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

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Abstract:

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 ichthyoplantkon communities at nearshore stations, near the Cerbère-Banyuls Marine Protected Area (France), during spring and summer 2003. Resulting datasets were analyzed 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 dataset 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 30m depth and is separated from the inner continental shelf. We propose the hypothesis that the rocky shore ecosystem is favorable 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).

Favorable 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; Sclafani 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 20m 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; Azeitero 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 30m 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, Lopez-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 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 9 radial transects coupling Bongo and fixed net collection sites. For the Bongo net collections, a grid of 18 stations (Fig. 1a) divided in nine transects of two stations each from the coast (on the 20

m isobath) to offshore (on the 40 m isobath). This framework was surveyed 12 times from May 7th to August 14th. 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 10m above the ocean floor (i.e., the "max depth") followrd by an up tow performed between this maximum depth and the surface. During this up tow, 3 horizontal tows of 5 minutes 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 (Sabatès, 1990a, Sabatès et al., 2007). 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 20m and 40 m within the sampling area. The catch of each tow (2 replicas) was sieved and fixed directly on board with 4% formalin-seawater leading to a total of 186 samples (one of the two replicas) analyzed from Bongo collections. The filtered volume was calculated by using flowmeters and the following formula:

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

The mean volume filtered was 268 ± 70 m^3 (mean ± SD).

At the same time as the Bongo net collections, fixed plankton nets (300 µm 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 to 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. (2001), is described in 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 July, 22nd to August, 20th. 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 harbor, leading to a total of 76 samples analyzed 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 2cm.s^{-1} were removed from further analysis. The mean volume filtered was 1185 ± 1392 m^3. The filtered volume was very variable depending on the current speed at each location (min=199 m³, max=5984 m³).

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 center of the area (Fig. 1b), recorded current strength and directions for the whole water column every 30 min. Wind data was kindly provided by Meteo-France. Strength and direction were recorded at 3-hour intervals at Cap Bear (Fig. 1). Bathymetric data were collected at a 1x1m resolution using multi-beam sonar, along the French coast up to the 30m 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; Sabatès, 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 1). 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 (MRT; 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 dataset. Results (Figure 2) show that variations between spring and summer lead to marked discontinuities in eggs and larvae. Both Bongo net datasets were split according to the season. The week has been also demonstrated to be the major temporal scale in density variations and was considered as the relevant time descriptor. As a result, six datasets were analyzed (Table 1 and 2). For eggs, eight 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 centered on the origin to reduce collinearity between terms following Legendre and Legendre (1998). Nine terms of a cubic surface trend analysis were included (X, Y, X^2, Y^2, XY, X^3, Y^3, X^2Y and Y^2X) (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 (Table 3 and Table 4). These cover four categories:

1) **Topography** (Table 3): 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 artifacts. 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 (CV around 0.30) of the three distances tried (100, 150 and 200 m) and found to be homogeneous between Bongo and Fixed nets.
- the *coast profiles* at *small and large scale* were used to characterize the topographic features of the coastline (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 artifacts. A 600 m and 2500 m radius circle was used for small and large scale respectively, centered 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 nearshore stations to the coast, the large scale distance to the radius of the biggest topographic feature of the area (Banyuls Bay).

2) **Hydrology** (Table 4): *Temperature*, *salinity*, *density*, and *fluorescence* were measured with the CTD. For each parameter, six descriptors were considered: values at 1 m, 10 m 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 3) and 4) **Currents** (Table 3): 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: The first was the average on the day when sampling occurred. The second is the average over three 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 datasets by compiling the mean of three depths (2 m, 3 m 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 analyze the partitioning of variance between spatial, temporal and environmental components, following Anderson and Gribble (1998). This is an extension of 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 (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 5 for both sampling methods. Coast profiles (CP) quantitatively describes topographic features such as capes, bays and straight coastlines in front of nearshore stations. At the small scale, all coast profiles (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 coast profiles (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 nets 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=15-17 °C, S=37.8 psu and σ_t < 28.5) and homogenous in the water column with little subsurface variation (Fig. 3.I). In early June (Fig. 3.II), variations of temperature and salinity were marked and the upper layer (0-10m depth) less saline. The stratification appeared first in the north, as shown by the pycnocline at 5-15m depth. By late June, salinity variations decreased but temperature variations still persisted, and a second, deeper, pycnocline appeared at 20-25m depth (Fig. 3.III). The upper layer (0-10m depth) was already homogenous. From July, the stratification was stable: the upper layer extended (0-20m 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 25m depth in late July at the southern stations, rising to 5-15m depth in August. Fluorescence levels were 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 Figure 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 3m 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 (1m depth) were much more variable in direction (Fig.4b). On average they were also 2.5 times stronger than recorded at 3m 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 1 and 4 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 Gobiesocidae 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 (Figure 2). Time had a greater influence than space for all datasets, although the influence of space was substantial, particularly in summer. The influence of space was also more obvious in fixed net datasets than in Bongo datasets. Moreover, models demonstrated the presence of spatio-temporal interactions.

Characteristic spatial homogenous clusters based on ichthyoplankton densities were defined for all datasets and closely matched topographic features. From these clusters three spatial structures were determined to characterize eggs and larval distributions (Table 1 and 2): 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 center of the study area, while the larval distributions 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 6. Negative variances estimated by adjusted R^2 were due to sampling error around a true population value of 0 (P. Peres-Neto, *comm. pers.),* 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 datasets. 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 datasets) or in combination with space (fixed net datasets). The combined effect of time and environment also significantly influences both Bongo egg datasets. 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 6). However, because of their combined effect with the environment, time and space may have contributed to an important fraction of the variation in some datasets (from 3.45% to 32.81% and from 3.02% to 31.75%, respectively).

Table 7 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 1m 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 two factors were detected in the RDAs. For all datasets, 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 datasets. 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, McPherson 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 one 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 datasets 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% for 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 behavior 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 Table 6 and Table 7, similarities and differences in the results can help to deduce two links between environmental factors and temporal and spatial variability. First, fixed net datasets 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 datasets, 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 datasets, 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 (24-36h, Marinaro, J-Y, Perpignan, *pers. comm.*), and may reflect timing spawning to ensure optimum environmental conditions for coastal species (Tremblay and Sinclair, 1984). The strong discontinuity in ichthyoplantkon communities between both seasons (July, 3rd for eggs and June, 23rd 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 (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. (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 datasets. 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 datasets 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 datasets (minimum sampling depth 20 m), belonging to the nearshore area, the limit between both domains should be located around 25-30m depth. This result is consistent with numerical modeling results of 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 20m and 30m 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 7). 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 Northwestern 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 it's 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.

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Legends for Tables and Figures

Table 1: Species and mean densities (± SD) of egg categories in number of egg per 1000 m³. Spatial structures of eggs have been identified with spatial models. Code: N north, S south, C center, N/S north-south gradient, Co/Sh coast-shelf structure. + zone of high density and ? unidentified structures. ✓ variable used in the dataset.

Table 2: Frequent and locally abundant larval taxa selected for the two sampling methods. 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 center, N/S north-south gradient, Co/Sh the coast-shelf structure. **+** zone of high density and **?** unidentified structures. ✓ variable used in the dataset.

Table 3: Topography, wind and currents descriptors used in analyses and corresponding abbreviations.

Table 4: Hydrology descriptors used in analyses and corresponding abbreviations

Table 5: Topography descriptors associated to each station for both sampling methods determined by GIS. CP coast profile and is influential for nearshore stations.

Table 6: Estimated percentages of variation in RDA explained by environmental (E), temporal (T) and spatial (S) fractions using adjusted R^2 for the six datasets. Explanations for negative variances are given in the text and correspond to a null contribution.

Table 7: Descriptors selected in RDA models with higher explanatory power for the six datasets according to each source of variation. Codes are given in Table 3 and 4, X and Y correspond to longitude and latitude respectively. The “total explained variation” is the sum of all previous parcels.

Figure 1: Study area with Bongo net (a) and fixed net (b) stations. Stars indicate CTD sampling stations and the grey triangle is the position of the ADCP. Dotted line represent the MPA border.

Figure 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.

Figure 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. Note: Turbidity not shown because of its homogeneity.

Figure 4: Wind rose (a) and currents roses during the study period at 1m depth (b) and 3m depth (c). Direction follows wind and current direction. Currents at 3m depth are the mean of currents at 2, 3 and 4m depth.

Table 1

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

Table 2

Taxa	*Bongo net Densities*		*Fixed net Densities*		*Bongo net Spring spatial structures*			*Bongo net Summer spatial structures*			*Fixed net spatial structures*		
	Mean	SD	Mean	SD									
Blennidae	93	± 115	28	± 46	C	+	✓	Co/Sh	-	✓	C	+	✓
Callyonimus sp.	16	± 18	1	± 2	N	+	✓	Co/Sh	-	✓	N/S	-	✓
Trachurus sp.	20	± 35	1	± 2	C S	+ -	✓	S	+	✓	Co/Sh	-	✓
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	+	✓
Scomber japonicus	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	+	✓
Anguiliforms	10	± 36	-	-	-	-	-	Co/Sh	-	✓	-	-	-
Arnoglossus sp.	3	± 8	-	-	N/S	-	✓	?	-	✓	-	-	-
Spicara sp.	5	± 11	-	-	C	+	✓	C	+	✓	-	-	-
Cepola macrophthalma	8	± 22	-	-	N/S	-	✓	Co/Sh	-	✓	-	-	-
Gobiesocidae	26	± 121	5	± 16	N/S Co/Sh	- -	✓	Co/Sh	-	✓	N/S Co/Sh	- -	✓
Mugilidae	8	± 15	1	± 2	-	-	-	C	+	✓	Co/Sh	-	-
Mullus sp.	3	± 10	-	-	-	-	-	Co/Sh	-	✓	-	-	-
Thunninae	5	± 12	1	± 3	-	-	-	Co/Sh	-	✓	Co/Sh	-	-
Scorpaena sp.	3	± 9	2	± 4	-	-	-	N/S	-	✓	N/S	-	-
Serranus hepatus	8	± 20	-	-	N	+	✓	Co/Sh	-	✓	-	-	-
Trypterigion sp.	9	± 34	-	-	-	-	-	Co/Sh	-	✓	-	-	-
Chromis chromis	-	-	4	± 22	-	-	-	-	-	-	?	-	-

Table 3

Topography		Wind		Currents	
Abbreviation	Descriptor	Abb.	Descriptor	Abb.	Descriptor
Depth	Depth	WindDirD	Wind direction averaged on the sampling day	CurDirD1m	Current direction at 1m averaged on the sampling day
DistCoast	Distance to the coast	WindDirW	Wind direction averaged 3 days before sampling	CurDirD3m	Current mean direction at 3m averaged on the sampling day
Slope	Bottom slope	WindSpdD	Wind speed averaged on the sampling day	CurDirW1m	Current direction at 1m averaged 3 days before sampling
BottComp	Bottom complexity	WindSpdW	Wind speed averaged 3 days before sampling	CurDirW3m	Current mean direction at 3m averaged 3 days before sampling
CoastProfSmall	Coast profile at small scale	-	-	CurSpdD1m	Current speed at 1m averaged on the sampling day
CoastProfLarge	Coast profile at large scale	-	-	CurSpdD3m	Current mean speed at 3m averaged on the sampling day
-	-	-	-	CurSpdW1m	Current speed at 1m averaged 3 days before sampling
-	-	-	-	CurSpdW3m	Current mean speed at 3m averaged 3 days before sampling

Table 4

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

Table 5

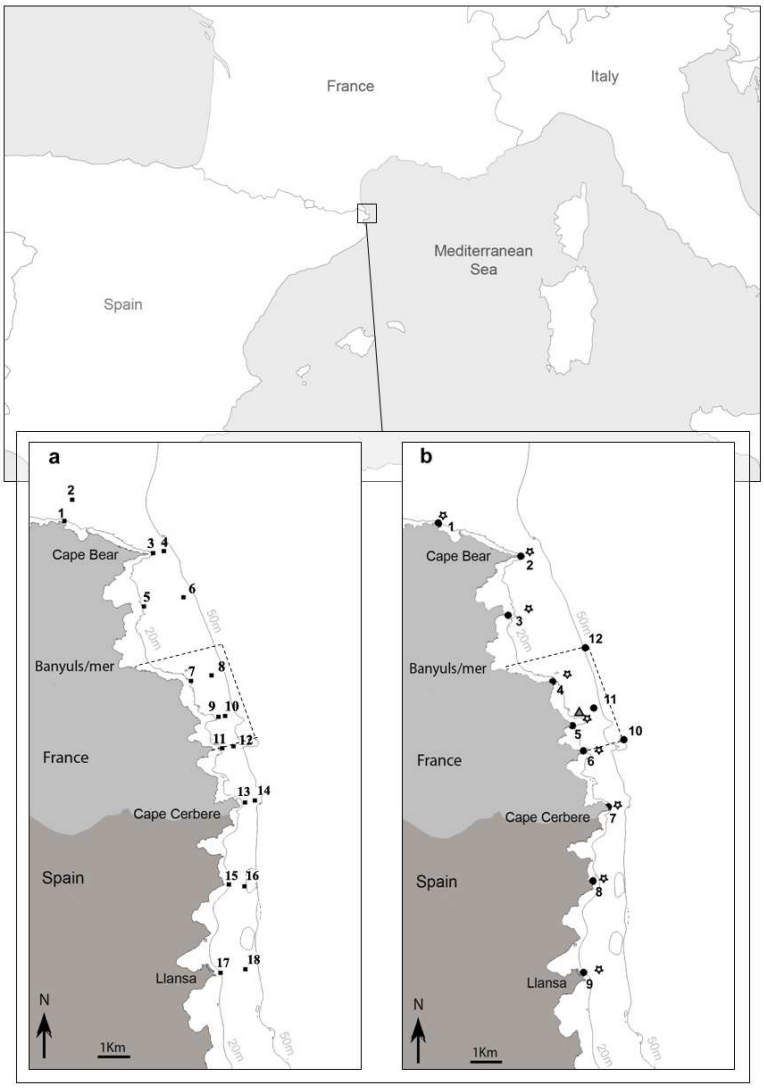
Sampling method	Station	Depth (m)	Distance to the coast (m)	Slope degrees	Bottom complexity	CP Small scale	CP Large scale
Bongo nets	1	16	68	10,83	388	32,79	31,07
	2	33	808	0,51	334	-	-
	3	20	152	7,54	166	3,38	12,07
	4	35	497	3,59	194	-	-
	5	22	409	3,94	231	14,25	68,28
	6	39	1732	0,88	251	-	-
	7	23	270	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
	18	44	963	0,00	293	-	-
Fixed nets	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	-	-

Table 6

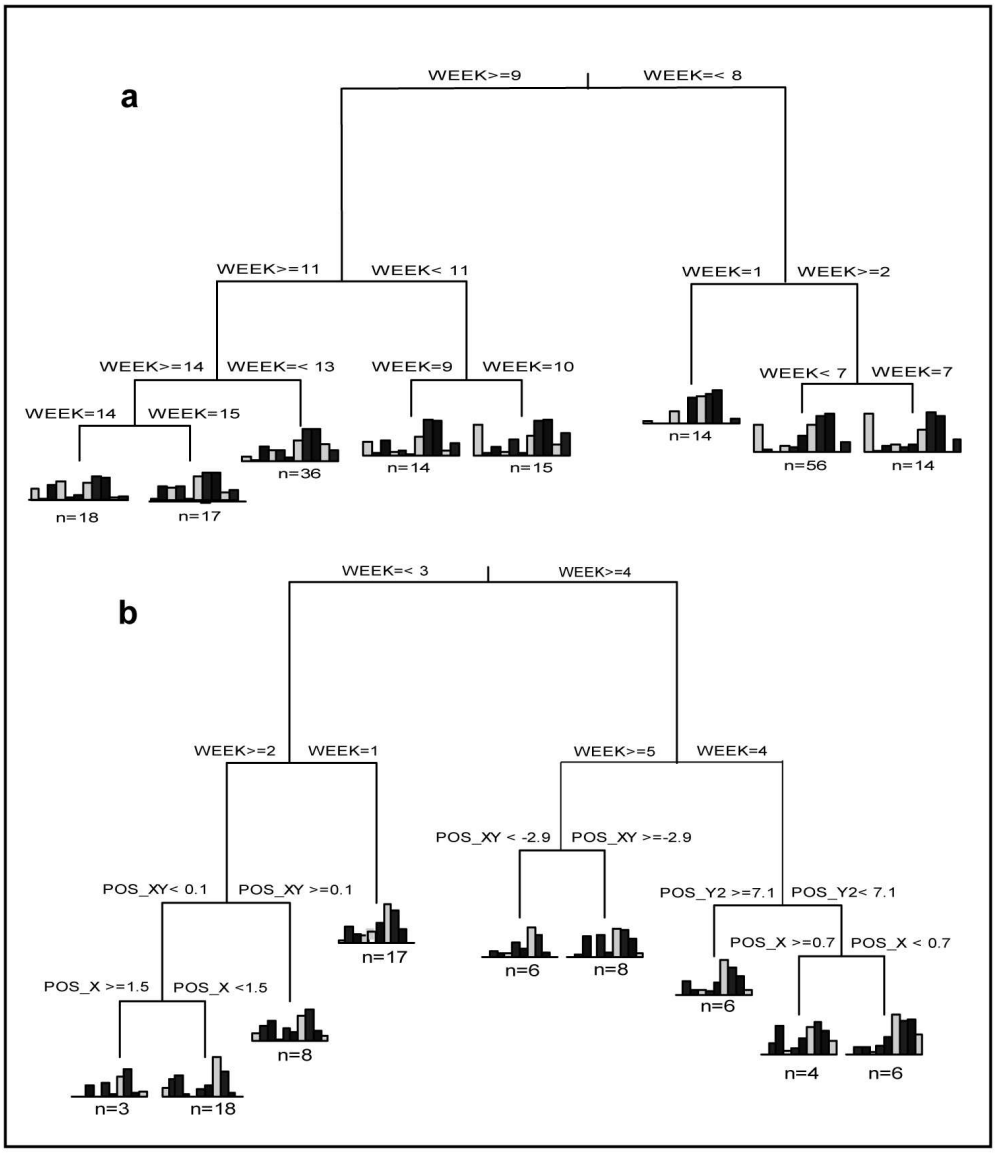
Dataset	Environ-ment (E)	Time (T)	Space (S)	E - T	S - T	E - S	E - S - T	Total Explained Variation	Residuals
Bongo net Spring Eggs	29.71	3.57	1.17	30.96	0.57	3.58	-2.29	67.26	32.74
Bongo net Summer Eggs	26.08	2.62	6.02	9.56	0.74	2.36	-0.74	46.65	53.35
Fixed net Eggs	11.99	2.08	1.39	3.68	0.28	31.55	-1.46	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

Table 7

Dataset	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 + Fluo20m	Week	Y^2
Fixed net Eggs	Depth + CurDirD1m + CoastProfLarge+ DensAbPycn	Week	X + Y3
Bongo net Spring Larvae	Depth + CurDirD1m + BottComp + Temp20m + FluoWatCol	Week	$XY^2 + Y3$
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



266x355mm (96 x 96 DPI)



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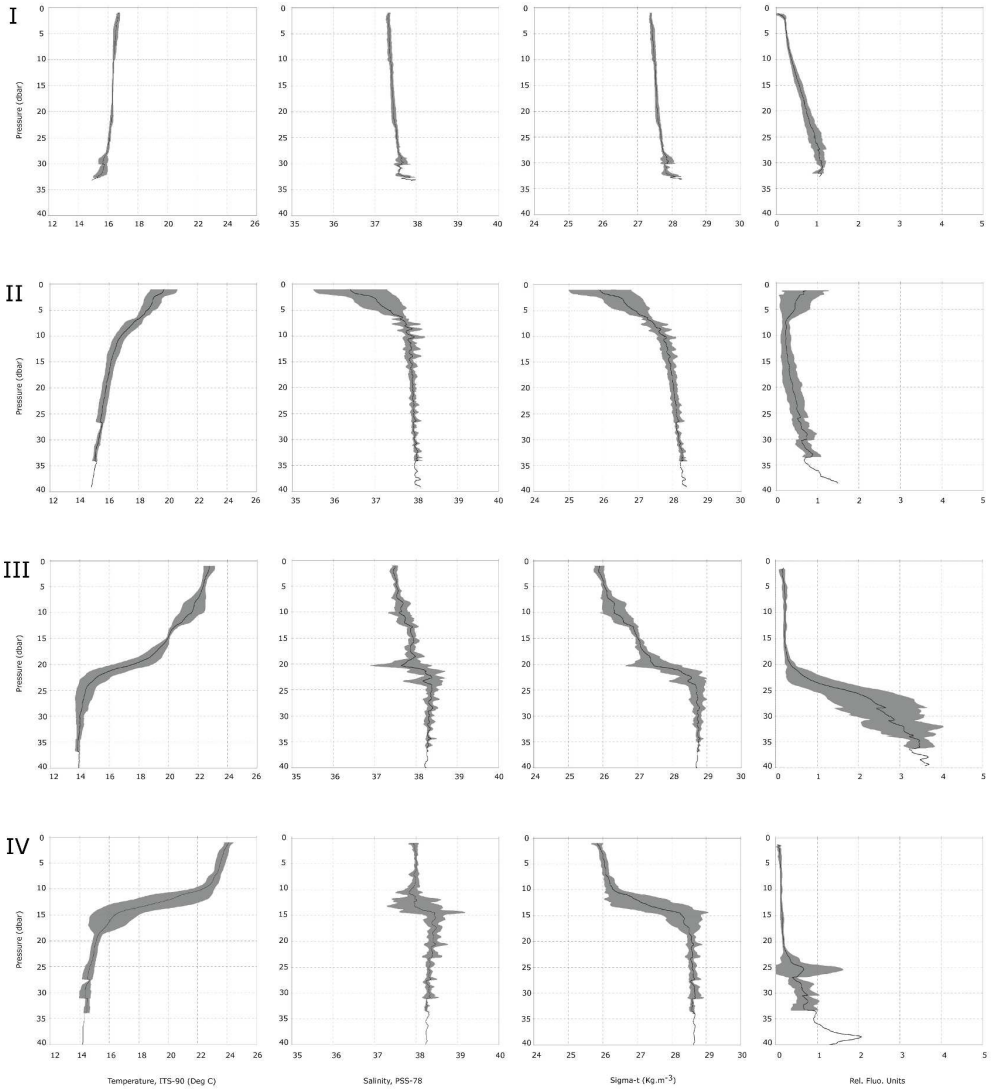

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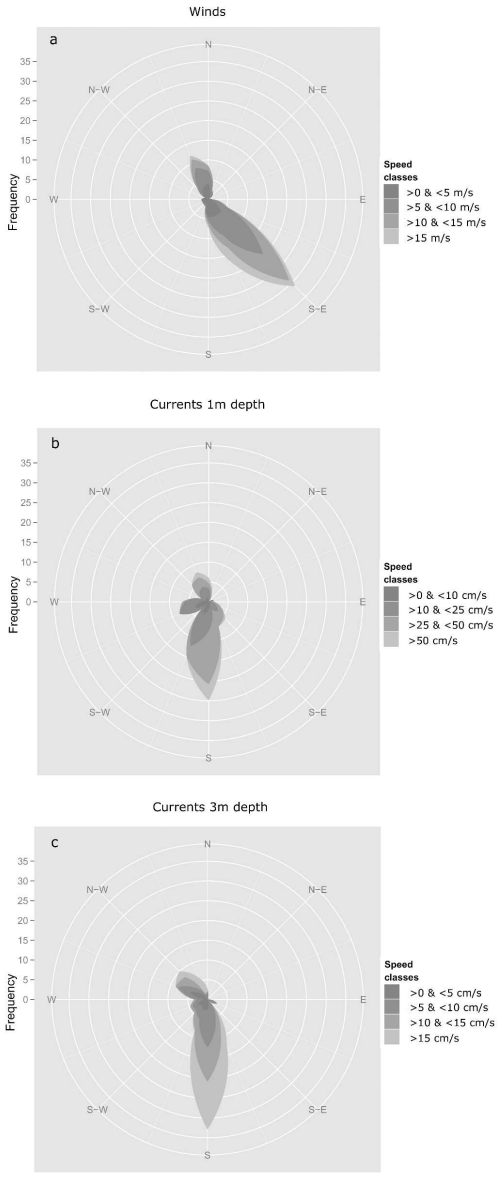

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