to provide a synoptic snapshot to assess the relative influences of space, time and environment on ichthyoplankton abundance on a typical temperate coastal area, by collecting the broadest possible data. The temporal extent of the study covered the period when most species spawn (late spring–early summer: Sabatés, 1990b; Somarakis *et al.*, 2002) and extended longer after this spawning peak to cover average larval duration (about 30 days, Macpherson and Raventos, 2006). Similarly, the spatial limit (25 km) lay within the range of appropriate scales for realistic dispersal distance (10–100 km), crucial for population connectivity (Cowen *et al.*, 2000). This work was limited to 1 year and undertaken at a site where inter-annual variability is known to be high. The differences between Bongo net and fixed net sampling lay in, (i) the location of stations with respect to bathymetry which increases the spatial extent of the study to the coastline, (ii) the sampling of the whole water column for Bongo nets or subsurface for fixed nets, which was expected to sample various potential ecological niches and catch various potential species and (iii) passive vs. active filtering, which was expected to bias some developmental stages because of the avoidance effect of passive filtering. However, spatio-temporal variations of winds, currents and water masses were not taken into account and may still play an important role in structuring the assemblages of eggs and larvae.

With so many factors taken into account, the proportions of total variance explained obtained here for the six data sets may appear quite low. Estimates based on adjusted R^2 will always be lower than those based on non-adjusted R^2 . The appropriate number of degrees of freedom is obtained by adjusting for the number of explanatory variables. The more variables used in the set of predictors, the more the adjusted R^2 will be lower than non-adjusted R^2 . Estimates of total explained variation based on non-adjusted R^2 are: Bongo spring eggs (71.99%), Bongo summer eggs

(53.11%), fixed net eggs (57.78%), Bongo spring larvae (51.63%), Bongo summer larvae (48.68%) and fixed net larvae (49.07%). The estimates of the total explained variation for the models are increased by 4.7–9.2% when non-adjusted R^2 are used rather than corresponding adjusted R^2 . These non-adjusted estimates are in the higher range of the total variation explained by environmental variables in RDA (25–48% in Lee *et al.*, 2005) and the middle range of the total variation explained by environmental variables in CCA (83% for the four first axes in Grothues and Cowen, 1999; 25–32% for the first axis in Alemany *et al.*, 2006), reported in the literature for the shelf areas. Nevertheless, the unexplained variation in the analyses remains important, and aside from sampling errors and unaccounted environmental variation, biological factors are likely to add a substantial influence to variability. Not surprisingly, the unexplained variation is more important in the case of larvae, for which unaccounted biological factors such as feeding and swimming ability add new sources of variation. The difficulties encountered in the taxonomic identification work can also explain the lack of relevance of space and time in explaining variability. In order to have a better interpretation of the results, the fact that species live in different habitats, with different biological behaviour and can belong to the same family must be taken into account.

In this study, the temporal evolution of currents and winds were used as descriptors, since the spatial component of variation for these factors was not available. Therefore, their contribution to ichthyoplankton variability can only be assessed based on the temporal dimension. Similarly, the direct effects of topography on eggs and larval distribution are purely spatial. It has been shown that individual influences of time and space were very low, but their combined effect with the environment was substantial in some cases. By comparing Tables VI and VII, similarities and differences in the results can help deduce two links between environmental factors and temporal and spatial variability. First, fixed net data sets are the only ones for which the combined space-environment component accounted for a greater degree of variability. They were also the only ones for which the coast profile at large scale is an influence. It seems straightforward that spatial structuring by the environment of eggs and larvae caught in fixed nets is dominant and due to topography. This supports the idea that the influence of the coast profile is limited to the nearshore ecosystem, since the location of stations is the only spatial difference between both sampling methods. Second, the combined time-environment component is only appreciable for Bongo nets eggs data sets, for which the simultaneous effect of winds and

currents appeared in the models. Hence the temporal variation of eggs sampled with Bongo nets is very likely to be caused by temporal variations of winds and currents and also spawning season. However, the short time-scale of wind fluctuations and egg duration may explain why this is not the case for Bongo nets larvae. Explanations why this link is not present for the fixed net data sets, or why in the case of Bongo eggs there is no collinearity between current and wind directions remain unclear.

Fluorescence is generally used as a proxy to estimate variations in phytoplankton concentration. Egg duration in the Mediterranean is generally very short (24–36 h, Marinaro, J-Y, Perpignan, personal communication), and may reflect timing spawning to ensure optimum environmental conditions for coastal species (Tremblay and Sinclair, 1984). The strong discontinuity in ichthyoplankton communities between both seasons (3 July for eggs and 23 June for larvae) occurs when stratification of the water column has established and stabilized (Fig. 2). Stratification has been identified as a prevailing factor on the shelf (Franco-Gordo *et al.*, 2002; Lee *et al.*, 2005), but Gray (Gray, 1996) found no effect of the thermocline on the vertical distribution of larvae. Here, density and temperature have been found to play a more important role than salinity. On the other hand, the best descriptor for the fluorescence factor is the average above the pycnocline. All these results can support the hypothesis that the pycnocline has a greater influence on ichthyoplankton horizontal distribution than the halocline or thermocline, as has been already shown by Munk *et al.* (Munk *et al.*, 2004). However, the relatively poor influence of hydrological descriptors requires that this be treated with caution. This is possibly related to the position of the CTD casts in the middle of the transect instead of being placed at each station, or because of small-scale temporal oscillation of the different parameters.

The results do, however, unequivocally demonstrate the influence of depth for all the data sets. The influence of depth on ichthyoplankton assemblages has been widely documented on temperate continental shelves and slopes elsewhere (e.g. Sabatés, 1990b; Espinosa-Fuentes and Flores-Coto, 2004; Auth and Brodeur, 2006), but it has only been suggested as a factor in the coastal domain (Koutrakis *et al.*, 2004). In fact, the data sets cover the nearshore area as well as the edge of the continental shelf, and the “depth” factor primarily discriminates both oceanographic domains. Since this influence is also detected in the Bongo data sets (minimum sampling depth 20 m), belonging to the nearshore area, the limit between both domains should be located around 25–30 m depth. This result is

consistent with numerical modelling results of Guizien *et al.* (Guizien *et al.*, 2006) who, in the same location, found separated nearshore and offshore dispersals of the annelid polychaete *Owenia fusiformis* larvae due to a physical barrier located between 20 and 30 m depth.

Other factors identified as influential by this study are the wind and current directions. The key element here is that the direction, much more than the speed of winds and/or currents, contributes to structure the ichthyoplankton community. Both wind (e.g. Dempster *et al.*, 1997; Dalley *et al.*, 2002) and current (e.g. Helbig and Pepin, 2002; Sanchez-Velasco *et al.*, 2006) factors are widely reported to have a major influence on pelagic eggs and larval distributions. All RDA models in this study have a current or wind direction as the second most explanatory environmental variable (Table VII). However, in most investigations, only speed is taken into account, probably because the circular nature of direction data prevents them to be included in standard statistical analyses. In other studies, U and V components of velocity have been used as descriptors (Dalley *et al.*, 2002). While they do take into account direction, they do not allow explicit discrimination of the relative influences between speed and direction. In the case of wind-driven current circulation which occurs in most coastal systems, the circulation is highly variable and this result has a strong implication for larval dispersal.

In conclusion, depth, wind and current directions as well as the topographic profiles of the coastline are among the factors most influential for ichthyoplankton abundance in this area of the north-western Mediterranean rocky shore. These results suggest that nearshore and continental shelf systems are separated, without being closed, and that alongshore transport of coastal eggs and larvae prevails. Since the direction of wind and/or current is dominant over their speed, the implications for dispersal of nearshore fishes in their early life are the following: if directions remain stable enough in comparison to pelagic life duration, there will be a coastal accumulation with advection in a direction parallel to the coast. If wind directions are unstable and change, changes in currents flowing toward the coast, eggs and larvae will be moved away and back, with a final result of retention near their spawning place. These outcomes can be enhanced or countered by the current speed: if the current speed is low when its direction is stable, as is usually the case in summer in the Mediterranean, transport will still be limited. Therefore, we propose the hypothesis that the nearshore ecosystem of rocky shores can be favourable for coastal accumulation and/or retention of ichthyoplankton, at least for a certain period of the larval life.

ACKNOWLEDGEMENTS

We also wish to thank the crew of the Research vessel “*Nereis IP*”, all the people who helped in field collection, sorting and identification. Météo-France kindly provided wind data. We are very grateful to Pedro Peres-Neto for his advice in interpreting fractions with negative variances and for his comments on the draft of this manuscript. We also thank Andrew L. Stewart, Clive D. Roberts, Vincent Zintzen and the two anonymous referees for language correction, advice and comments that enhanced this paper.

FUNDING

We thank the European community during the Biomex Programme under contract QRTL-2001-0891 and the Cerbere-Banyuls MPA for funding.

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