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**“Caracterización de la distribución espacial y temporal del meroplancton  
en la costa asturiana”**

**“Characterization of the spatial and temporal distribution of meroplankton  
in the Asturian coast”**

**TESIS DOCTORAL**

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A mis abuelos, Obdulia y José Antonio.



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“No es la última ola con su salado peso  
la que tritura costas y produce  
la paz de arena que rodea el mundo:  
es el central volumen de la fuerza,  
la potencia extendida de las aguas,  
la inmóvil soledad llena de vidas.  
Tiempo, tal vez, o copa acumulada  
de todo movimiento, unidad pura  
que no selló la muerte, verde víscera  
de la totalidad abrasadora.”

Pablo Neruda, de “El gran océano”.

“He sido un niño pequeño que, jugando en la playa, encontraba de tarde en tarde un guijarro más fino o una concha más bonita de lo normal. El océano de la verdad se extendía, inexplorado, delante de mi.”

Isaac Newton.







La fase larvaria de los animales bentónicos costeros forma una componente importante en la comunidad planctónica marina denominada meroplancton. Durante mucho tiempo, la capacidad de estos organismos para nadar se ha considerado irrelevante frente a la turbulencia promedio del ambiente pelágico, siendo por tanto equiparable a la de una partícula pasiva que deriva con las corrientes. Por lo tanto, la distribución del meroplancton se ha estudiado en relación a las corrientes oceánicas y los procesos que las originan, como los afloramientos costeros. Las distancias de dispersión resultantes responden a escalas de cientos de kilómetros, lo que concuerda en apariencia con la función ecológica fundamental de éste estadio: la dispersión y conectividad entre las poblaciones adultas. Sin embargo, nuevos estudios desde distintos campos como la ecología evolutiva, la genética y la oceanografía costera sugieren que la dispersión a larga distancia no es la regla general sino la excepción, y que no es un requisito primordial en el sostenimiento de las metapoblaciones. La retención de las larvas en la franja costera es el resultado de complejos comportamientos de natación activa en la vertical. Hay también un componente pasivo en dicha retención: la misma costa es refractaria a las corrientes marinas lo que deriva en la formación de masas de agua diferenciadas muy costeras caracterizadas por una circulación más lenta y mayor tiempo de residencia (Franja Límite Costera).

Las altas abundancias del meroplancton en la franja costera implican que el estudio de sus distribuciones ha de desarrollarse a escalas espaciales más pequeñas y con mayor resolución. Solo recientemente se ha comenzado a muestrear exhaustivamente los primeros cientos de metros desde la línea de costa y a entender los procesos que afectan a la distribución de las larvas en este ambiente. La topografía costera dista mucho de ser uniforme a lo largo del litoral, lo que introduce una heterogeneidad potencial en la capacidad de retención de las franjas de agua costera que podría repercutir en las distribuciones meroplanctónicas. El comportamiento activo de las larvas puede llevar a su acumulación en zonas de convergencia frontal, donde la natación contra la corriente vertical de hundimiento permite al organismo permanecer en superficie y agregarse. Estos frentes costeros pueden además transportar dichas agregaciones si son móviles, como es el caso de las estructuras generadas por ondas internas que se propagan en la termoclina. Otro factor importante es la escala temporal a la que interpretar las distribuciones. Los procesos de acumulación y transporte en frentes ocurren en pocas horas a través de la plataforma costera y las corrientes generadas por el viento cambian en unos pocos días. Pero para entender su relevancia es necesario integrar estos procesos respecto al tiempo al que la larva está sometida a los mismos en el plancton, consideración

esta que pocas veces se tiene en cuenta. Por otro lado, es necesario el conocimiento de la estacionalidad de las larvas y de los procesos oceanográficos costeros para entender su posible efecto en los patrones de distribución y dispersión.

En el **Capítulo 1**, se aborda la caracterización de la distribución de los taxones más comunes a través de la plataforma costera por medio de transectos mensuales, lo que también permite una aproximación a la estacionalidad de los procesos costeros y de la comunidad larvaria. En lo relativo a la estacionalidad, la diferenciación más clara se estableció entre las comunidades de verano y primavera con nauplius del cirrípedo *Verruca stroemia* y veliger de moluscos como taxones más abundantes, respectivamente. Este patrón podría obedecer a cambios en la estructura de tamaños del alimento potencial, es decir, el fitoplancton, durante el periodo de estratificación. Por otro lado, al extraer la variación temporal y analizar las distribuciones en el eje costa- océano, las concentraciones de los organismos difieren marcadamente entre especies y estadios. La mayor parte de los taxones más abundantes no muestran variaciones importantes en su posición respecto a la costa con las corrientes inducidas por el viento, lo que en principio se interpreta como el resultado de comportamientos activos a través de la columna de agua que evitan la exportación. Sin embargo, las larvas cypis de *Verruca stroemia* y las veliger de litorínidos se acercan a la costa en situaciones de afloramiento, lo que sugiere que utilizan la corriente de capas profundas. La escala temporal a la que actúan estas corrientes tanto para las cypis como para las veligers es de semanas, equiparable al tiempo de residencia de esos estadios larvarios en el agua. Esta representividad de las escalas temporales relativamente largas muestra que las distribuciones de las larvas han de ser relacionadas con procesos integrados a lo largo de toda su vida en el plancton, especialmente si estos procesos son extremadamente variables durante ese periodo (p.e. el transporte de Ekman en nuestro area de estudio).

En el **Capítulo 2**, examinamos las distribuciones meroplanctónicas a lo largo de 200 kilómetros de costa y relacionamos sus patrones espaciales con las variables oceanográficas clásicas de la columna de agua, pero también con descriptores de la topología costera, cuantificadas por vez primera en este tipo de estudios. Los patrones de autocorrelación espacial de la comunidad larvaria se corresponden con la estructura espacial de las variables de columna de agua que a su vez esta definida por un gradiente Este-Oeste especialmente marcado en Cabo Peñas. Las distribuciones de muchas especies se explican en gran medida por las variables topográficas calculadas a distintas escalas, en detrimento de la

autocorrelación espacial intrínseca por procesos biológicos (p.e. la emisión simultánea de larvas en porciones concretas de la costa). La importancia de estas variables no hidrográficas a escalas diversas, especialmente la orientación y la complejidad de la línea de costa, implica que una parte significativa de la variabilidad no explicada en anteriores estudios puede deberse a efectos topográficos. Estos efectos generan áreas de retención larvaria al Este de los cabos y en líneas de costa simples donde la entrada de larvas podría ser facilitada por una mayor magnitud de la componente perpendicular de las corrientes mareales y una menor anchura de la Capa Límite Costera. A medida que el tiempo de residencia de la larva en el plancton aumenta, aumenta significativamente la influencia de la topografía y disminuye la importancia de la estructura espacial de las variables hidrográficas sobre su distribución. Interpretamos estos resultados como adaptaciones a la gran variabilidad temporal en el ambiente pelágico para periodos largos y/o efectos de retención dependientes del tiempo y dirigidos por la topografía costera.

En el **Capítulo 3**, analizamos la distribución de una gran variedad de especies y estadios larvarios en las inmediaciones de frentes de convergencia muy costeros. Se analizaron 4 de éstos frentes, observándose importantes diferencias en las velocidades de las corrientes que convergen hacia la línea del frente. El proceso hidrográfico causante de la formación de estos frentes es probablemente la progresión hacia la costa de ondas internas que se propagan en la termoclina y alcanzan la superficie. En nuestro area de estudio, el la convergencia frontal parece ser asimétrica, y mucho más marcada en el lado costero del frente, lo que promueve la retención larvaria. Por otro lado, se estudio otro tipo de estructura frontal, probablemente relacionada con la convergencia de corrientes opuestas desviadas por la topografía local, en la que la acumulación sucede potencialmente desde ambos lados del frente. Para todos estos eventos, las distribuciones de las larvas variaron entre especies y estadios desde patrones difusivos a la retención costera, la acumulación en el frente o la retención hacia el mar. La capacidad de agregación de larvas en un frente responde según un patrón unimodal a la ratio velocidad de la larva: velocidad de la corriente de convergencia. Esto sugiere que la acumulación resulta de un compromiso entre la velocidad del organismo y la de la corriente a la que es sometido, con un máximo para valores de la ratio alrededor de 1:3 Por lo tanto, cada taxón larvario se caracteriza por un rango propio de corrientes de convergencia a la que se da su agregación dada su velocidad de natación, lo que evidencia hasta que punto las larvas son activas e influyen en su propia distribución. Las acumulaciones en los frentes de estadios



tardíos podrían ser de gran relevancia en el proceso de reclutamiento en el hábitat adulto ya que todos los frentes se desplazaban en dirección a la costa.

Esta Tesis proporciona una descripción cuantitativa de la distribución del meroplancton a escalas espaciales y temporales ajustadas al ámbito espacial y al tiempo de residencia de éstas larvas en el plancton. Los patrones encontrados apoyan la idea de que la capacidad de natación de las larvas influye directamente sobre los patrones de distribución, lo cual se contrapone a la visión tradicional de las larvas como trazadores pasivos de los movimientos del agua. La natación en contra de la corriente vertical conduciría a la retención en aguas costeras y a la agregación en frentes de convergencia. Nuevos datos de corrientes tomados muy cerca del litoral apuntan al papel de la Franja Límite Costera como atenuadora de las corrientes inducidas por los vientos, contribuyendo probablemente a la retención costera sin necesidad de un comportamiento activo de las larvas (Discusión General). Las distribuciones a lo largo de la costa son dirigidas por procesos pasivos pues la migración vertical no evita ese tipo de transporte; sin embargo, lo reduce potencialmente a través de la retención en costa. Otra importante aportación de este estudio es cuantificar la importancia de la topografía en las distribuciones a lo largo de la costa y proporcionar una primera aproximación paisajística a su estudio.





## General Introduction





## Why a planktonic larva?

Most of the approximately 170,000 species in 23 of the 31 phyla which present living marine forms have indirect development being their life cycles “biphasic” (Young 2002). The first phase from the embryonic development to the metamorphosis is called larva (Hickman 1999) and develops as a free-swimming individual within the so-called meroplankton. Larvae usually differ from the adult in their size, perception of the environment, feeding performance or locomotion.

The preponderance of complex life cycles among marine invertebrates has two possible interpretations in terms of evolutionary biology: 1) larvae may be in fact the primitive, plesiomorphic condition resembling the hypothetical holoplanktonic ancestors from which sessile and mobile-benthic adults evolved or were “added” (the trochaea theory and other “terminal addition” theories: Nielsen 1979, Nielsen & Norrevag 1985, Nielsen 1995, Nielsen 2009); 2) direct life cycles with benthic forms were first and larvae emerged in many different taxa independently and convergently (“intercalation” theories: Salvini-Plawen 1980, Ivanova-Kazas & Ivanov 1988, Rouse 1999, Sly et al. 2003). Although the debate is still open and has to be individualised for each lineage, the probability of independent convergent development of some larval characteristics shared by several phyla, like the ciliar bands in trocophore-like larvae, is low and it is easier to suppose that larvae were first (Nielsen 1995). However, no environmental pressures which would have triggered the evolution of a benthic form have been proposed. Moreover, fossils from the early Cambrian show marine communities dominated by benthic animals without any planktonic living forms. Peterson 2005 used both a molecular clock and the fossil record to find at least 4 independent origins of larvae from the late Cambrian to the middle Ordovician which correlate in time with novel modes of benthic predation. Thus, high predatory pressures at the bottom would drive the intercalation of pelagic larvae in the life cycles, a development that took place in a new environment where these pressures are several orders of magnitude lower (Johnson & Shanks 2003). Considering evolutive traits for different lineages separately, indirect development with planktotrophic veligers may be the basal condition from which direct development derived in the case of littorinids (Reid 1990), but free living nauplii secondarily evolved from direct ontogenesis in euphausiids and dendrobranchiate (Scholtz 2003). Then, we can give two different short answers to the question of why there are larvae: they were there since the origin of life as

holoplanktonic organisms; or they are the evolutive response to new high predation rates in the benthos during the early Paleozoic.

## Larval dispersal and connectivity

The understanding of larval evolution has profound implications in the way we study and interpret larval distributions in space and time. Note that, despite which of the two prevalent theories of the origin of larvae we assume as correct, dispersal, defined as the spread of larvae from the spawning to the settlement site (Pineda et al. 2007), does not play an important role in any of them. However, the tendency among marine biologists has been to consider larvae itself as an adaptation to dispersal and high inter-population gene flow (Thorson 1950, Thorson 1961, Scheltema 1971, Roughgarden et al. 1985). This traditional point of view was based on an overestimation of the relative importance of cohesion and uniformity for the viability of benthic populations compared with genetic drift and local adaptations, a balance previously enounced by Wright 1931. Such an overestimation was partially due to the lack of knowledge about the connectivity of the subpopulations, that is, the exchange of individuals between them, a concept that takes into account both dispersal and post settlement survival (Pineda et al. 2007). New studies show that very little exchange of individuals between subpopulations is required to maintain a minimum genetic homogeneity to ensure viability: few individuals per generation (Slatkin 1993, Cowen and Spognaule 2009). These low connectivity requirements are probably achieved with short dispersal ranges and may not represent a mayor force in the evolution of larvae. In addition, Pechenick (1999) revised the advantages and disadvantages of larval development in benthic marine invertebrates and found that the risk of transport to non suitable areas and the decreasing capacities of adaptation to the local habitat largely overcome the presumably benefits of extensive dispersal. In fact, this study remarks the evolutionary trend towards losing the larval stage in many clades and explains the dominance of biphasic life cycles on on the basis of difficulties to simplify the ontogenies, not on positive selection in favour of larvae. This new body of theories has been fully supported by a set of studies which better measured larval dispersal and connectivity patterns using different techniques: significant microgeographic genetic heterogeneity was found for the lobster *Homarus* and the barnacle *Balanus glandula* (Hedgecock 1986); biophysical models indicate very high self recruitment in coral reef fishes (Cowen 2006); and biochemical fingerprinting points to short dispersal distances in mussels (Becker et al. 2007).

## Larval distributions

An important feature that supported the view of great dispersal distances was the high magnitude of the coastal currents that would act transporting larvae passively far away the source population (Hannan 1984). This interpretation influenced in great extent the studies from which cross-shore and alongshore meroplanktonic distributions were inferred. The across shelf distributions were supposed to respond to powerful mesoscale processes that would transport newly released larvae to oceanic larval pools far offshore where they mix and randomly recruit onshore (Roughgarden et al. 1988). The main mesoscale physical process invoked to cause this two-ways transport across the shelf was wind induced currents (Ekman transport). Due to Earth rotational effects, winds blowing parallel to the coast generate a surface flow approximately perpendicular to it and to the right of the wind direction in the Northern hemisphere (Ekman 1905, Pond and Pickard 1983). When this flow is directed onshore, it is forced downwards at the coast and then offshore at depths below the thermocline in stratified waters (downwelling, negative Ekman transport); contrarily, when surface currents are directed offshore, there is a shoreward flow at depth and then upward to replace the volume of water exported at the surface (upwelling, positive Ekman transport; Thompson 1978). Upwelled mixed waters can reach the surface forming a cold, high-nutrients, high-chlorophyll coastal band separated from the stratified offshore waters by the upwelling front. Positive Ekman transport would cause the offshore displacement of early larvae and reversals in the wind speed and direction driving the transitions up-downwelling (upwelling relaxations) would move the upwelling front onshore with old stages competent to settle (Gaines and Roughgarden 1985, Roughgarden et al. 1988, Farrell et al. 1991, Roughgarden et al. 1992). Roughgarden's et al. 1988 paper was supposed to demonstrate this hypothesis in the field using samples from the California Cooperative Fisheries Investigation (CalCOFI) but they were not collected closer than 9km from the coast. In addition, this theory already contained arguments against its own principles: larvae seemed to passively drift with the surface currents but the oceanic larval pool would be aggregated at the upwelling front (Roughgarden et al. 1992, Shanks et al 2000), a feature that requires active resistance against the downward flow in the convergence that characterizes the front (Franks 1992). Contrarily to horizontal currents, the vertical flow could be faced by typical larval swimming speeds in the order of mm/s or even cm/s (Mileikovsky 1973, Chia et al. 1984). Then, there is an implicit control in the vertical position of the organism throughout the water column, a behavioural mechanism that



could also allow larvae to descend to the onshore flow layer during active upwelling (Grantham 1997). Finally, when very coastal domains were surveyed and very nearshore larval distributions were found to be the rule (Poulin et al. 2002, Shanks and Brink 2005, Genin et al. 2005, Morgan et al. 2009, Shanks & Shearman 2009), researchers recognised the real potential of the active vertical positioning: it provides coastal retention by remaining in depth layers which ensure onshore transport, both at downwelling and upwelling conditions. This latest theory evolved parallel in time respect to those showing short larval dispersal ranges, thus being supported each other and pointing to clear effects of nearshore retention on ecological patterns. Not only behavioural patterns may favour inshore retention but also very coastal circulation features recently discovered by physical oceanographers. Wind induced cross shore transport dramatically decreases as the coast is approached (Austin & Lentz 2002, Largier 2003), probably due to coastal boundary layer effects. This concept was defined as the layer of the ocean adjacent to the coast where viscosity significantly affects water circulation enhancing turbulence (Csanady 1972). Wolanski (1994) remarked its lower dynamism and permeability coining the term “sticky water”. The role of this physical process in limiting cross shore transport is currently being debated. Rilov et al. (2008) similarly defined the surf zone as a semi-permeable barrier but, despite high turbulence, they also found that very shallow waters remained stratified with respect to cross shore currents.

Several factors may significantly contribute to differentiate alongshore distributions from those in the perpendicular axis: the apparent lack of strong hydrographic gradients along the coast, the higher magnitude of the parallel flow and the different temporal and spatial scales of water motion among others (Winant 1983, Lentz et al 1999, Pineda et al. 2007). Largier (2003) extensively revised these concepts using advection-diffusion models and found that the diffusive component of the larval transport had been largely sub-estimated and it seemed to limit population wash out by advection. In addition, he noticed that retention patterns in the cross shore axis driven by active larval behaviour may disproportionately reduce alongshore transport. White et al. (2010) gave another step and explicitly introduced coastal heterogeneity in these models defining retention zones, which resulted in shorter dispersal distances. This more complicated model was consistent with field evidence pointing to the effect of coastal topography on meroplankton distributions. Different coastline configurations may result in different widths and permeabilities of the coastal boundary layer. For example, high reef density regions in the Great Reef Barrier are more refractory to the entraining of tidal and low frequency currents compared with low density ones, thus affecting the distributions of coral

reef fishes (Wolanski & Spagnol 2000). This kind of processes may be of relevance in other nearshore systems, but have been poorly studied. The magnitude and direction of the tidal currents was shown to be dependent on coast orientation with respect to prominent headlands (Rosenfeld & Beardsley 1987), another process that may potentially interact with the circulation of larvae but has not been explored. By far, the most common mechanisms invoked to explain zooplankton patterns in abundance around capes have been the wakes observed in their lee (Pritchard et al. 2007). Their origin is the flow separation at the tip of the headland because, due to inertia, the main current describes a meander at a certain distance past the cape. Thus there is an area of weaker flow and increasing water residence time in the lee (the wake). Retention is often aided by the convergent flow around the front which separates the wake from the free stream current. Usually, in this retention zone the flow is reversed and gyres are generated (Wolanski et al. 1984). When the outer alongshore circulation is driven by strong upwelling, these structures are called “upwelling shadows” (Graham et al. 1992), extensively studied because of their potential to accumulate meroplankton (Wing et al. 1998, Mace & Morgan 2006). This potential of topographic variability to alter larval alongshore distributions has never been incorporated in models describing meroplankton patchiness. Typical zooplankton patches along the coast have been reported to achieve sizes of 80-100km (Mackas 1984) as the organisms would be linked to the size of mesoscale hydrographic structures (Ayata et al. 2011). Alternatively, intrinsic spatial autocorrelation effects specific of each taxa, like localized, synchronized spawning and aggregative behaviours, have been invoked to explain other patterns (Legendre 1993, Bjørnstad et al. 1999). A third component constituted by coastline configuration descriptors would probably account for significant amounts of variability in the abundance patterns. The knowledge of alongshore distributions, especially focused on the typical spatial scales of retention, is critical in the emerging science of marine reserve design (Bostford 2001; Bostford et al. 2003; Largier 2003, Lubchenko 2003, White et al. 2010).

## Spatial and temporal scales

The time and space scales of an ecological process are of paramount importance for the design of meaningful studies (Wiens 1989). It is usually difficult to identify the correct scale to describe a pattern because it becomes evident at scales which are not those typical of the underlying mechanism responsible of it (Levin 1992). This is especially true in the plankton, where the organism perceives the environment and responds to it on scales resembling its body size, but the apparent distribution patterns arises at scales of hundreds of meters (Pineda et al 2009). The increasing evidences previously commented coming from the study of larval evolutive trends, dispersal, connectivity and distributions, all point to the relevance of small spatial scales on larval ecology. Surprisingly, the oceanographic processes occurring at these scales (hundreds of meters to few km's) present a very similar functioning compared with those in the mesoscale: high turbulence in the water column in shallow waters triggers both the presence of the “sticky water” layer close to little high density reef zones (Wolanski & Spagnol 2000) and large tidal fronts (Pingree et al. 1975); retention zones originated by flow separation are originated in the lee of large capes (Wing et al. 1998, Harms & Winnant 1998) and small headlands (Largier 2003); and the convergence flow structure around very nearshore foam lines associated with internal waves and topographic features is of the same nature to that developed across upwelling fronts along entire continental margins (Zeldis & Jillet 1982, Pineda 1999, Shanks et al 2000). Internal waves consist of tidal or lower frequency deformations propagating along the thermocline which often reach the surface causing a characteristic, weak convergent circulation. In fact, each wave crest could be seen as a little upwelling of deep waters below the thermocline. Pineda (1999) demonstrated that the accumulation capacity of these features was related to the ability of resisting the downwards flow in the crest of the wave, as it happened in the upwelling fronts. Probably, this pattern could be extended to other very local convergences which seemed to alter meroplanktonic distributions following Shanks et al. (2003). In less than 1 km along the coast of Oregon, these authors found striking differences in the physical origin, effects on plankton community and frequency of coastal fronts, pointing to an extremely high spatial heterogeneity at the small scale. Such variability probably underlies the decoupling between nearshore larval abundances and intertidal recruitment observed in more general studies at greater spatial scales (Rilov et al. 2008).

Intuitively, the time and space scales of a process are coupled. In the case of meroplankton, planktonic larval duration (PLD) seems to correlate with larval dispersal distances (Siegel et al. 2003). However, that simple assumption has been questioned as cross shore retention during significant periods in the water column reduces dispersal distances (Sponaugle et al. 2002, Largier 2003, White et al. 2010). On the other hand, the PLD is not strictly fixed for a given species, but it varies with the metabolism of the larvae, which is in turn influenced by temperature (O'Connor et al. 2007). The life time in the pelagic environment defines a temporal framework where physical oceanography processes may affect larval ecology. However, there are few studies integrating those processes over time scales that are relevant to the distribution patterns of larvae (but see Lagadeuc 1992 and Thiébaud et al. 1994). Moreover, usually the only time scale considered is the one typical of the physical event and this could be particularly wrong for meroplankton due to the mismatch between space and time: for larvae developing several weeks in the plankton the spatial dynamics which matter are probably those with periods of hours (internal waves, foam lines) or few days (upwelling relaxations). Then, the periodicity of such events during the larval life may be critical to evaluate their influence. Largier 1993 remarked that the ecological importance of short-lived coastal fronts may depend on their recurrent periodic nature over longer time scales. Another relevant time-dependent feature in the biology of larvae is the spawning timing which seems to follow the seasonality of temperate seas like the other plankton components (Highfield et al. 2010). Recent studies indicate that larval release to the pelagic environment may respond not only to adult population requirements but also to larval characteristics (Starr et al. 1990).

## Study area

The Central Cantabrian Sea is characterised by a narrow shelf with a mean depth of approximately 150m. This coastal platform is wider to the west, but never more than 55 km, and presents an abrupt shelf break in the Aviles Canyon. The main topographic coastal feature is Cape Peñas, a 20 km wide headland in the middle of the domain. The system follows the usual seasonal dynamics in temperate seas, with some particularities. In winter, the Iberian Polar Current, IPC, is well defined going eastward along the shelf break and enhanced by predominant southwesterly winds, generating meanders and eDDies (Botas et al. 1990, Pingree & Le Cann 1990, González-Quiros et al. 2004). Intense bloom events during the stratification period (typically from March to October) are driven by coastal upwelling

generated by episodes of strong sea breezes from the northeast (Botas et al. 1990, Varela et al. 2005). These events are stronger to the west of Peñas and restrained to a nearshore stripe of colder water coincident with the shelf width. The coastal waters off Cudillero are of particular interest to study very coastal processes as a shoreward lengthening of the cross shore transect monthly surveyed since December 1992 by the University of Oviedo in collaboration with the Spanish Institute of Oceanography (PROYECTO RADIALES; <http://seriestemporales-ieo.net>). Three stations are sampled, E1, E2, E3 at the shelf, the shelf break and the open sea on a transect of only 23km, due to the proximity of the Avilés Canyon. The hydrographic and biological processes studied here (Llope 2005, Valdes et al 2007) can be directly compared with those analysed inshore. The area is particularly affected by the Nalón river, the most important hydrographic system in the Cantabrian Sea in terms of outflow and input of nutrients (Prego & Vergara 1998), whose estuary is located 10km to the east.

The intertidal community in the Cantabrian Sea is characterized by a high diversity of invertebrates, mainly annelids, molluscs and crustaceans (Anadón & Fernández 1986, Arrontes & Anadón 1990, Fernández et al. 1990). Among crustaceans, barnacles reach the highest densities in the rocky shores. Some species are edible and have great economic importance, mainly the gooseneck barnacle *Pollicipes pollicipes* but also the crab *Necora puber*, the mussel *Mytilus galloprovincialis*, the sea snail *Littorina littorea*, the limpet *Patella vulgata* and the sea urchin *Paracentrotus lividus* (Molares & Freire 2003, Sanchez & Olasso 2003, González-Irusta 2009).

## Objectives

The main objective of this thesis is to describe very coastal meroplankton distributions as a function of the physico-chemical properties of the pelagic environment but also of the species-specific biological characteristics and landscape configuration. The spatial resolution and proximity to the coast reached in the cruises together with the consideration of other non-hydrographic variables are the novel aspects of these studies.

Here, the particular objectives of the chapters 2, 3 and 4 are briefly resumed:

**Seasonality and cross shore distributions in the inner shelf:** an approach to the seasonality of the larval community and a description of the cross shore trends in abundance as a function of the Ekman transport.

- Seasonality of the environmental properties of the water column.
- Seasonality of the larval community.
- Ekman transport time-series.
- Cross shelf distributions of larvae and their correlation with Ekman transport at different time scales.
- Other very coastal processes.

**Alongshore coastal distributions:** a description of the larval distribution patterns along the coast mediated by water column properties, landscape configuration and spatial autocorrelation.

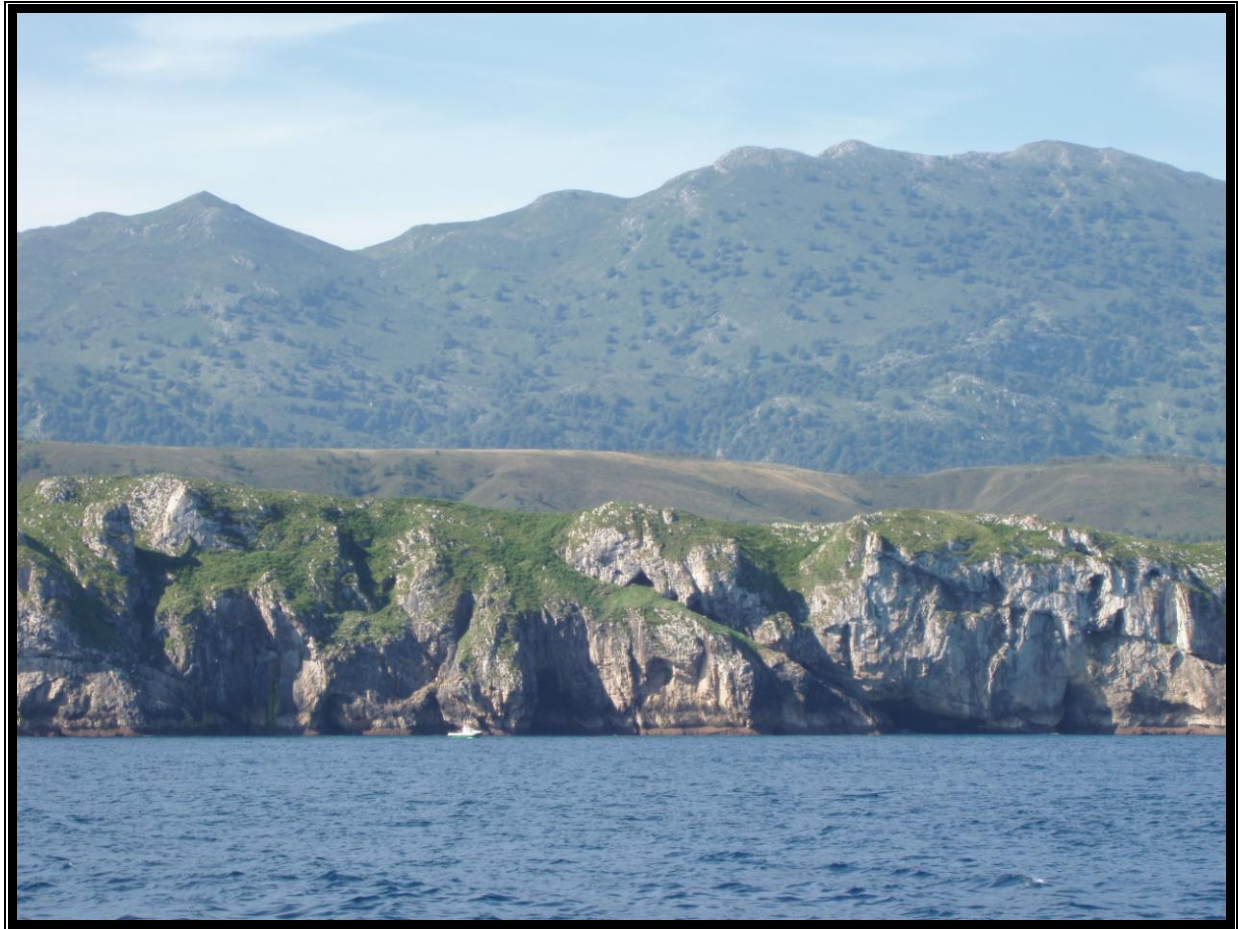
- Alongshore distribution of the water column properties.
- Alongshore distribution of the topographic descriptors at different scales.
- Alongshore distribution of larvae.
- Larval distribution variability decomposition in spatially intrinsic, topographic and water column components.
- Topographic effects: relevant descriptors and spatial scales.
- Trends of the variance components with the planktonic larval duration.

**Spatial distributions around very coastal convergence structures (slicks and foam lines):** a description of larval distributions across coastal fronts.

- Description of the physical structures and convergent flows around very coastal fronts.
- Larval distribution patterns across the front: retention, frontal accumulation, non altered patterns.
- Origin of larvae.
- Origin of the fronts.
- Larval distribution patterns across the front: relative swimming speeds dependence and its ecological implications.



## Chapter I: Seasonality and cross shore larval distributions







### **Introduction**

The distribution of the larval stages of coastal benthic populations determines the dispersal and connectivity patterns (Becker 2007) and in turn the whole structure of the adult communities (Largier 2002). Larvae are in fact the unique linkage among distant benthic coastal populations. Knowing the processes which affect meroplanktonic distributions in space and time is necessary to develop a methodology for the design of marine reserves (Bostford et al. 2001, Bostford et al. 2003, Lubchenko 2003).

Many different physical oceanographic processes have been studied in relation with larval distribution patterns in the coastal ocean. Seasonality in temperate waters seems to rule planktonic composition and larvae are not an exception (Byrne 1995, Highfield et al. 2010). The breeding season has been considered a characteristic determined by adult requirements (Todd & Doyle 1981). However, new studies reveal that the timing of spawning may have evolved to maximize larval survival. For example, spawning has been observed to coincide with phytoplankton blooms (Starr et al. 1990, Highfield et al. 2010). Storms are also supposed to trigger spawning as an adaptation that enables larvae to settle on new free surfaces generated by great waves (Barry 1989, Gyory & Pineda 2011).

The cross-shore distribution of larvae determines the alongshore dispersal (Largier 2003) and the depth of the adult populations in the shelf (Shanks et al. 2002). Traditionally, intermittent wind induced coastal upwelling has been suggested as the mechanism that may control these patterns (Gaines & Roughgarden 1985, Farrell et al. 1991, Roughgarden et al. 1992). Larvae are supposed to be advected offshore by the surface Ekman transport. The upwelling front, which delimits offshore waters from those newly upwelled inshore, presents a characteristic convergent current circulation which leads to the accumulation of the zooplankton (Shanks et al. 2000). Larvae would remain in the front if capable of swimming upwards against the downward flow at the convergence, which is much weaker than the horizontal current (Franks 1992). Relaxation of the upwelling leads to downwelling, pushing the front against the coast, where larval recruitment may take place (Roughgarden et al. 1992). Little is known about the effectiveness of this process, especially for species which settle in the intertidal and have to be transported across the whole shelf. Alternatively, Grantham (1997) suggested the possibility of a return to the shore mediated by deep currents during active upwelling (the onshore flow hypothesis). This would imply an ontogenic vertical migration at the upwelling front to a

depth ensuring onshore transport. Such stage-dependent vertical distribution with later, competent stages located deep underneath the upwelling front, have been observed by Lindley et al. (1994), Grantham (1997) and Morgan et al. (2009). However, new studies have revealed larval spatial distributions restrained to very nearshore waters regardless of the presence or absence of upwelling conditions (Poulin et al. 2002, Shanks & Brink 2005, Genin et al. 2005, Morgan et al. 2009). Larvae would swim against the vertical flow and, guided by the the surface-bottom gradient of turbulence within the Ekman layer (Pringle 2007), would search for those depth layers where transport is shoreward. In this scenario, the distribution of larvae would be defined by other processes, like topographically induced fronts (Shanks et al 2003), internal waves (Kingsford and Choat 1986, Zeldis and Jillet 1992, Shanks 1995, Scotti et al. 1997, Pineda 1999) Langmuir circulation cells (Lafarriere 2007) or river plume fronts (Govoni et al. 1989, Egglestone et al. 1998, Tillburg et al. 2009). Even if upwelling was determinant for the spatial distribution of some larvae, little is known about the temporal scale which really governs the dispersal dynamics. Settlement rates have been found to correlate with upwelling indexes averaged over 3-4 days (Largier et al. 1993) but it is unlikely that this time interval may describe the distribution patterns of larvae, especially for those larvae characterized by long planktonic lives.

The aim of this study is to describe the seasonality and cross-shore distribution of meroplanktonic taxa at a monthly time scale and at the spatial scale range of hundreds of meters, to investigate the role of upwelling on the generation of these patterns and to identify the relevant temporal scale at which it operates.

### **Material and Methods**

A monthly survey has been carried out from July 2007 to September 2008 aboard the R. V. “José Rioja” (with the exception of May and July 2008) off Cudillero, Central Cantabrian Sea (Fig. I.1). We sampled 11 stations, the five more coastal ones separated 200m from each other, the rest of them 500m apart. The farthest station from the coast (4 km) has been sampled monthly since 1993 within the long term monitoring program RADIALES (Llope et al. 2006; Fig. I.1).

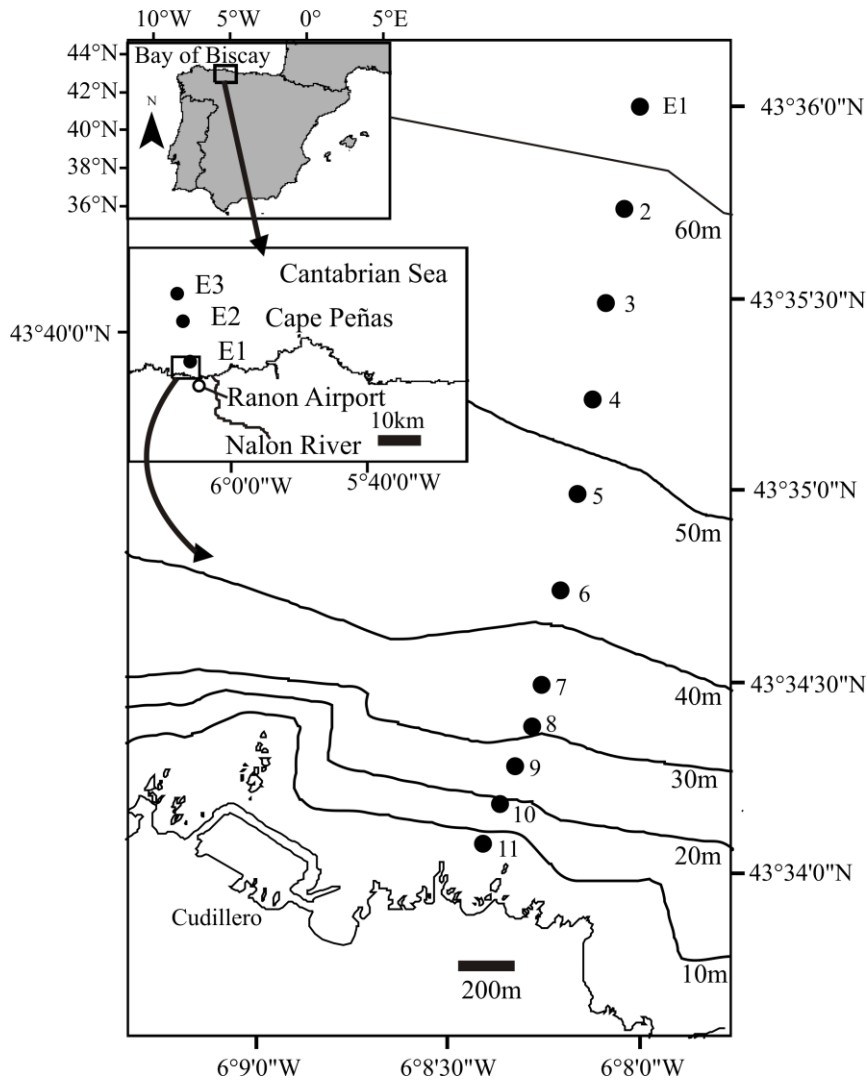


Figure I.1. Geographical location of the eleven coastal stations. Long term monitoring stations (E1, E2, E3) and topographic features are also shown, as well as the meteorological station in the Ranon Airport.

For logistic reasons, the transect was sampled twice in every survey. First, we conducted CTD casts while steaming offshore and sampled meroplankton with nets while steaming inshore. Each pass took less than 1.5 h, and the nearshore stations were sampled with a very small time difference between passes. During the first pass we sampled fluorescence, temperature, salinity and density using a SBE 25 CTD mounted on a Niskin bottle rosette. We also calculated a stratification index (SI) by subtracting surface from bottom sigma-t (Albaina & Irigoien 2007). Fluorescence was transformed to chlorophyll-a concentrations in  $\text{mg m}^{-3}$  by calibration against fluorometric chlorophyll-a measurements ( $n=120$   $R^2=0.74$   $p<0.0001$ ) from water samples obtained from the Niskin bottles at 0, 10, 20, 30, 40 and 50m depth at station 1. Each 200 ml-sample was filtered onto  $0.2\mu\text{m}$  GF-F filters, frozen, extracted in 5 ml 90% acetone during 24 h in dark and  $-20^\circ\text{C}$  and the chlorophyll-a concentration measured in a

Turner Designs 10 fluorometer following the acidification method of Yentsch and Menzel (1963). During the second pass we towed a 100 $\mu$ m, 40 cm in diameter WP2 net from the bottom to the surface at every station. The net was designed to avoid clogging in coastal waters (Sameoto et al. 2000). Plankton concentrated in the codends were poured into 250 ml plastic bottles and preserved by adding formaldehyde to a final concentration of 4%. At the laboratory, the whole sample was analysed on a counting plate to determine and count individuals belonging to each meroplanktonic taxa. Our taxonomic resolution varied depending on the group, from coarse (e.g. littorinids and decapod larvae) to species-level (e.g. in barnacles). Although fish larvae and eggs are not strictly meroplankton, they have been included in the analysis because they are larval stages, sometimes very common, and are not commonly studied at this small resolution. We took into account the visual observations of foam lines or slicks observed along the transect and compared them with CTD data.

We used the PRIMER software package to analyze the multivariate structure of the meroplanktonic assemblage and its relationship with the physical-biological structure of the water-column (Clarke and Gorley 2006). Squared root-transformed larval abundances were used to derive a Bray Curtis similarity distances matrix between samples of the whole temporal series from July 07 to September 08. We used this matrix to conduct an ordination analysis (MDS) and to search for groups of samples (hierarchical cluster analysis), whose characteristic species were found using the SIMPER procedure. On the other hand, we took into account surface temperature (ST), chlorophyll-a (SCHLA), salinity (SS) and the stratification index (SI) of each station. With the normalized environmental data, we calculated a semi-matrix of euclidean distances among stations which we used to conduct MDS, CLUSTER and SIMPER analyses, to arrive at groups of stations based on physicochemical properties of the pelagic environment. Last, Bioenv and Stepwise analysis (BEST) was carried out to match the larval and water column matrixes. The significance of the match was tested with 1999 random permutations of the rank correlation coefficient  $\rho$ . In addition, multiple linear regression models were performed for the most abundant species and stages with their log +1 transformed abundances as dependent variables and all the water column variables as independent predictors. To this set of explanatory variables we added the distance to the coast of every station (D).

To characterize the cross shore distribution patterns of the most common larval taxa, (minimum abundances of 5 ind.m<sup>-2</sup> at least in one out of the 11 stations) we calculated the average distance offshore for the most abundant taxa following Shanks & Shearman (2009).

$$\bar{D} = (\sum_{i=1}^{11} n_i d_i) / (\sum_{i=1}^{11} n_i)$$

where  $\bar{D}$  is the average distance from the coast,  $n_i$  is the population density at sampling station  $i$ , and  $d_i$  is the distance of sampling station  $i$  from the coast. Average distances were calculated for each month and grouped by species and stages to look for taxa-specific cross shore distributions using ANOVA and Fisher *post-hoc* tests. To keep the statistical design balanced with the highest power of analysis, only those taxa consistently present in 12 out of 13 cruises were considered for the ANOVA.

We hypothesised that Ekman transport may explain the cross-shore abundance patterns to some extent. Thus,  $\bar{D}$  was submitted to a linear regression analysis against upwelling indexes calculated from wind data (reported in the Ranón Airport, Fig. 1) according to equation in Bakun (1973) and averaged for time intervals ranging from 1 to 120 days prior to sampling using the R software package.

## **Results**

### **Physical structure**

Seasonality and coastal hydrographical processes affected the physical environment in the region. Vertical temperature profiles from July and August 2007, and August and September 2008 profiles show column structure with the thermocline well established at 40 m depth, a typical summer situation in the Cantabrian Sea (Albaina and Irigoien 2007). Temperature peaked in August 07 at the surface (20° C), when the highest SI was observed (1.5). Foam lines were identified at a range of distances between 800 and 1500 m from the coast in August 2007 and 2008 but the presence of surface density gradients was also observed in July 2007 and September 2008 at similar distances (Fig. I.2, Fig I.3).

September 2007 was characterized by the upwelling of deep water, caused by strong NE winds which blew sustainably during the three days prior to our survey (Fig. I.4), causing the lowest

summer surface water temperature and the highest surface chlorophyll-a concentration (12.2 C° and 8.4 mg m<sup>-3</sup>, respectively; Fig. I.4) in 14 years of time series sampling. Vertical temperature profiles showed a weak stratification and a surface salinity gradient coincident with a foam line located at 1500m from the coast (Fig. I.2)

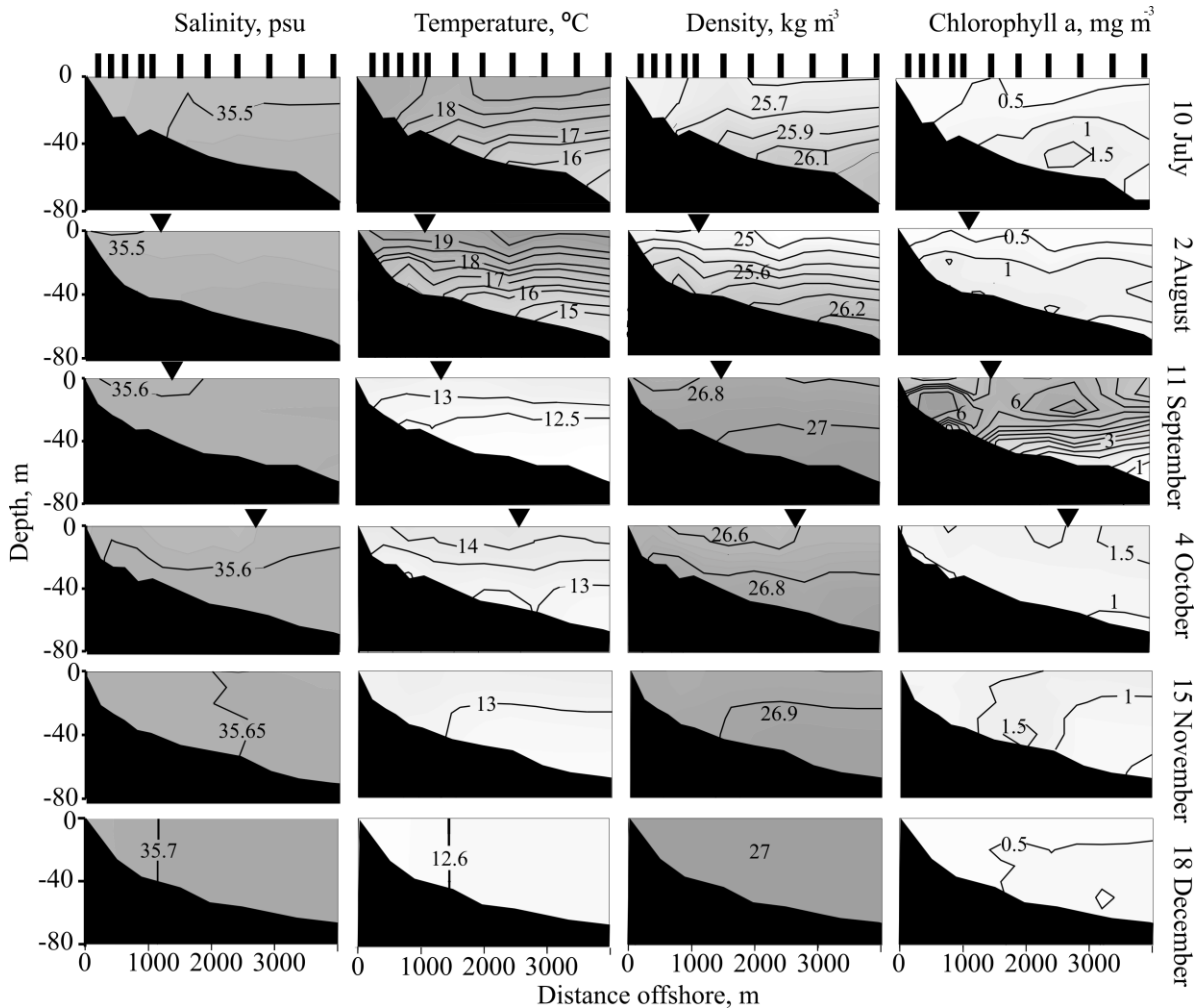


Figure I.2. Contour profiles of salinity, temperature, density sigma-t and chlorophyll-a at every sampling from July 07 to December 07. Dark triangles show the location of the slicks or foam lines observed.

In October 2007, the sections revealed a surface lens of warmer water with lower salinity, limited by two areas of marked surface physical gradients at 1000 and 2700 m from the coast (Fig. I.2). The latter was clearly associated to a foam line close to station 3.

In November and December 2007 and in January 2008, no stratification was observed and no frontal structures or surface gradients were apparent (Fig. I.2, Fig. I.3). During February and March 2008 there were marked physical gradients surrounding surface lenses between 1000 and 3000 m (Fig. I.3). A slick was observed during March 2008 at 800 m from the coast,

associated with an incipient, 10-15 m deep thermocline and a corresponding subsurface chlorophyll maximum (Fig. I.3).

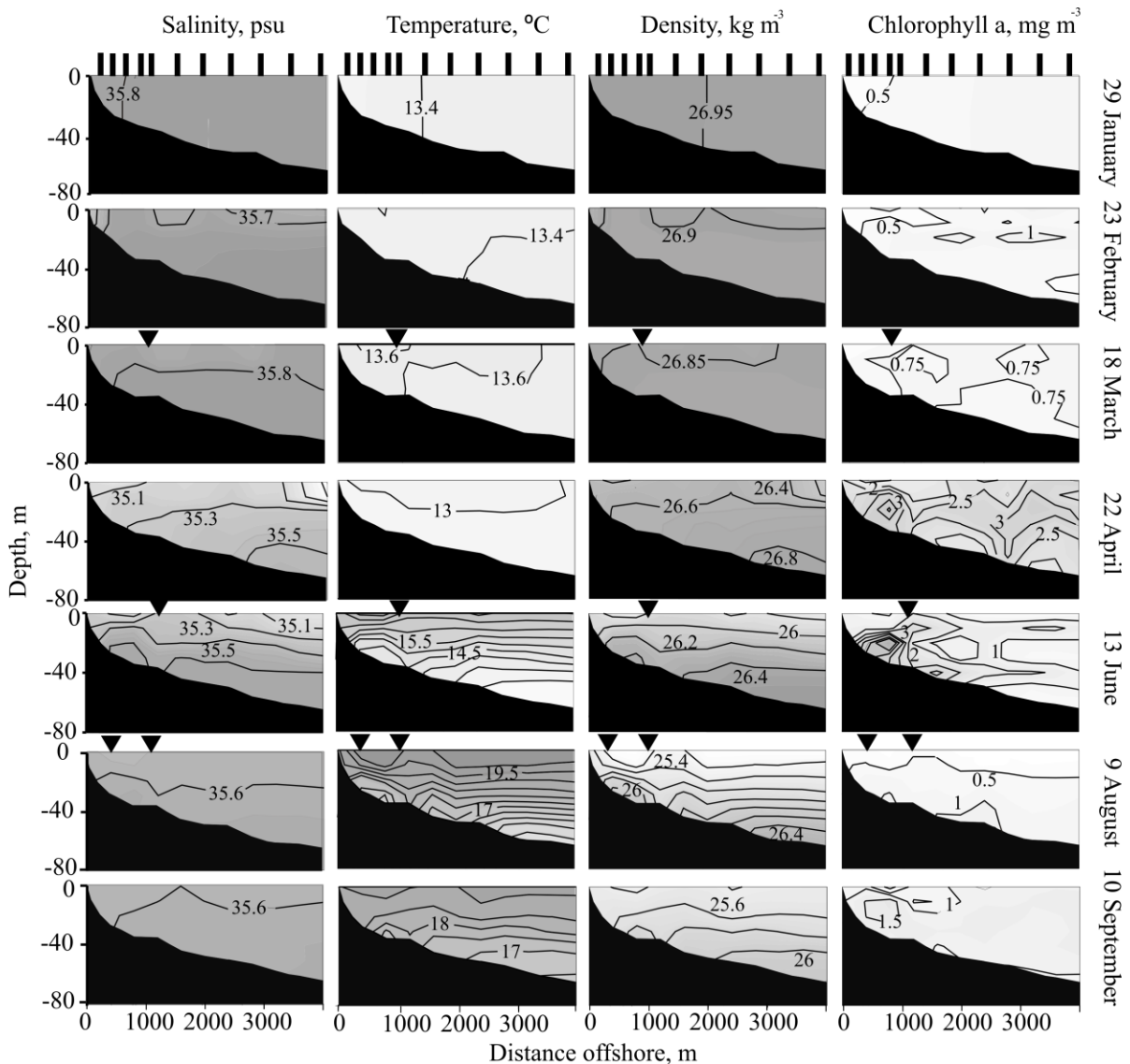


Figure I.3. Contour profiles of salinity, temperature, density sigma-t and chlorophyll-a at every sampling from January 08 to September 08. Dark triangles show the location of the slicks or foam lines observed.

During April and June 2008, surface salinity was low due to continental runoff probably originating at the Nalón River (Fig. I.1), with strong cross-shore salinity gradients situated at 1000 and 3500m from the coast in April and 1000m in June (Fig. I.3), this last coincident with a conspicuous slick. Stratification was only established in June with a 30 m deep thermocline and markedly fresh waters at the surface.

During 2007 and 2008, downwelling prevailed in winter, with onshore, wind-induced transport exceeding  $-2000 \text{ km}^{-1} \text{ s}^{-1}$  and reaching  $-9000 \text{ m}^3 \text{ km}^{-1} \text{ s}^{-1}$  in March 2007. Conditions



were more prone to upwelling during the summer, although transport rarely exceeded  $1000\text{m}^3\text{ km}^{-1}\text{ s}^{-1}$ , with a notorious peak of  $2000\text{ m}^3\text{ km}^{-1}\text{ s}^{-1}$  in September 2007 (Fig. I.4).

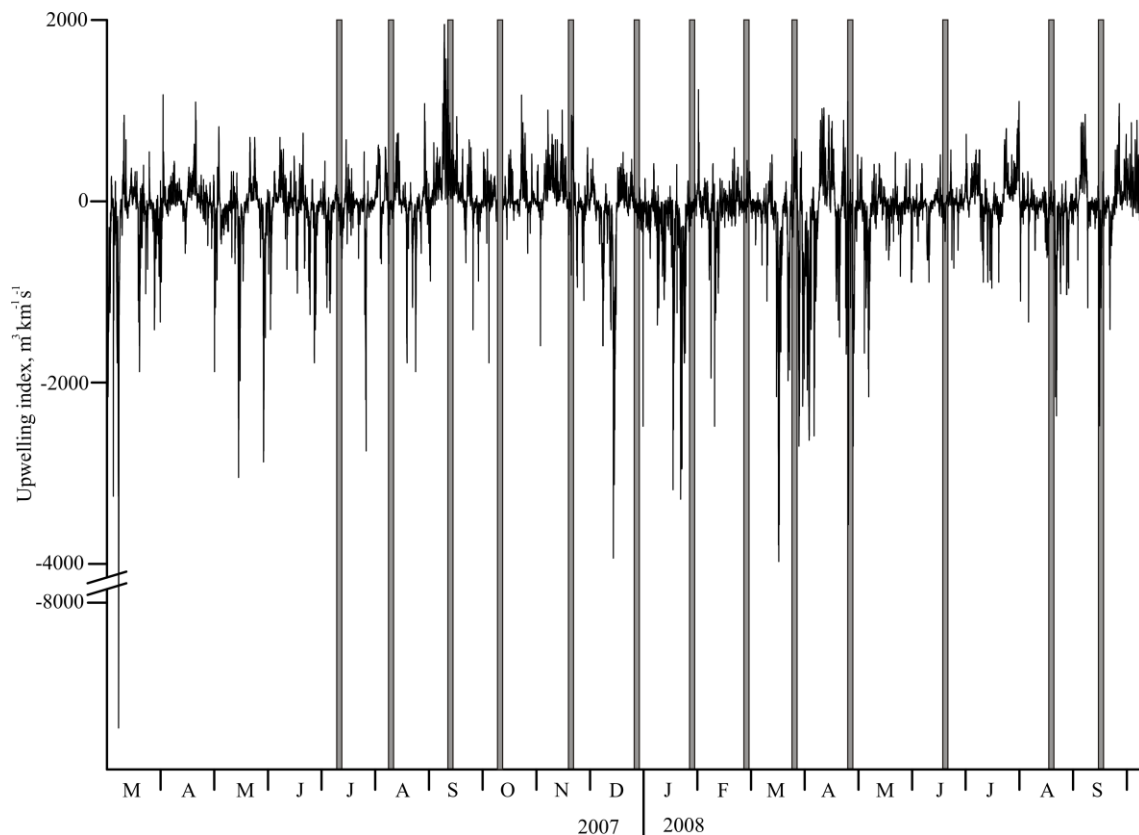


Figure I.4. Ekman transport time-series from March 07 to September 08 from Ranón Airport hourly wind data. Month initials are represented.

### Meroplankton assemblages

Seasonality variation predominated over the cross shore gradient in determining the structure of meroplankton assemblages. Littorinids, *Hiatella spp.* bivalve veligers, *Pollicipes pollicipes*, *Chthamalus spp.*, porcellanid zoeas, *Liocarcinus spp.* megalopae and echinoderms in general peaked in spring/summer while segmented larvae of spionid annelids, the barnacle *Verruca stroemia*, zoea of *Liocarcinus spp.* zoea, cyphonauts of *Membranipora spp.* and larval fish were more abundant in autumn and winter (Fig. I.5). *Hiatella spp.* veligers and juvenile flatworms present maxima coincident with frontal structures especially in summer (Fig. I.5), while the highest abundances of *Echinocardium cordatum* plutei were found close to a marked slick in March 08 (Fig. I.5). The abundances of the most common taxa significantly correlate with water column predictors and distance to the coast but the amounts of variability explained varied considerably from 13.5 to 74.1% for *Liocarcinus spp.* zoeae to *Hiatella spp.* veligers,

respectively (Table I.1). The variables which significantly entered the models were predominantly SS and SST in 5 and 4 out of the 6 taxa analysed, respectively. SST explained more than 50% of the variance in the case of both mollusc taxa (Table I.1).

Table I.1. Results of the multiple linear regression analyses for the most abundant taxa. For each variable, we show the variance explained, the significance level ( $p^* < 0.05$ ;  $p^{**} < 0.01$ ;  $p^{***} < 0.001$ ) and the sign of the correlation. For each taxa, the total variance explained is also shown. See Material and Methods for the acronyms of the independent variables.

Taxa	SST	SS	SI	SCHLA	D	Total
<b>Spionids</b>	9.2*** -		6.5*** +			15.7
<b>Littorinids</b>	45.7*** +	14.9*** +				60.6
<i>Hiatella spp.</i>	49.0*** +	1.6** -	14.9*** +	8.6*** +		74.1
<i>Verruca stroemia</i> early nauplii		21.8*** -			8.8*** -	30.6
<i>Verruca stroemia</i> late nauplii		13.0*** -		5.4** +		18.4
<i>Verruca stroemia</i> cyprids	2.8* -	2.4** +	6.1*** +		2.6* -	13.9
<i>Liocarcinus spp.</i> zoeae				6** -	7.5*** +	13.5

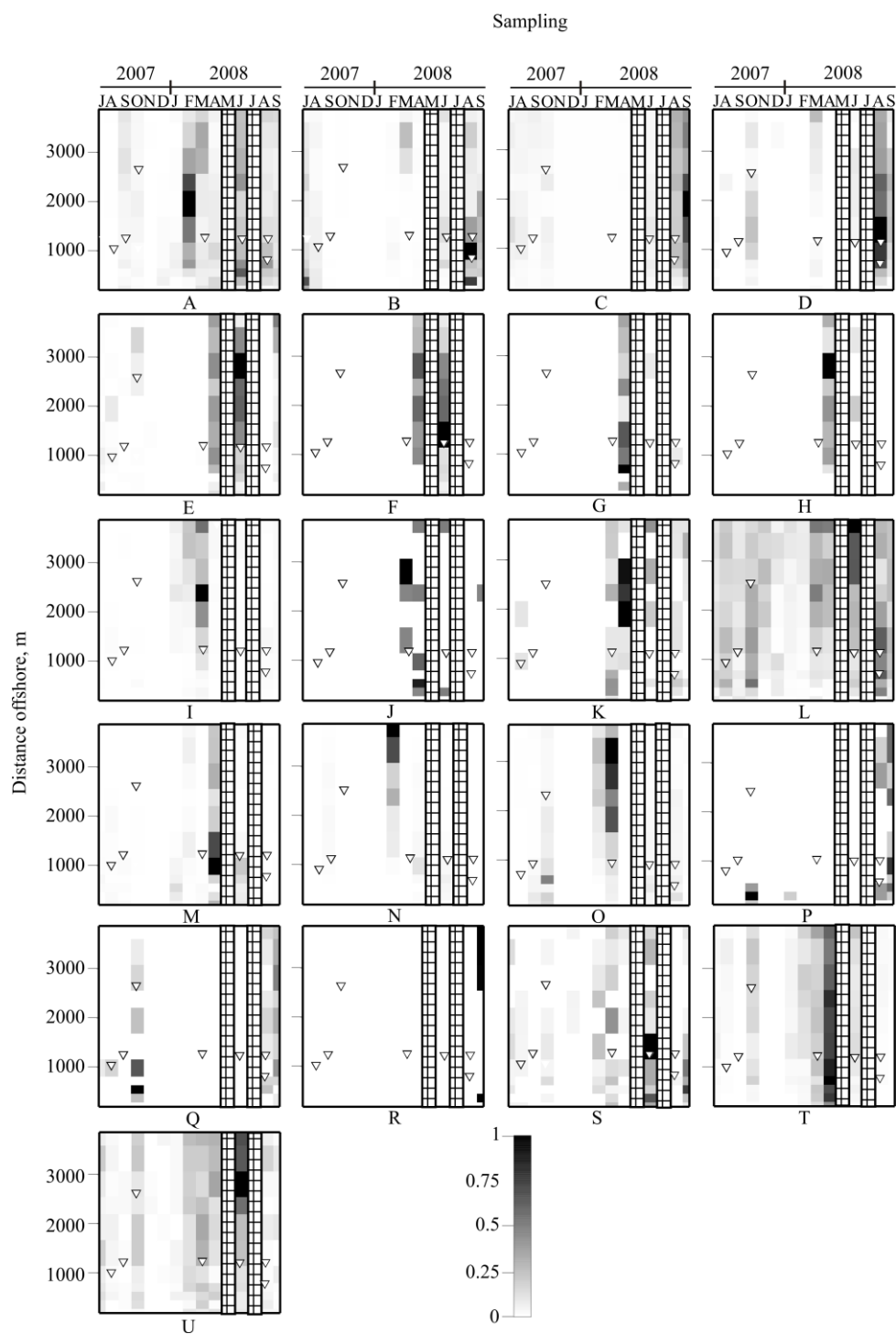


Figure I.5. Abundance mosaic profiles of different taxa and stages. The colour bar shows the proportional abundance respect to the maximum of each taxa. Stripped bars represent failed samplings on May and July 2008. Month initials are represented. White triangles show the location of foam lines and slicks A) Spionids (maximum=4900 ind m<sup>-2</sup>); B) littorinids (m=26650); C) *Hiatella spp.* (m=134400); D) flatworms (m=330); E) *Amphiura spp.* (m=630); F) *Echinocardium cordatum* (m=580); G) *Paracentrotus lividus* (m=100); H) *Holothuria sp* (m=80); I) *Liocarcinus spp.* zoea (m=6150); J) *Liocarcinus spp* megalopae (m=16); K) porcelanids (m=80); L) other decapods (m=1800); M) *Verruca stroemia* early nauplii (m=50900); N) *Verruca stroemia* late nauplii (m=40600); O) *Verruca stroemia* cyprids (m=3700); P) *Chthamalus spp.* early nauplii (m=40); Q) *Chthamalus spp.* late nauplii (m=100); R) *Chthamalus spp.* cyprids (m=8); S) *Membranipora spp* (m=170); T) fish eggs (m=2600); U) fish larvae (m=550)

There were 3 groups of stations, according to the composition of their meroplankton assemblages (CLUSTER and MDS analysis, Fig. I.6):

-**W**: Low density, winter assemblage defined at a similarity level of 28%. Characterized by low larval densities of all the taxa and comprising samples from late Autumn to Early winter. The taxa which contributed the most to the similarity inside this group of samples were decapod larvae (average abundances around 100 ind. m<sup>-2</sup>, 20,79% of average similarity)

-**N**: naupliar assemblage defined at a similarity level of 38%. Characterized by high densities of *Verruca stroemia* early nauplii (around 2500 ind. m<sup>-2</sup>, 12.17% of average similarity) with samples from mid winter to late spring.

-**V**: veliger assemblage defined at a similarity level of 38%. Characterized by high densities of *Hiatella* spp.. (around 10000 ind. m<sup>-2</sup>, 22.85%) and littorinid veliger larvae (around 1600 ind. m<sup>-2</sup>, 8.88%) from summer to mid Autumn.

The best match between water column variables and larval assemblages was for a subset containing SS and SST (BEST,  $p=0.0005$ , Fig. 6), although it only explained 26.4% of the variance in meroplankton composition.

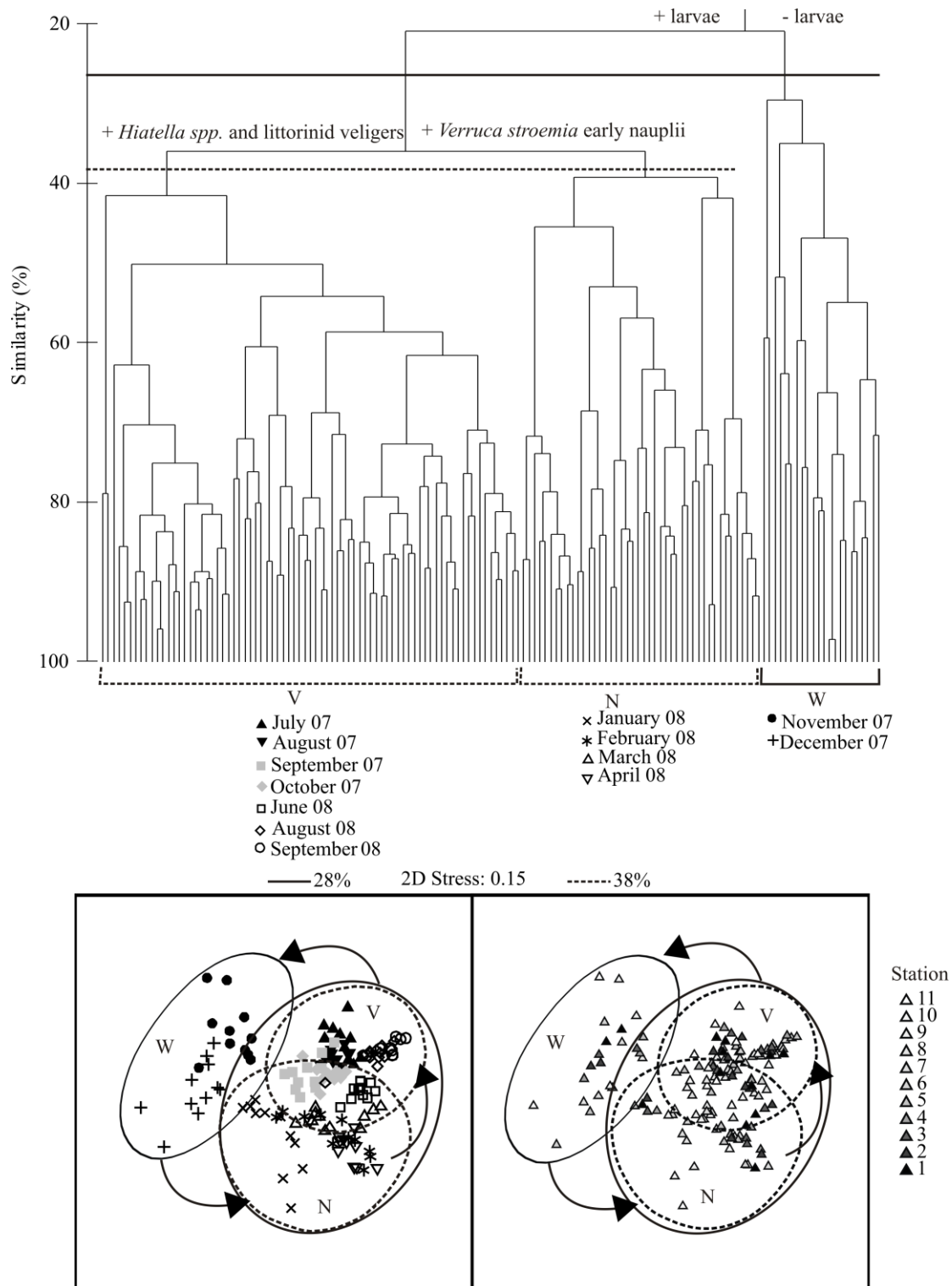


Figure I.6. Results of the multivariate analyses. The cluster carried out with larval abundances is shown with the levels of similarity used to define different meroplanktonic assemblages: 28% (dark line) and 38% (discontinuous line). Three assemblages were obtained: W (winter), N (naupliar) and V (veliger). The main taxa driving the differences between groups of samples are shown in the branches of the cluster. The biological MDS is represented with different symbols for sampling date and station number (1-11). Arrows are drawn to represent the transitions between the three assemblages as an approach to the larval seasonality.

### **Cross shore abundance trends and time-dependent Ekman transport**

We calculated average distances offshore for the most abundant taxa and/or stages for each monthly cruise: veligers of littorinids and *Hiatella* spp., early nauplii, late nauplii and cyprids of *Verruca stroemia*, spionid annelid segmented larvae and *Liocarcinus* spp. zoeae. These distances varied between species, stages and cruises (Table I.2). Only *Verruca stroemia* early nauplii, spionid annelid segmented larvae, littorinid veligers and *Liocarcinus* spp. zoeae (Table I.2) were considered for the ANOVA. Distances were not transformed as they were normally distributed and there was homogeneity of variance between the different taxa. Significant differences among these species were found ( $p=0.0007$ ): early nauplii were consistently located landwards and *Liocarcinus* spp. seawards respect to annelids and littorinids (Table I.2).

Table I.2. Average distance offshore for each abundant taxa and sampling. Species-specific mean distances with their standard deviation are also shown. Mean distances in bold show values of those taxa that were taken into account in the analysis of variance (present in 12 out of 13 cruises), being “a”, “b” and “c” consistent groups defined by the Fisher post-hoc test. The significance levels arising from the pair wise comparisons between groups are represented in parenthesis following an alphabetic order ( $p < 0.05$ ;  $** < 0.01$ ;  $*** < 0.001$ )

Cruise	Spionids	Littorinids	<i>Hiatella</i> spp.	<i>Verruca stroemia</i> early nauplii	<i>Verruca stroemia</i> late nauplii	<i>Verruca stroemia</i> cyprids	<i>Liocarcinus</i> spp.
10 July 07	1627.45	969.06	1932.23	893.02	1297.78	—	1077.9
2 August 07	2110.66	1223.74	1951.94	1098.33	—	1631.05	1553.82
11 September 07	2204.61	752.66	2897.73	822.55	2062.88	753.29	2404.19
4 October 07	1902.37	2400.45	1919.06	1548.4	2529.91	1025.52	1161.26
15 November 07	—	1533.51	1646.35	952.01	—	—	—
18 December 07	869.61	—	2726.22	—	—	—	3006.21
29 January 08	1290.42	2051.76	—	632.2	—	—	2701.15
23 February 08	1888.25	1678.18	—	2305.49	3258.01	2698.85	3001.5
18 March 08	2284.58	3060.33	1961.31	736.13	1344.31	2559.02	2528.73
22 April 08	1227.5	1865.64	2672.75	1612.32	1388.45	—	2688.35
13 June 08	1654.7	1877.96	1588.53	939.53	957.44	1159.3	2347.06
9 August 08	1493.23	1171.99	2161.63	969.42	2045.03	1251.72	1368.18
10 September 08	1715.66	1450.92	1896.82	1061.63	2499.98	1636.26	2278.75
Mean	<b>1689.09 ± 423.28</b> a (*,*)	<b>1669.68 ± 642.47</b> a (*,*)	2123.14 ± 443.3	<b>1130.92 ± 471.21</b> b (*,***)	1931.53 ± 746.75	1589.38 ± 706.2	<b>2176.42 ± 700.68</b> c (*,***)

In littorinids, the regression coefficient between the average population distance from the coast and the time-averaged upwelling index varied widely from nearly 0 for an integration time of 1 day to a maximum of 0.41 ( $p < 0.05$ ) when integrated 9-21 days (Fig. I.7). A similar pattern could be observed for *Verruca stroemia* cyprids, whose correlation peaked (0.80,  $p < 0.01$ ) for an integration time of 20-34 and 36-94 days (Fig. I.7). Both significant correlations corresponded to a negative linear relationship (Fig. I.7), indicating that sustained upwelling conditions were associated with populations being closer to the shore. Similar patterns were apparent for spionids and *Liocarcinus* spp. but those correlations were never significant (Fig. 7). No clear patterns were observed in *Hiatella* spp. and *Verruca stroemia* nauplii (Fig. I.7).

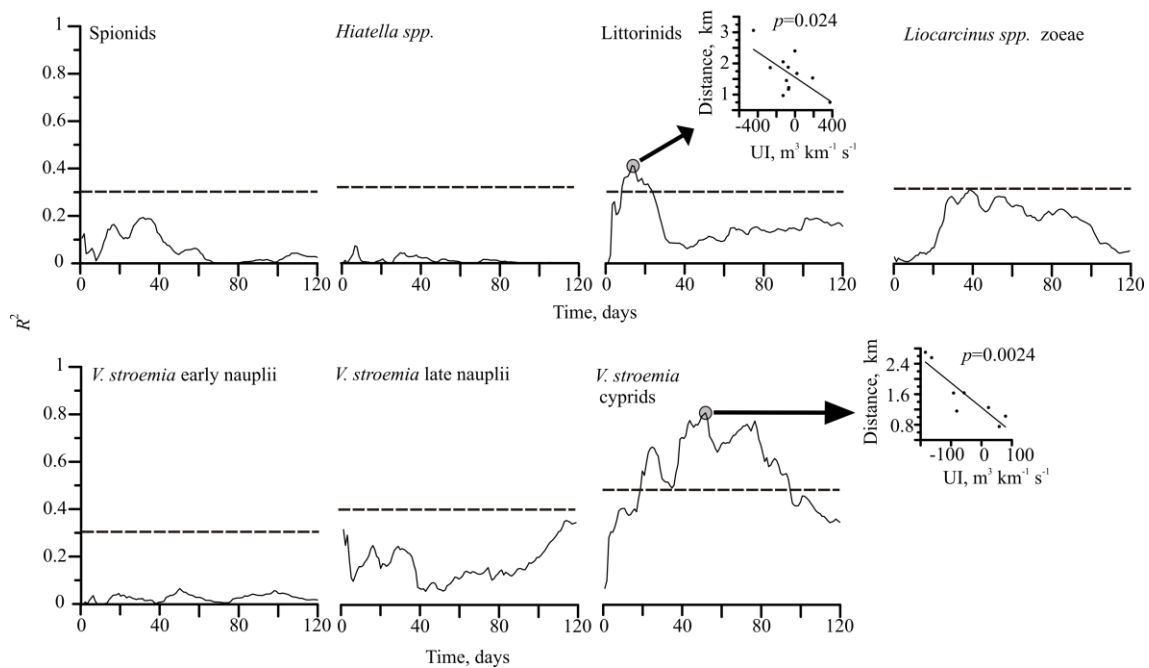


Figure I.7.  $R^2$  values obtained from the simple linear regressions between average distance offshore and upwelling indexes represented against the time scale used to average wind data from 1 to 120 days prior to each sampling. These plots are represented for the most abundant taxa. Discontinuous lines mark the  $R^2$  values that achieve signification ( $p$  value=0.05). For those taxa presenting significant relationships, the maximum  $R^2$  value is marked with a grey circle and the best fit between average distance offshore and average upwelling index (UI) is represented. Time scales used for these regressions are 13 and 52 days for littorinids and *Verruca stroemia* cyprids, respectively.



## Discussion

In our study, seasonality was the primary source of variability in meroplankton distributions. Multivariate analyses with larval abundances produced a temporal arrangement of groups of samples with no spatial structure (Fig. I.6), and distance from the coast explained a lower proportion of variance in meroplankton abundance than water column variables (Table I.1). Nevertheless, larval concentrations within each monthly transect were far from uniform, adopting spatial patterns which were related to the upwelling-downwelling regime in two taxa (Fig I.7). This relationship emerges only when integrating the upwelling dynamics across temporal scales comparable to the lifespan of the planktonic larvae.

### *Seasonality*

Changes in the abundance of the most common larvae (*Hiatella* spp., littorinids and *V. stroemia* early nauplii) define the biological seasonality, dominated by nauplii in late winter and spring and veligers in summer and early autumn (Fig. I.6). A similar temporal pattern has been described in coastal waters off Ireland (Byrne 1995), England (Highfield et al. 2010) and Southern Spain (Gilabert 2001), and is likely a response to prey availability. For example, many european barnacles spawn when there is a higher abundance of prey for their larvae (Stone 1989, Vargas et al. 2006). Larvae of *V. stroemia* are generalist feeders (Stone 1989) and spawn throughout the year (Fig. I.5). In contrast, larvae of *Chthamalus* spp. are specialized in small flagellates, which become important in warm, nutrient-poor summer waters (Stone 1989, Agawin et al. 2000; in the Cantabrian Sea, Casas et al. 1999, Calvo-Diaz and García-Morán 2006). Accordingly, *Chthamalus* spp. spawns mostly during the July-October period (Fig. I.5). *Pollicipes pollicipes* also spawns during summer (Fig. I.5, Macho et al. 2005) and their feeding appendages resemble those of *Chthamalus* spp. (personal observations). Likewise, veligers, which consume phytoplankton smaller than 5 $\mu$ m (Raby et al. 1997), were more abundant during summer in our study (Fig. I.5, Fig. I.6).

*Upwelling-mediated cross shore distributions*

Classical models of larval transport involve the generation of a convergent upwelling front which separates coastal, outcropped deep waters from the surface waters carried offshore by Ekman transport (e.g. Roughgarden et al. 1988). Swimming larvae and other floating objects capable of counteracting the convergent vertical flow would accumulate at the front and be carried offshore, being dispersed far from the origin (Roughgarden et al. 1988). If the upwelling conditions are prolonged until completion of the larval phase, reversal to downwelling would carry the front onshore, favouring recruitment of the competent larvae to the adult habitat (Roughgarden et al. 1992). However, those conditions do not apply in the Central Cantabrian Coast, which lies at the fringe of the NW Iberian Upwelling system. Here, outcropping of the thermocline and formation of upwelling fronts rarely happens, even during episodes of significant Ekman transport (e.g.  $2000 \text{ m}^3 \text{ km}^{-1} \text{ s}^{-1}$  in September 2007; Fig. I.2, Fig. I.3, Fig. I.4). In addition, wind reversal typically happens at scales of 3-4 days (Fig. I.4) much shorter than larval lifetimes of most benthic species, to which we must add substantial diel variability due to thermal sea-land breezes (Varela et al. 2005). In summary, upwelling fronts are unlikely and, if present, the time scale of the process is unfavourable for the existence of dispersal-recruitment cycles (Roughgarden et al. 1992.).

Our larval distributions also suggest that classical theories based on upwelling-mediated transport across the whole shelf are not valid in our study area. Maximum abundances of veligers and barnacle nauplii in our coastal cruises are in the order of those found for closely related species in the West coast of North America, where larval nearshore retention was observed across the inner shelf (thousands of individuals  $\text{m}^{-2}$ , Fig. I.5; Shanks & Shearman 2009). In agreement with these observations, nearshore distributions in 5 out of 7 abundant larval taxa were uncorrelated from the upwelling activity (Fig. I.7). To our knowledge, this can only be explained by active attachment to the shore by opposition to vertical currents (e.g. Poulin et al. 2002, Shanks and Brink 2005, Morgan et al. 2009 for meroplankton; see Genin et al. 2005 for an empirical test for the whole zooplankton community). Note that all the organisms studied would be able at least to resist the vertical flow in the water column (Chia et al. 1984) and may potentially behave as active organisms in this way. In contrast, in the case of *V. stroemia* cyprids and littorinid veligers spatial distributions were affected by Ekman transport and larvae were closer to the coast during sustained upwelling conditions (Fig. I.7). It is plausible that ontogenic migration to deep water layers by these larvae may have favoured

onshore transport during upwelling, following Grantham's hypothesis (1997). We have not sampled the vertical distribution of these species, but this type of pattern has been clearly documented at the upwelling system off California, both for cyprids (Shanks & Shearman 2009, Tapia et al. 2010) and for competent gastropod veligers (Fuchs 2005). In the case of *Verruca stroemia*, the ontogenic change in behaviour is clear: contrarily to cyprids, the distribution patterns of the naupliar stages are not correlated with Ekman transport (Fig. I.7). Thus, nauplii may actively swim against the vertical currents remaining in very coastal waters (Table I.2). This means that, for this species, the metamorphosis to the cyprid and its associated vertical migration to the bottom layers may occur quite close to the coast and not offshore at the upwelling front as Grantham (1997) suggested.

Our analysis reveals that the cross shore distribution of cyprids and littorinids is significantly correlated with the upwelling activity, but only when the latter is averaged over certain intervals of time. This is apparent in our plots of correlation coefficient vs. time lapse of integration, which shows a smooth increase from nearly 0 at 1 day averaging time to a peak correlation at some species-specific time interval (Fig. I.7). This result may be spurious to some extent, since estimations using long time averages include the data from shorter time averages and since meteorological systems are essentially autocorrelated at different time scales (Brett & Tuller 1991). However, peak correlations are obtained for averaging periods which are biologically meaningful. For example a peak negative correlation between distribution and upwelling was obtained when using a 13-day average Ekman transport in littorinid veligers. Littorinid larvae remain in the plankton 30 days (Janson 1987), but a significant fraction as trocophora, thus development times in the order of tens of days make sense for veligers. Moreover, peak correlations were achieved at 52 days integration time in cyprids (Fig. I.7), which is roughly consistent with planktonic duration times of 1-2 months in *Verruca stroemia* (Anderson 1992; cyprids may delay metamorphosis over longer periods, Pechenick et al. 1993). A similar sensitivity to the temporal scale of integration has been observed for the dependence of equinoplutei larvae on wind dispersal events in the English Channel (Lefevre et al. 2003). Likewise, differences in transport rates among short and long-lived annelid larvae have been attributed to the time scale of integration of physical events in the Bay of Seine (Lagadeuc 1992, Thiébaud et al. 1994). Thus, in the context of short-lived upwelling pulses prevailing in the Central Cantabrian Coast, larval distributions would reflect the average transport resulting from the series of "push and pull" events within the larvae development time. Due to the high wind variability in our study area, net offshore export

should be more reduced than in strong upwelling areas, where wind direction and velocity are more consistent (Mann & Lazier 1996). This would certainly contribute to the very nearshore larval distributions observed in our study.

*Very coastal larval retention and nearshore dynamics*

Active larval behaviour and the nature of the Ekman transport in our region are the most plausible causes for the very coastal meroplankton distributions. Theories based on long dispersal trajectories driven by the upwelling activity (Roughgarden et al. 1988, Roughgarden et al. 1992, Grantham 1997) are not supported by our biological and meteorological data. Contrarily, our results suggest that local retention patterns and short dispersal distances are the rule, which agrees with the new insights in coastal population ecology. Extensive dispersal is not required for the cohesion of the coastal metapopulations (Pechenick 1999). It has been shown that a reduced larval exchange between populations is sufficient to keep their viability and genetic diversity (Cowen et al. 2000, Cowen et al. 2005). Thus, the benefits of remaining close to the parental habitats for settlement (higher survival, higher fitness in local habitats) may largely overcome those of extensive dispersal (Pechenick 1999).

Our observed nearshore meroplankton distributions seem to be defined by coastal physical processes. We have observed repeatedly that the abundances of *Hiatella* spp. veligers, juvenile flatworms and *Echinocardium cordatum* plutei peaked close to slicks and foam lines (Fig. I.5). These structures coincided with vertical uplifting of the thermocline (Fig. I.2, Fig. I.3) that we interpret as internal waves. Zooplankters have been shown to accumulate in the crest of internal waves by resisting the vertical currents in the convergence area associated with the slick (Zeldis & Jillet 1982, Shanks 1995, Pineda 1999). It is the same behaviour that potentially reduces offshore export by Ekman transport. Unfortunately, we lacked the resolution to confirm the accumulation of some species in the crest of the internal waves. Future studies focused on the interaction between nearshore physical features and biological characteristics such as lifespan of the planktonic stage or prey characteristics are required given the increasing evidence for larval retention at the coast. This evidence clearly contradicts the idea of meroplankton as passive tracers of water movements.



## Chapter II: Alongshore larval distributions





### **Introduction**

The study of larval distribution patterns in the coastal ocean has important implications for the understanding and management of the intertidal benthic communities, allowing the link between oceanic larval pools and adult populations to be made (Botsford et al. 2001, Botsford et al. 2003). Traditionally in plankton studies, water column variables like temperature, nutrients, chlorophyll are included in regression models to explain the spatial distribution of planktonic organisms (e.g. Gili et al. 1991, Thibault-Botha et al. 2004). However, many studies suggest that the topographic characteristics of the coast also determine to a great extent the distribution of planktonic larvae of benthic, coastal organisms, and their subsequent settlement patterns (Archambault and Bourget 1998, White et al. 2010).

There are several physical mechanisms that may potentially mediate the effect of coastal topography on larval distributions. The permeability of the coastal boundary layer ("sticky water" *sensu* Wolanski 1994) has been related to coastline complexity (Wolanski and Hammer 1988, Wolanski 1994, Wolanski and Spagnol 2000, Lambrechts et al. 2008). Its across shore width may depend on viscosity, current velocity and length scale of a topographic feature (Becker 1991, Penven et al. 2000). Two properties, permeability and thickness, define the strength of the layer as a barrier for larvae. In addition, there have been observations of flow recirculation patterns and larval retention at the lee of headlands (Roughan et al. 2005, Mace and Morgan 2006). Therefore, topographic characteristics of the coast may have an effect on physical processes which in turn modify the water residence time affecting larval dispersal (Largier 2004). In spite of these potential and important effects, a generalized, quantitative approach to the relationship between coast topography and meroplankton distribution has never been attempted. Examples abound on the effect of individual features as bays and capes (St. John 1958, Byrne 1995, Mace and Morgan 2006) but not as much in a generalized, landscape approach (but see Archambault and Bourget 1998) and never quantitatively or involving a spatial scale component. In addition, samples for the estimation of larval abundance are usually collected far from the coastal boundary layer (Shanks and Brink 2005), where larval retention patterns are taking place (Wing et al. 1998, Morgan et al. 2011).

Here we have followed a landscape, multi-scale spatial regression approach to explore the quantitative relationship between topographic characteristics of the coastline and the distribution of meroplanktonic taxa and stages. This approach has been applied to a set of very



nearshore stations sampled during summer 2008 in a 200 km coastal stripe along the Central Cantabrian Sea, and has allowed us to separate the effects of *in situ*, water column properties from the effects of coastal topography and of species-specific spatial autocorrelation patterns (Legendre 1993, Bjørnstad et al. 1999). Our results confirm our initial hypothesis that topography explains significant variability in the spatial distribution of meroplankton, and suggest that interaction between currents and larval behaviour play an important role in the fate of larvae.

## **Material and methods**

### **Meroplankton sampling**

We carried out a 13 days survey from July 3 to July 15 2008. We planned to conduct sampling once at each of 42 transects perpendicular to the coast at 4 km intervals covering the total length of the Asturian coast (200km; Fig. II.1). Each transect had two stations located at 200 and 1000m offshore, approximately, sampled with the 9.40m boat “Nueva Asturias” and the research vessel “Garcia de Cid”, respectively. At each station, we towed vertically from the bottom to the surface a triple WP2 net, 100µm pore width and a radius of 20cm, adequate to catch small larval taxa like early barnacle nauplii. Net length and width were specially designed to avoid clogging in coastal waters (Sameoto et al. 2000). Samples were preserved in 250 ml bottles in 4% formaline with sea water. We searched for all the larvae in the entire sample, and identified them to the lowest possible taxonomic level, which was species or at least genus in most of the cases. We calculated the total volume filtered from net width and station depth and larval abundances were expressed as individuals m<sup>-3</sup>.

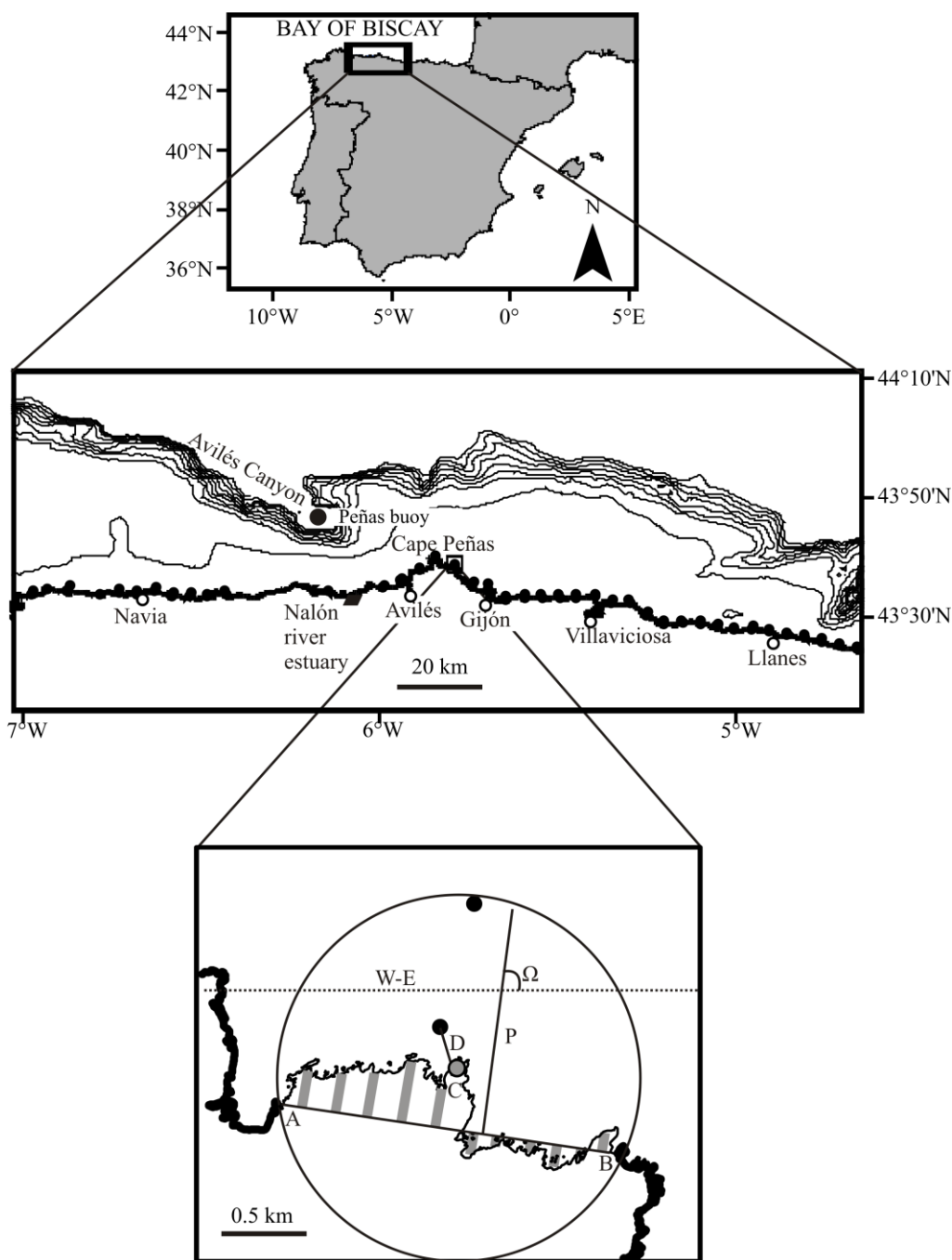


Figure II.1. Study area along the Central Cantabrian Sea. Main topographic features and coastal towns are shown together with the position of an oceanographic buoy, the isobaths every 100m till 800m and the position of every transect. In the map below, we show the components used to calculate the topographic variables (see material and methods). Dark points mark the stations. In this case, the method is applied to the most coastal station on a scale of 2000 m diameter of the circumference. A and B are the intersection points between the line and the circumference. C is the closest point in the coastline, marked in grey, at a distance D and also the circumference centre. P is the perpendicular to the A-B line. A dotted line shows the longitudinal axis W-E). The barred surface is the area used to obtain the convexity index and the coastal segment analysed to calculate the fractal dimension is represented with a thinner line.  $\Omega$  is the angle that approximates the coastal orientation.

### Water column variables

In every station, we employed a SBE25 CTD to measure the main water physical properties: temperature, salinity, density and fluorescence (Table II.1 for the acronyms). Sea surface temperature (SST) was obtained directly from the CTD casts at 1m depth. Dilution factor (DF) was calculated as follows (Pettine et al. 2007):

$$DF=100 (SSb-SS/SSb)$$

where SSb is the mean background surface salinity (35.7) and SS is the surface salinity in situ. DF is a proxy for the influence of continental runoff on the coastal ocean. An index of stratification (SI) was measured as the bottom minus surface sigma-t densities in  $\text{kg m}^{-3}$  (Albaina and Irigoien 2007) and gives us an estimation of the water column structure. Fluorescence values were transformed to chlorophyll-a concentrations in  $\text{mg m}^{-3}$  by calibration against fluorometer chlorophyll-a measurements ( $R^2=0.82$   $p=0.001$ ) from Niskin bottle water samples taken at 0 and 20m depth in every station. These water samples were filtered onto 0.2 and 5  $\mu\text{m}$  GF-F filters and the filters were frozen and extracted in 5 ml 90% acetone during 24 h in dark and cold conditions. Chlorophyll-a concentration was measured with a Turner Designs 10 fluorometer following the acidification method of Yentsch and Menzel (1963). We then, integrated chlorophyll-a averaged over the depth of the station to calculate CHLA in  $\text{mg m}^{-3}$ . As we fractionated it, we obtained CHLA<5 as the percentage of chlorophyll a between 0.2 and 5 $\mu\text{m}$ . Both variables measure the amount and size composition of larval potential food. We used wind data recorded every 50 min aboard the “Garcia de Cid” to calculate daily means of the Bakun’s upwelling index 1973 (UPW) in  $\text{m}^3 \text{km}^{-1} \text{s}^{-1}$ .

Table II.1. Acronyms of the variables, models and components of the variation

Acronym	Meaning
SST	Sea surface temperature
DF	Dilution factor
SI	Stratification index
CHLA	Chlorophyll a concentration
CHLA<5	Percentage of chlorophyll a in particles smaller than 5 $\mu$ m
UPW	Upwelling index
OR	Orientation
CO	Convexity
FR	Fractal dimension, complexity
D	Distance to the coast
BS	Bottom slope
T	Variance explained by models with topographic variables only
W	Variance explained by models with water column variables only
E	Variance explained by models with all the environmental variables
S	Variance explained by models with spatial coordinates only
T+S	Variance explained by models with topographic variables and spatial coordinates
W+S	Variance explained by models with water column variables and spatial coordinates
E+S	Variance explained by models with all the environmental variables and spatial coordinates
<i>t</i>	Pure topographic component of the variation
<i>w</i>	Pure water column component of the variation
<i>s</i>	Pure spatial component of the variation
<i>txw</i>	Interaction component of the variation between topography and water column
<i>txs</i>	Interaction component of the variation between topography and space
<i>wxs</i>	Interaction component of the variation between water column and space
<i>txwxs</i>	Interaction component of the variation between topography, water column and space

We know that, as the survey lasted 13 day, the spatial trends obtained from these data are intrinsically influenced by changes with time. To know if spatial gradients at least in temperature and in chlorophyll are consistent for a given moment and also to look for mesoscale relevant features, we explored SST and chlorophyll-*a* concentration maps derived from daily images retrieved by the MODIS sensor (MODerate Resolution Image Spectroradiometer). The data was obtained from the Ocean Colour Web (Feldman and McClain 2008; Goddard Space Flight Center, NASA; [oceancolor.gsfc.nasa.gov](http://oceancolor.gsfc.nasa.gov)).

### Topographic variables

Coastal topography was quantified using a Geographic Information System (GIS) software to calculate three indexes: orientation, convexity and complexity. For each station, we first located the closest point on the coastline and drew a circumference centred on this point with diameter equal to the spatial scale under consideration (either 0.5, 2, 5 or 20 km). The acronym for each variable (Table II.1) is depicted with these numbers to know the spatial scale of interest. We drew a straight line between the two farthest points of intersection between the circle and the coastline, hereafter called A and B, and set a straight line between them. Orientation (OR) was obtained as the angle formed by the perpendicular to this line and the E-W axis, ( $\Omega$ , Fig.II.1). Note that  $0^\circ$  means a pure east orientation and  $180^\circ$  a west one. A proxy for convexity (CO) was inferred subtracting the sea surface down the A-B line from the land surface above it. To standardise we divided this difference by the total area of the circle. Positive values of this index point indicate convex coastlines. To measure the complexity of the coastal segment between A and B we used a proxy of its fractal dimension (FR), a method that has been found useful in previous studies (e.g. Mandelbrot 1967, Jiang and Plotnick 1998). This method assumes that the measured length of the coast increases with increasing map scale, due to an increase in the level of detail shown in the map. The fractal dimension measures the pace at which the length changes with the scale of measurement, thus a complex coast will have a higher fractal dimension than a simple one. We approached the fractal dimension of each fragment of the coastline with the “box-counting” method implemented in MATLAB (Moisy 2008). This method superimposes a regular grid of boxes of length R on the image of the line and counts the number (N) of occupied boxes. This routine is repeated with box sizes that are powers of 2 (i.e. 1, 2, 4, 8, ...). The number N of boxes of size R needed to cover a fractal set follows a power-law function

$$N = N_0 * R^{(-df)}$$

with  $df \leq 2$ .  $df$  is known as the Minkowski-Bouligand, Kolmogorov or simply box-counting dimension. If the set has some fractal properties over a limited range of box size R, this may be appreciated by plotting the local exponent, obtained as follows

$$df = - d \ln N / d \ln R$$

as a function of R. We chose the range of R with a relatively constant value of  $df$  and averaged the values of  $df$  to obtain the fractal dimension of the line (FR).

To this set of topographic variables we added distance from the station to the closest point in the coast (D) and bottom slope (BS). This last one was calculated as the closest known depth to every station obtained from bathymetry profiles divided by the distance to the coast.

### **Statistical analyses: meroplankton community**

This pool of statistical methods was done with PRIMER v6 software (Plymouth Routines In Multivariate Ecological Research) following Clarke and Gorley 2006. To characterize larval assemblages, we carried out a multidimensional scaling analysis (MDS) on the Bray Curtis similarity distances matrix among samples, calculated with  $\log + 1$  transformed abundances. Simultaneously, a hierarchical cluster was done to search for clear groups of samples corresponding to distinct meroplankton assemblages. In such a case, we carried out a similarity percentage routine (SIMPER) to examine the contribution of the abundance of each species to the dissimilarities among groups. Same procedures were used to characterize the stations by their water column, in situ variables (SST, SI, DF, CHLA and CHLA<5) and topography (OR, CO, FR, D, BS) at the four spatial scales tested, now based on Euclidean distances with previously normalised data. These five sets of explanatory variables were forced to explain the larval resemblance matrix one by one using the BEST procedures (Bio-Env and Stepwise analysis), which link the abiotic with the biotic pattern. The significance of every match was tested with 1999 random permutations of the rank correlation coefficient  $\rho$ .

With the resemblance matrixes obtained from the previous analyses, we looked for the intrinsic spatial autocorrelation of meroplankton, water column variables and topography at the 4 spatial scales. We employed Mantel correlograms built with the Pearson's R coefficient calculated for a limited range of distance classes (from 4 to 170 km). Their significance was tested with 1999 random permutations. Typical patch size was estimated using the distance class at which the coefficient first passes below 0 (Zhang et al. 2006). These procedures were carried out with SAM v4 software (Spatial Analysis in Macroecology) following Rangel et al. 2006.

### **Statistical analyses: species-specific procedures**

To assess spatial autocorrelation in each taxon and each environmental variable, we plotted the Moran's I coefficient of autocorrelation against the distance classes in km. Significance was achieved again with Mantel's test using 1999 random permutations and patch size was inferred as before.

We studied the importance of environmental variables as predictors of spatial distributions for the most abundant species. SAM v4 software performs Generalised Least Squares Analyses (GLS) which takes into account autocorrelation. Due to potential multicollinearity, variable selection was carried out by a manual stepwise, backward elimination retaining those that were significant. To validate the multiple regression model, all the variables previously rejected were added one by one to the ones remaining to examine their effect on the  $r^2$ . We also introduce the 4 spatial scales separately in the case of OR, CO and FR in order to avoid dependence between scales. Finally, we checked that the residuals fitted a normal distribution and that Condition Number was well below 4. This last parameter measures how the solution model changes if original data are slightly modified (Cheney and Kincaid 2008). The variance corresponding to every significant variable was achieved removing them from the model following an increasing standard coefficient order. We checked that the sum of these variances equals the total  $R^2$  of the whole model.

We have followed the statistical methods used in Lagos et al. 2008 and Ayata et al. 2011 but with two personal adaptations. First, we considered another set of variables, the topography descriptors, separately from the classic water column variables. That makes our results more complete but also more complex, as more components of the variation arise. Second, we used multiple linear regression analyses retaining only significant variables with the spatial coordinates. Previously mentioned authors used third order polynomial functions with both x and y coordinates. We think that with these functions we may get overfitted models respect to those based on linear expressions that are used for the rest of variables and thus increase artificially the variance explained by space. In addition, we think that the main spatial structures in our region are alongshore longitudinal gradients, which can already be extracted with linear fits.

Seven kinds of models arise from all the possible combinations between water column predictors, topographic variables and spatial coordinates (Tables II.1 and II.2). GLS were repeated under these 7 assumptions, which enable a simple way to calculate the different components of the variation explained for every taxon by subtraction among corresponding  $R^2$  (Tables II.2 and II.3). Our aim is to discern between these paths by which larval patterns can be structured. The components of variation (Table II.1 for acronyms) include the pure, direct effects on larval distributions of topography ( $t$ ), water column characteristics ( $w$ ) and space ( $s$ ). This variance explained only by space points to aggregations driven by larval behaviour or other environmental variables that we have not taken into account. The four interactions between these pure components were also taken into account. The topographically structured water column effect ( $txw$ ) points to the importance of water column, in situ variables mediated by topography as coastal shape characteristics may influence larval spatial patterns changing the physicochemical properties of the water masses. Similarly, in some extent, the variance explained by topography could be mediated by the space if the coastal shape properties are aggregated. This component is the spatially structured topography effect ( $txs$ ). The spatially structured water column component ( $wxs$ ) measures the effects of water column properties aggregated in the space and reflects the spatial structure of larval distributions that is shared with that presented by the physicochemical properties of the pelagic environment. Finally, we expect a three ways interaction component ( $txwxs$ ), which points to the effects of aggregated topographic features on the water column that affect larval distributions. Although this partitioning of the variance is arbitrary, this procedure allows us to infer the relative importance of topography, water column and space and how they interact on larval distributions.



Table II.2. Description of the regression models performed to obtain the different components of variation. Note that, although UPW has been included in the W model, it is not strictly a water column, *in situ* variable. See Table I for the acronyms.

Kind of model	Variables included	Implicit components of variations
T	OR, CO, FR, D, BS	$T = t + txw + txs + txwxs$
W	SST, DF, SI, CHLA, CHLA<5, UPW	$W = w + txw + wxs + txwxs$
E	OR, CO, FR, D, BS, SST, DF, SI, CHLA, CHLA<5, UPW	$E = t + w + txw + wxs + txs + txwxs$
S	Space X, Space Y	$S = s + txs + wxs + txwxs$
T+S	OR, CO, FR, D, BS, Space X, Space Y	$T+S = t + s + txw + wxs + txs + txwxs$
W+S	SST, DF, SI, CHLA, CHLA<5, UPW, Space X, Space Y	$W+S = w + s + txw + wxs + txs + txwxs$
E+S	OR, CO, FR, D, BS, SST, DF, SI, CHLA, CHLA<5, UPW, Space X, Space Y	$E+S = t + w + s + txw + wxs + txs + txwxs$

Table II.3. Calculations of the different components of variation. (\*)  $txwxs$  was calculated from the total variance of any of the regression models once the rest of the components are known. See Table II.1 for the acronyms.

Component of variations	Calculations
$t$	$t = (E+S)-(W+S)$
$w$	$w = (E+S)-(T+S)$
$s$	$s = (E+S)-E$
$txw$	$txw = (W+S) - ((E+S)-(T+S))-S$
$txs$	$txs = E - ((E+S)-(W+S))-W$
$wxs$	$wxs = (T+S)-S-T$
$txwxs$	(*)

### Trends with larval age

We examined the effects of the time spent as planktonic larvae in the water column on their spatial distribution. As accumulations can be driven by topographic and/or hydrographic processes that increase water residence time in a given place, we regressed total larval abundances with the mean planktonic larval duration (PLD) for each station. The PLD for each species and stage was obtained from the literature (Table II.4). As we also hypothesized a time-dependent shift of the characteristics that define larval distributions, different components of the variation were regressed with the PLD.

Table II.4. Planktonic larval duration (PLD) of all the taxa considered in the individual analyses.

Taxa	PLD	Reference
Spionids	45	Blake and Arnovsky 1999
<i>Nephtys</i> sp.	84	Ruth and Lindholm 2002
Littorinids	30	Janson 1987
<i>Hiatella</i> spp..	90	Scheltema 1971, B. Campos, personal communication
<i>Amphiura</i> spp.	88	Sköld et al. 1994
<i>Paracentrotus lividus</i>	19	Gosselin and Jangoux 1998
<i>Chthamalus</i> spp. early nauplii	9	Burrows et al. 1999
<i>Chthamalus</i> spp. late nauplii	14	Burrows et al. 1999
<i>Chthamalus</i> spp. cyprids	30	Burrows et al. 1992, Crisp 1950
<i>Balanus perforatus</i> early nauplii	4.5	Anil et al. 1995, Bassindale 1936
<i>Balanus perforatus</i> late nauplii	9.5	Anil et al. 1995, Bassindale 1936
<i>Balanus perforatus</i> cyprids	25	Anil et al. 1995, Bassindale 1936
<i>Liocarcinus</i> spp. zoeae	26.5	Lindley 1988

## **Results**

We were able to sample a total of 67 stations along the Central Cantabrian Sea coast. There was a 30km length gap located close to the Aviles Canyon (Fig. II.1) that was not surveyed due to severe bad weather.

We identified a total of 16 different meroplankton taxa and/or stages. Only common and abundant groups (usually far above 1 individual m<sup>-3</sup>) were used for the species-specific procedures, their alongshore distribution was plotted and described, and we look for an approximated planktonic larval duration (PLD) for every one of them in the literature (Table 4). These were the segmented larvae of the annelids of the spionid family and *Nepthys sp.*, mollusc veligers of litorinids and the bivalve *Hiatella spp.*, the plutei larvae of the brittle star *Amphiura spp.* and the edible sea urchin *Paracentrotus lividus*, the barnacles *Balanus perforatus* and *Chthamalus spp.* separated by their larval stages: early nauplii (stages I to III), late nauplii (stages IV to VI) and cyprids, and the zoeal stages of the crab *Liocarcinus spp.* We found other less abundant organisms which were only included in the meroplankton community analyses: cyphonaut larvae of the bryozoan *Membranipora spp.*, juvenile flatworms, possibly included in the genus *Convoluta*, early nauplii of the barnacles *Verruca stroemia* and the edible *Pollicipes pollicipes*, and different decapod larvae.

### **Distribution of the topographic variables**

At scales of 0.5 km (Fig. II.2) topographic variables seemed evenly distributed, with clearer patterns arising at larger scales probably due to geomorphological characteristics of the coast. On the 20 km scale, the highest and lowest orientation values were found at the western and eastern sides of Cape Peñas, respectively; convexity peaked in Cape Peñas and presents low values to the east of the cape, around Gijón; complexity increased in the western coast close to Navia while decreases markedly around Villaviciosa (Fig. II.2)

### **Distribution of the water column, *in situ* variables**

We found that SI values were more variable in the western domain of the study region while around Llanes they are grouped around an average value of  $0.2 \text{ kg m}^{-3} \pm \text{SD}$  (Fig. II.3). About DF, it seems to be evenly distributed, although we observed a clear peak on the western side of Cape Peñas (around 2.5%), possibly due to the proximity of the Avilés and Nalón river estuaries (Fig. 3). Both SST and CHLA<sub><5</sub> increased eastwards from 17.5 to 19C° and from 20 to 70%, respectively (Fig. II.3). However, CHLA seems to decrease eastwards from values around  $1 \text{ mg m}^{-3}$  near Navia to values below detection in coastal waters in the proximity of Llanes (Fig. II.3). We are aware that these trends are partially due to temporal changes in the properties of the water masses in our region. However, satellite imagery for a given moment (Fig. II.4) indicates that there is also a pure spatial component of variation. Daily data point to clear oscillations in surface Ekman transport, although it was mainly positive with maximum values around  $700 \text{ m}^{-3}\text{km}^{-1}\text{s}^{-1}$ . Close to Cape Peñas and in the eastern limit of our survey, we recorded slightly negative values pointing to upwelling relaxations (Fig. II.3). These fluctuations in the prevalent direction of wind induced currents can already be observed in the satellite imagery: the coastal stripe of cold, high chlorophyll a upwelled water was wider and more evident in the western half of our domain on July 3 and July 16 but not on July 8 (Fig. II.4). On July 8, when we were sampling the western side of Cape Peñas, downwelling dynamics evidenced by satellite imagery agreed with our measured negative UPW values. During both upwelling and downwelling situations, there was a clear alongshore gradient in temperature and chlorophyll (Fig. II.4).

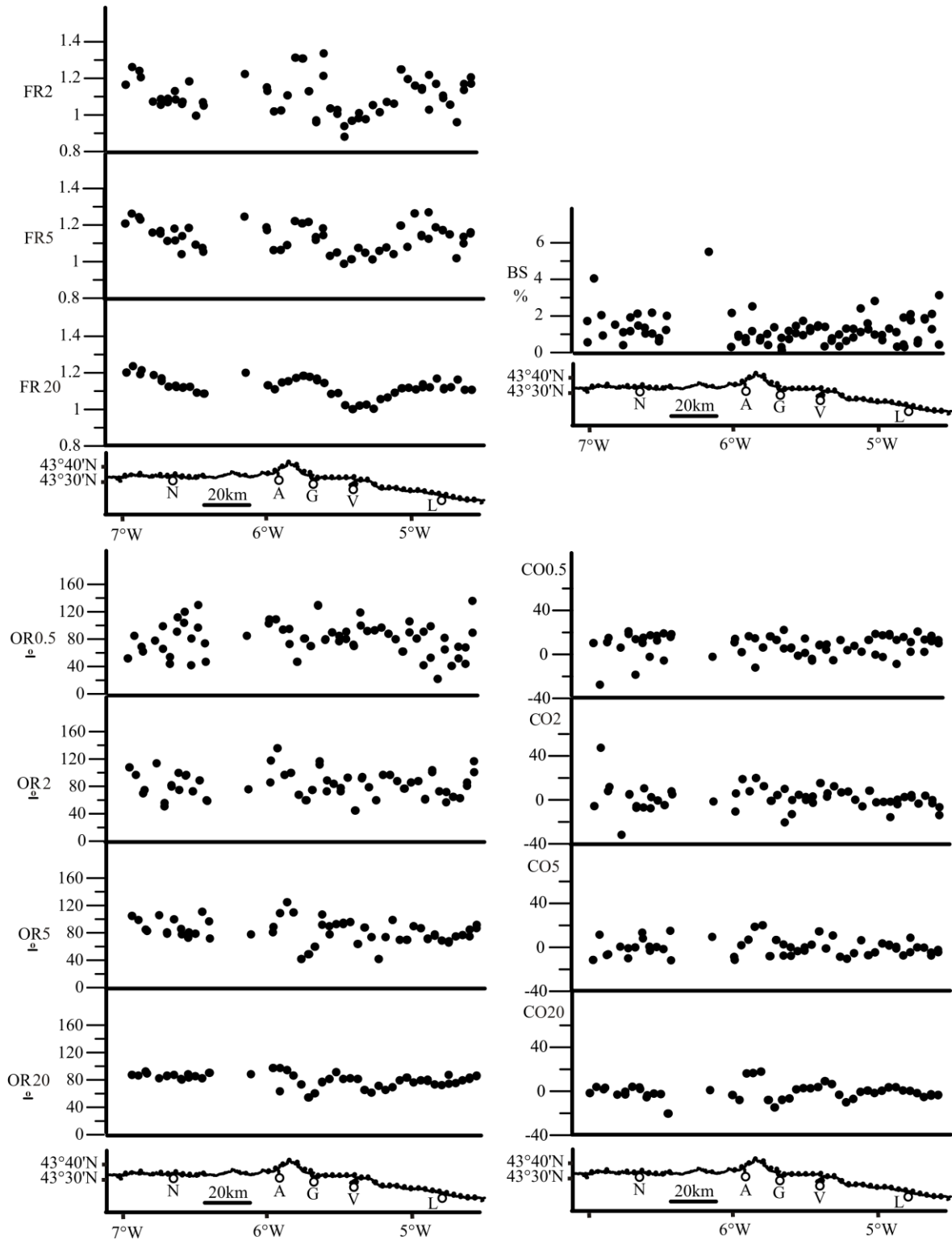


Figure II.2. Alongshore spatial distributions of topographic variables that were found to be significant in any regression model. The map below shows the location of the transects along the coast and the main coastal towns (N:Navia, A:Avilés, G: Gijón, V: Villaviciosa, L: Llanes). Note that both fractal dimension and orientation do not present units as they are non dimensional. See material and methods for the acronyms of the variables.

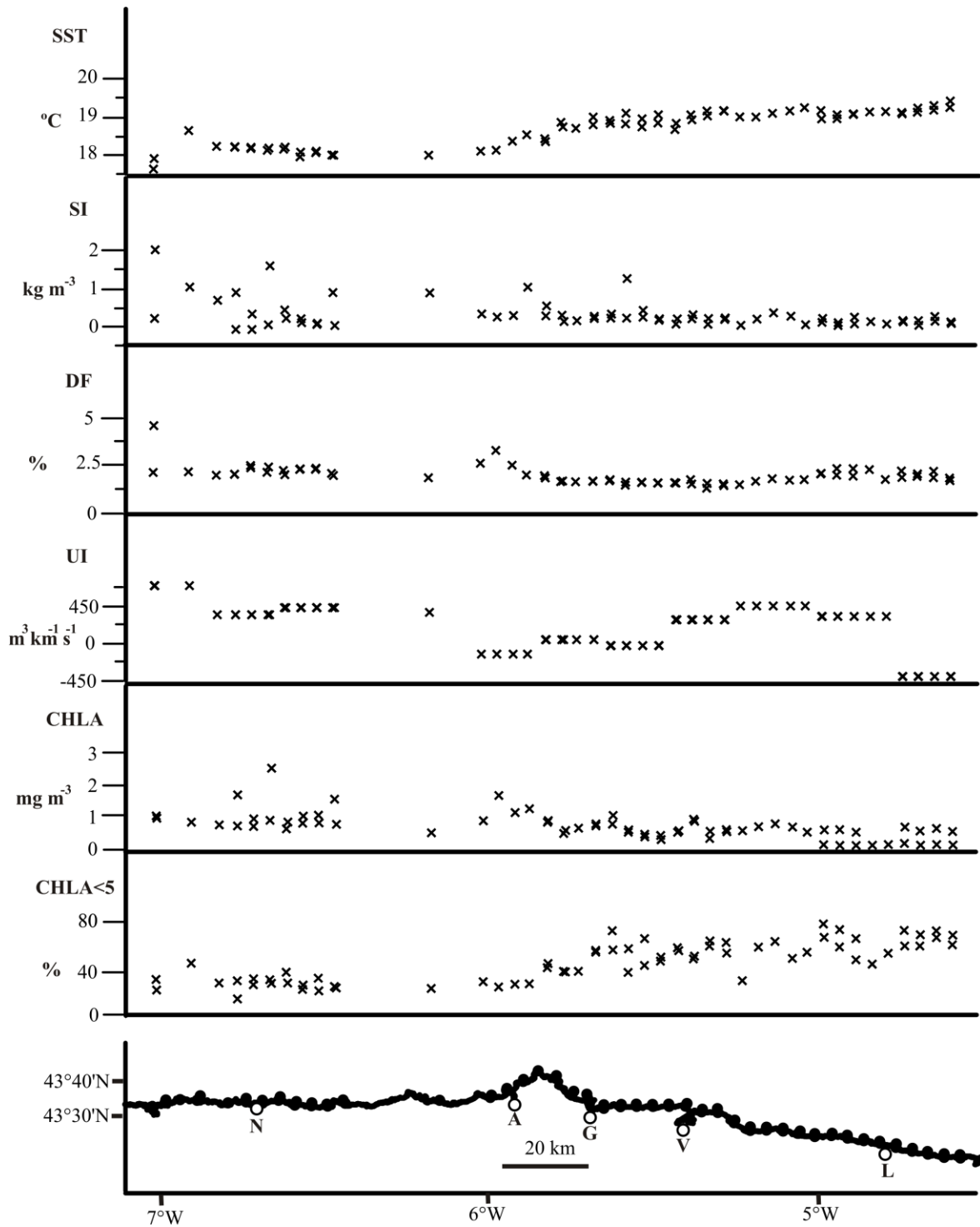


Figure II.3. Alongshore spatial distributions of water column variables that were found to be significant in any regression model. The map below shows the location of the transects along the coast and the main coastal towns (N: Navia, A: Avilés, G: Gijón, V: Villaviciosa, L: Llanes). See material and methods for the acronyms of the variables.

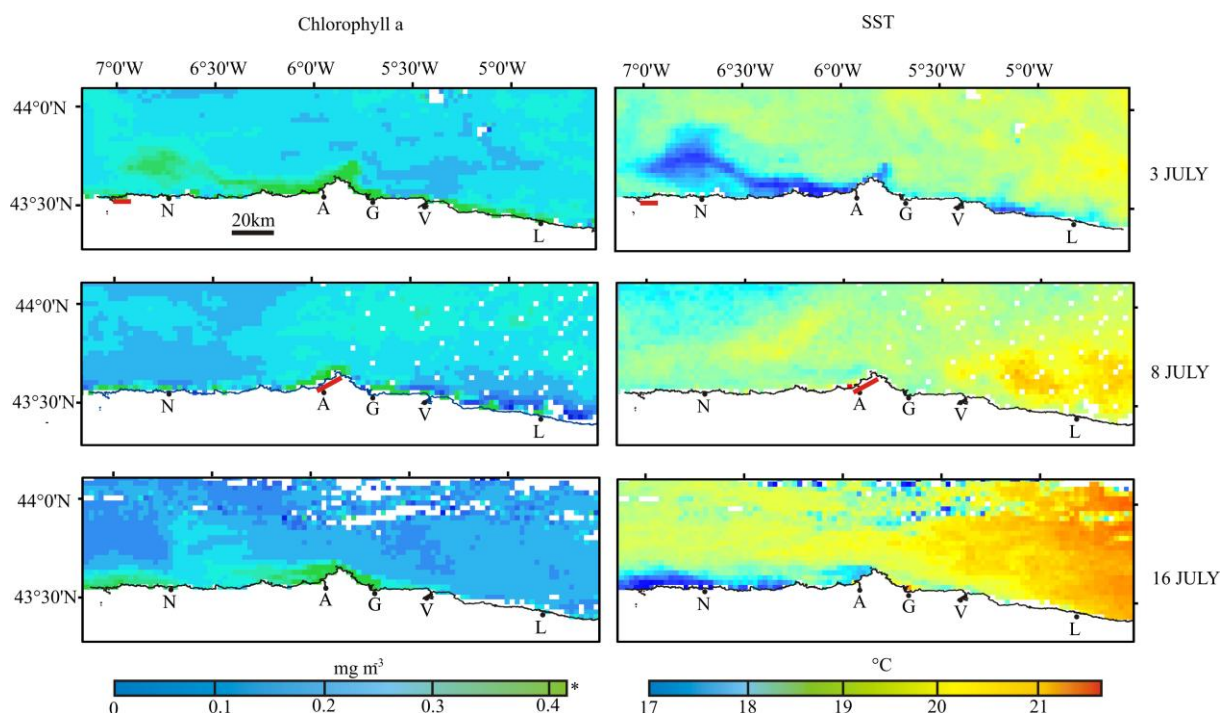


Figure II.4. MODIS satellite imagery of chlorophyll a and surface sea temperature for three different days. Red thick lines represent the coastal segment that was surveyed each day. Note that on 16<sup>th</sup> of July this line is not represented as we have already finished our study two days before. Each map shows the main coastal towns N: Navia, A: Avilés, G: Gijón, V: Villaviciosa, L: Llanes).

### Meroplankton distribution

Mollusc veligers of litorinids and the bivalve *Hiatella* spp., were the most abundant larvae in our survey, with maximum abundances above 1000 ind m<sup>-3</sup> (Fig. II.5). Meroplankton was more abundant in the eastern half of the study area (Fig II.5, Fig. II.6). This pattern is especially evident for *Balanus perforatus* cyprids, *Amphiura* spp. and *Paracentrotus lividus* in a region between Villaviciosa and Llanes, where veligers also peak. Exceptions are the spionid annelids, with more uniform alongshore larval densities; *Chthamalus* spp. early and *Balanus perforatus* late nauplii, with higher abundances to the west; *Balanus perforatus* early nauplii, peaking around Cape Peñas; and, finally, *Liocarcinus* spp. and *Nephtys* sp were evenly distributed (Fig. II.5, Fig. II.6).

### Meroplankton community analyses

The main result of these analyses is the greater importance of the water column predictors in setting a longitudinal differentiation in the larval community, an alongshore pattern also reflected in the pure distributions of both species and variables (Fig. II.5, Fig. II.6).

Larval community assemblages were defined on the between-samples Bray-Curtis distance matrix. The resulting MDS shows a very clear pattern when we overlap the groups obtained from the respective cluster: Samples from the western half of our study area (group 1) and those from the eastern side (group 2), with the limit set at Cape Peñas (Fig. II.7). SIMPER procedure shows that veligers, due to their high abundances, are the main components providing the similarity inside both groups: litorinid contribution is 19.51 and 21.28% and *Hiatella* spp. contribution is 15.8 and 21.68% for groups 1 and 2, respectively. Differences between groups 1 and 2 are mainly based on changes in the mean abundances of *Balanus perforatus* early nauplii (15.13 to 1.77 ind m<sup>-3</sup>), *Hiatella* spp. (34.67 to 151.35 ind m<sup>-3</sup>), *Chthamalus* spp. early nauplii (15.13 to 5.88 ind m<sup>-3</sup>) and litorinids (54.95 to 138.03 ind m<sup>-3</sup>), explaining 11.36, 9.08, 7.44 and 7.01% of the total dissimilarity between groups, respectively.



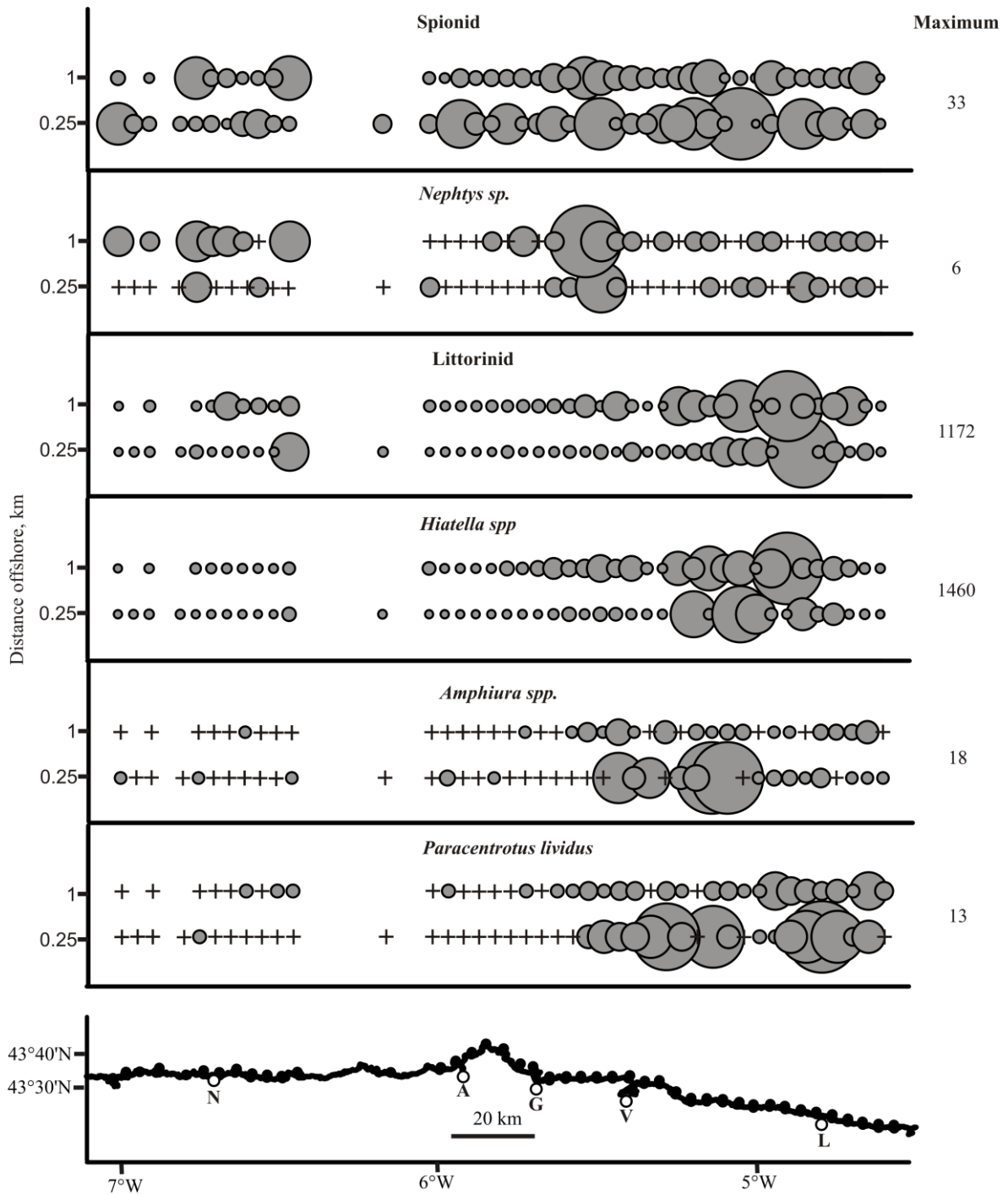


Figure II.5. Alongshore spatial distributions. The map below shows the location of the transects along the coast and the main coastal towns (N: Navia, A: Avilés, G: Gijón, V: Villaviciosa, L: Llanes). For every taxa, approximated distance offshore is represented. Circles point to relative larval abundances respect to the maximum indicated in ind m<sup>-3</sup>, while crosses mark 0 values.

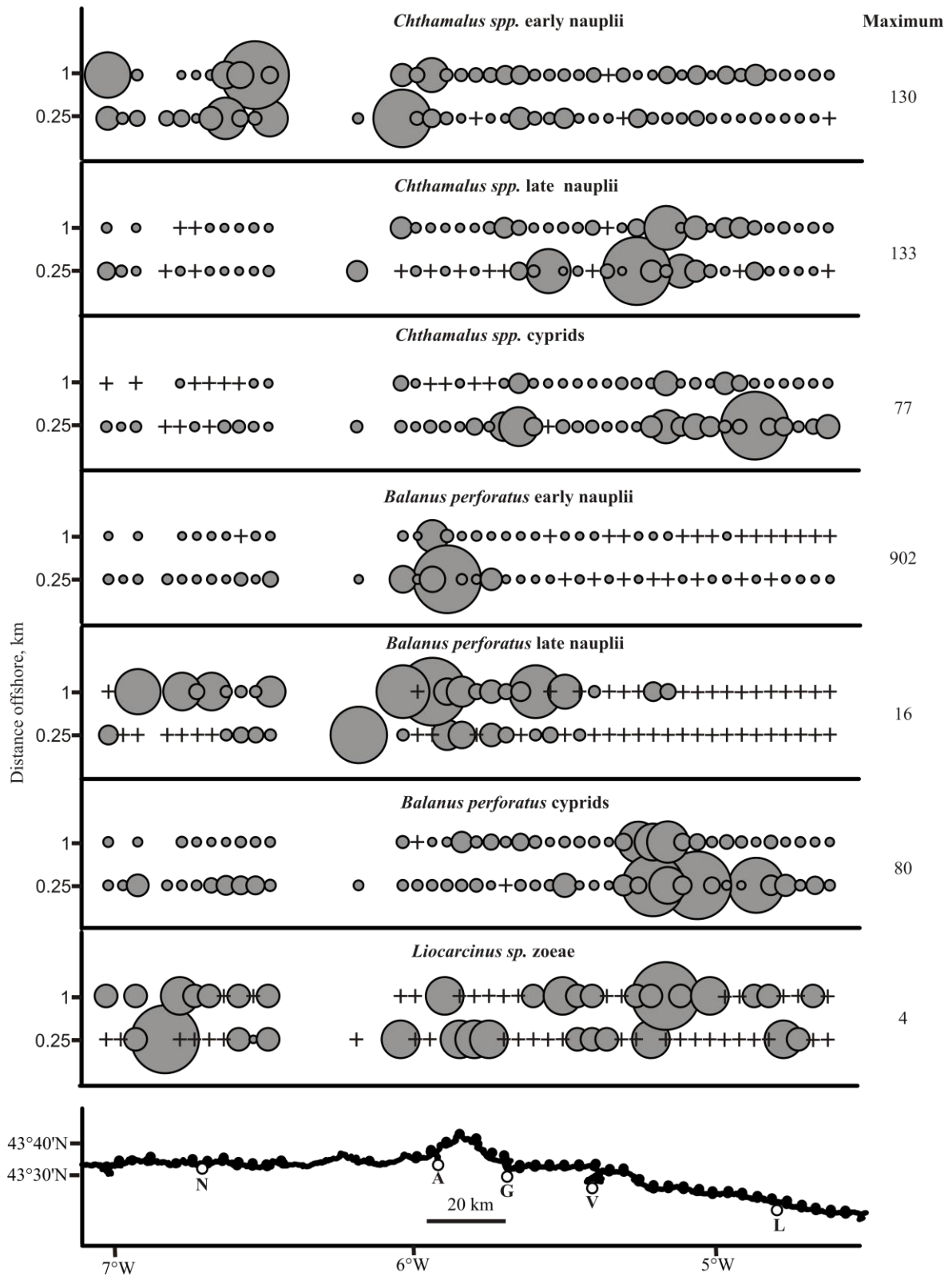


Figure II.6. Alongshore spatial distributions. The map below shows the location of the transects along the coast. For every taxa, approximated distance offshore is represented. Circles point to relative larval abundances respect to the maximum indicated in  $\text{ind m}^{-3}$ , while crosses mark 0 values.

On the other hand, multivariate analysis made with *in situ*, water column variables show a very similar pattern (Fig. II.7) with western and eastern locations in two different groups (groups A and B, respectively). SIMPER procedure points to CHLA<5 and SI as the variables which contribute the most to the average similarity inside each group with 40.20 and 30.24% for groups A and B, respectively. Differences between groups A and B are mainly based on changes in the mean values of SST (18.19 to 19.04°C), CHLA<5 (29.58 to 57.53 %) and CHLA (0.95 to 0.49 mg m<sup>-3</sup>), explaining 31.35, 26.99, and 17.77% of the total dissimilarity between groups, respectively. We also carried out these analyses for the topographic variables at the 4 spatial scales previously selected: none of them show clear patterns with distinctive groups of locations. Thus, BIOENV results show clear linkages between meroplankton and water column matrixes because both presented differentiation based on west-east grouping. As most of the locations in group 1 appear in group A, and those included in group 2 are coincident with those in group B, the  $\rho$  statistic using these groupings was the highest achieved (Fig. II.7). SST on its own provided the best match: any other combination of water column variables reduces  $\rho$ , pointing to their minor role in the spatial larval community assemblages. BIOENV procedures between the biotic matrix and those obtained from the topographic variables on each scale were statistically significant, but values of  $\rho$  are lower and more than a single explanatory variable is required, indicating worse matches between matrixes (Fig. II.7). Both BS and D appear at every spatial scale, while OR contributes to the match at 0.5 and 5 km scales, CO on 0.5 and 2 km, and FR only on 20 km (Fig. II.7).

The results of Mantel's tests indicate that distributions of larvae and water column variables also share very similar spatial structures (Fig. II.8). Note that the spatial correlograms for both kinds of data were the only significant ones, in detriment of those made with topographic variables. The size patch for both is set at 88 km, as that is the distance where R first becomes negative (Fig. II.8).

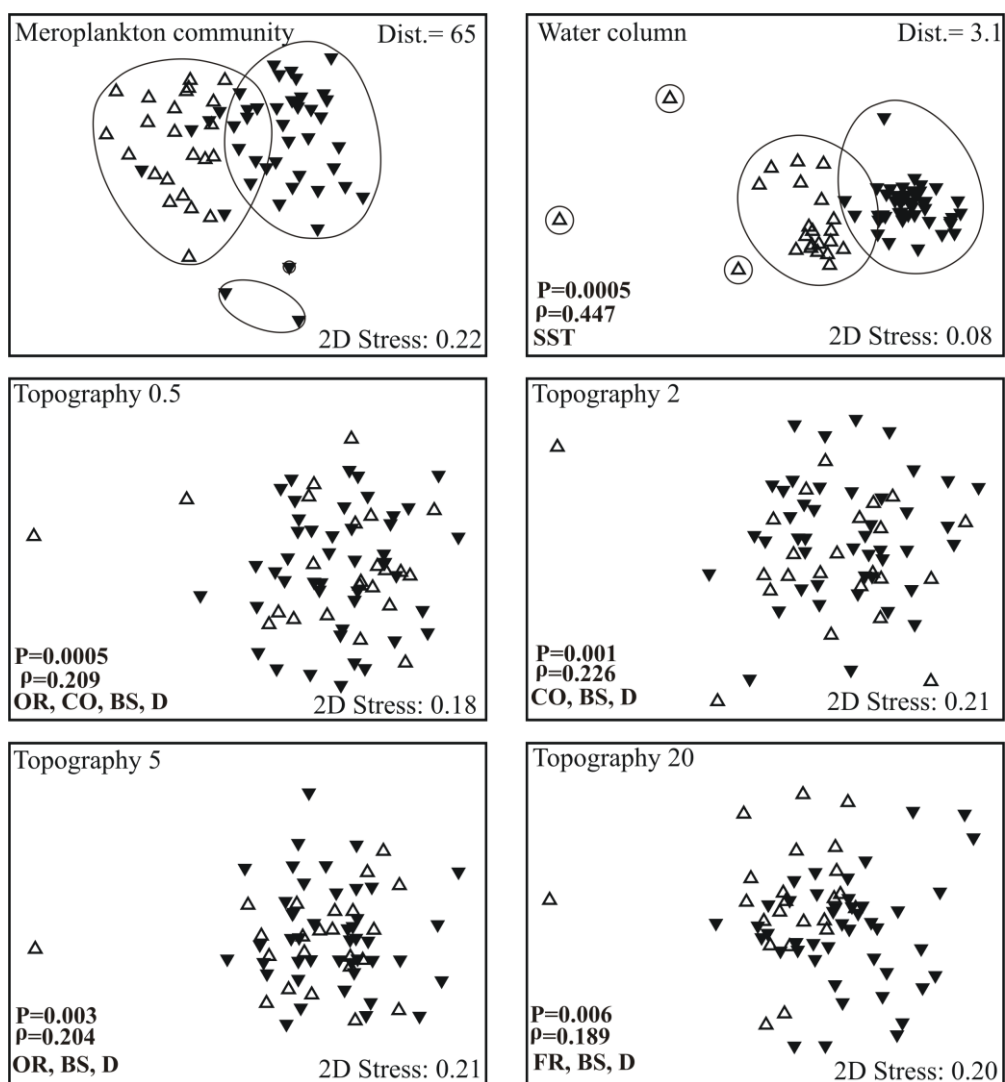


Figure II.7. Multidimensional scaling analyses for meroplankton community, water column variables and topography on the four scales studied. Plots are shown in two dimensions with their respective stress. Every triangle marks the relative position of each station to the others in terms of the similarity distance between them. White triangles and dark inverted ones point to stations to the west and east of Cape Peñas, respectively. When clear groups of stations are obtained from cluster analyses, we show them delimited with dark thin lines. The level of similarity distance used to infer the groups is shown on the upper right corner of the plot. The results of BIOENV analyses carried out to measure the agreement between each matrix and the meroplankton community one are shown:  $p$  value, rank correlation coefficient and significant variables (see material and methods for acronyms).

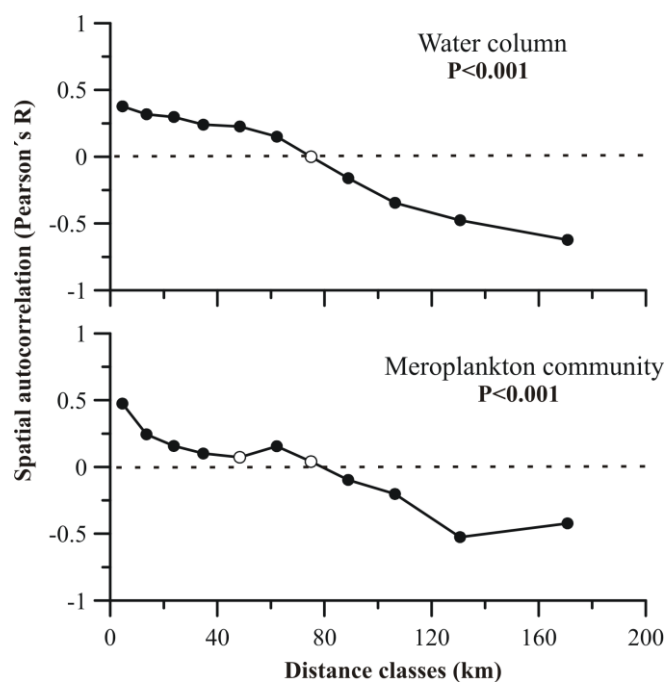


Figure II.8. Spatial structure obtained from water column variables and meroplankton community similarity matrixes. P value is shown, obtained from Mantel's test. Pearson's R was plotted as a measurement of spatial autocorrelation and standardised dividing each value by the range. Dark and white circles show the significant and nonsignificant Pearson's R, respectively.

### Species-specific analyses: spatial autocorrelation

Spatial correlograms based on Moran's I (Fig. II.9) show that, in general, water column predictors are more consistently structured in the space than topographic descriptors. Note that all the water column variables together with UPW presented quite significant spatial autocorrelation patterns, with patch sizes varying between 34 and 88km (Fig. II.9). However, among the topographic variables, only correlograms for OR0.5 and FR0.5 were found to be significant, but the pattern followed by Moran's I along the distance classes is less clear. Patch size is 34 and 13km for OR0.5 and FR0.5, respectively.

The same procedures performed for every abundant larval taxa point to spatial patterns that correspond to those found for the water column variables (Fig. II.10). However, not all the taxa showed significant spatial configurations. Patch size ranges between 23 to 88km for early nauplii and cyprids of *Chthamalus* spp., respectively (Fig. II.10).

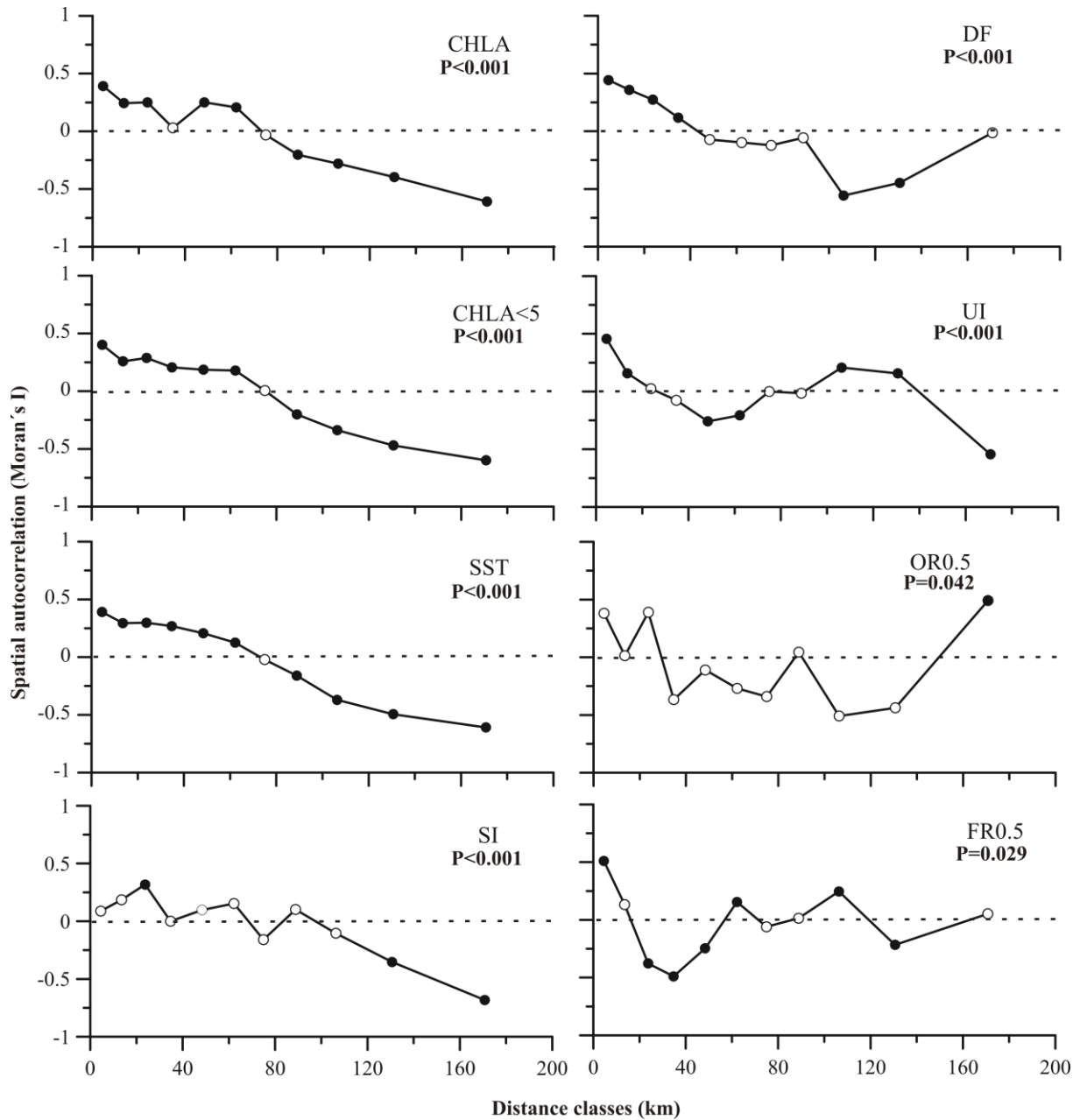


Figure II.9. Spatial structure of environmental variables which were found significant in Mantel's test (P value shown). Moran's I was plotted as a measurement of spatial autocorrelation and standardised dividing each value by the range. Dark and white circles show the significant and non-significant Moran's I, respectively.

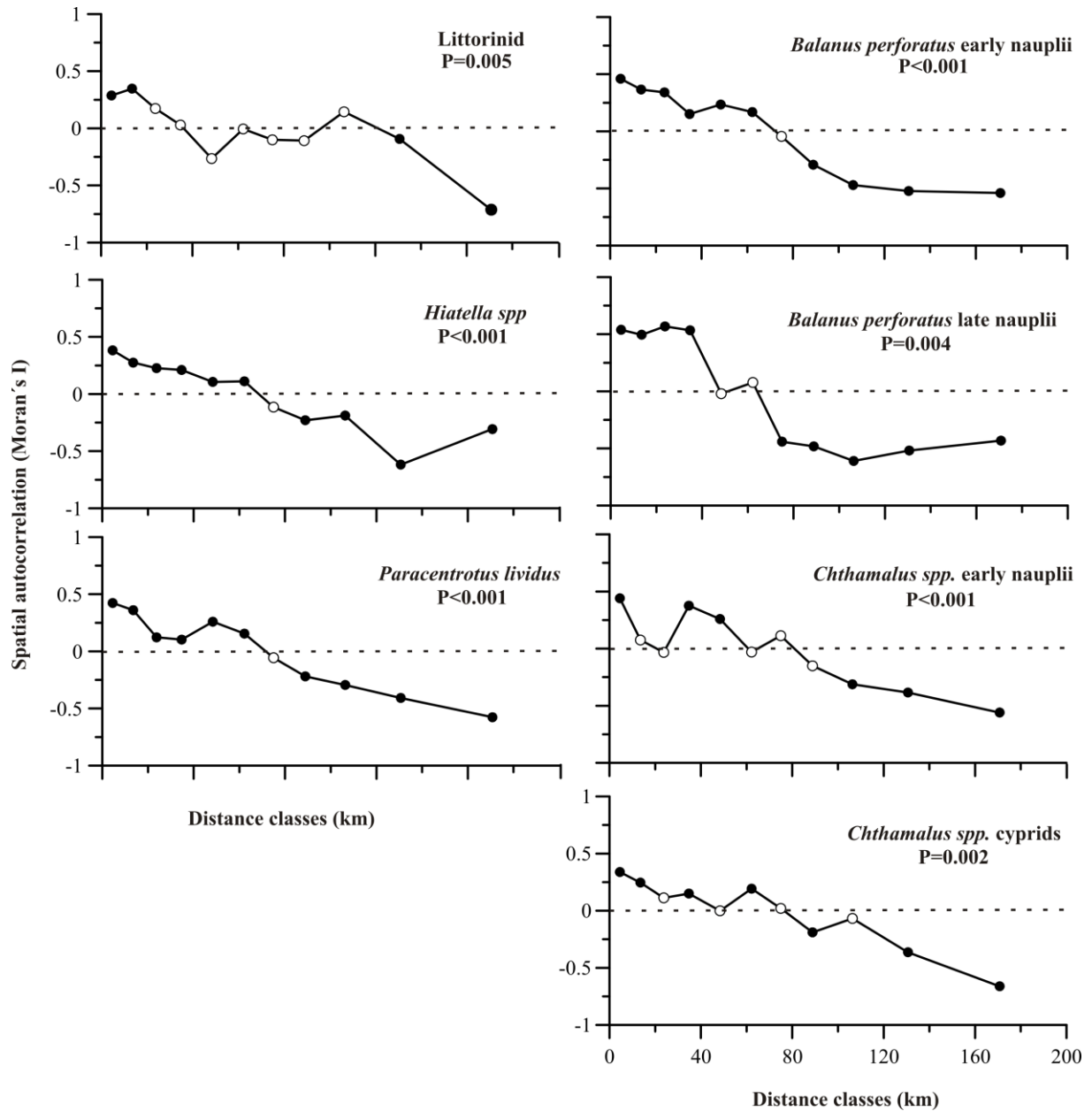


Figure II.10. Spatial structure of larval abundances ( $\log \text{ind m}^{-3}$ ) which were found significant in Mantel's test (P value shown). Moran's I was plotted as a measurement of spatial autocorrelation and standardised dividing each value by the range. Dark and white circles show the significant and nonsignificant Moran's I, respectively.

### Species-specific analyses: GLSs

General Least Squares (GLS) regression models explained between 6.1 and 59.9% of the total variance under the 7 different assumptions (Table II.5, Table II.6). *Chthamalus* spp. late nauplii was a clear exception, as no variable was significant in any model. Spatial coordinates usually explained high percentages of variance (i.e., up to 35% and 44.8% for latitude and longitude respectively in the distributions of *Balanus perforatus* late nauplii and *Paracentrotus lividus*; Table II.5, Table II.6). According to the sign of the regression coefficients, molluscs, equinoderms and cyprids of cirripeds increased eastwards, early stages of cirripeds increased westwards, while late naupliar stages of *Balanus perforatus* increased northwards and littorinids increased southwards (Table II.5, Table II.6). In general, when longitude and latitude were added to the models, the percentage of variance explained by water column predictors that presented consistent alongshore trends decreased markedly (like sea surface temperature, chlorophyll in less than 5 µm particles, total chlorophyll; Table II.5, Table II.6).

Orientation of the coastline explained up to 10.2% in the distribution of late nauplii of *Balanus perforatus* when only topographic predictors were used (Table II.5), an entered regression models in 9 out of 13 taxa analysed (Table II.5, Table II.6). Nauplii of *Chthamalus* spp. and *Balanus perforatus* were more abundant in coasts facing west at scales of 2 and 20km, respectively, while cyprids of *Balanus perforatus*, zoeae of *Liocarcinus* spp., spionids, *Nephtys* sp., *Hiatella* spp., *Amphiura* spp. and *Paracentrotus lividus*, were more abundant at east-facing coasts, mostly at a 0.5km scale (Table II.5, Table II.6).

Coastline convexity entered some of the 7 regression models in 5 out of the 13 taxa examined (Table II.5, Table II.6), explaining up to a maximum of 10.6% in the abundance of littorinids (full environmental model, Table II.5). Littorinids, early nauplii of *Chthamalus* spp., late nauplii of *Balanus perforatus* and zoeae of *Liocarcinus* spp., were more abundant in convex coasts at various scales, while cyprids of *Chthamalus* spp. were more abundant at concave coastlines at a 2km scale (Table II.5, Table II.6).

Coastline complexity entered regression models in 8 of 13 taxa, explaining a maximum of 21.1% of the total variance in *Amphiura* spp. at a 20km scale (Table II.4). Larvae of spionids, *Nephtys* sp., littorinids, *Hiatella* spp., *Amphiura* spp. and *Paracentrotus lividus* were more abundant at simpler coastlines, mostly at a scale of 20 km (Table II.6). In contrast, nauplii of



*Balanus perforatus* were more abundant at complex coasts at a 20km scale. Note that coastal complexity never entered the models when measured at the smallest scales. The distance from the coast entered the models in 4 out of 13 taxa and explained up to 23% of the variance in the abundance of cyprids of *Chthamalus* spp. Both these cyprids and *Nephtys* sp. larvae increased their number onshore, while abundances are higher offshore for *Hiatella* spp. and *Balanus perforatus* late nauplii. BS had minor contributions to the regression models (Table II.5, Table II.6)

Among the water column environmental variables, SST was included in the regression models in 8 taxa, and explained up to 50.4% of the total variance in the abundance of early nauplii of *Balanus perforatus* (E and W models; Table II.5, Table II.6). The abundance of larvae of littorinids, *Hiatella* spp., *Amphiura* spp., *Paracentrotus lividus* and *Chthamalus* spp. cyprids, increased with temperature while it decreased for naupliar stages of both barnacle species (Table II.5, Table II.6). CHLA presented maximum values of  $R^2$  in the case of *Balanus perforatus* cyprids (8%) and correlates negatively with its abundances. However, zoeae of *Liocarcinus* spp. and veliger of *Hiatella* spp. correlates positively with total chlorophyll (Table II.5, Table II.6). CHLA<5 entered the models for *Amphiura* spp. and *Chthamalus* spp. cyprids showing positive relationships with higher percentage of small size particles and negative correlation for littorinids. For the cyprids, CHLA<5 explains 22.4% of the total variability (Table II.6). The rest of water column variables played minor roles in the regression analyses

Chapter II: Alongshore larval distributions

Table II.5. Variance explained by the environmental variables for all the taxa. Note that significance is indicated  $p^* < 0.05$ ;  $p^{**} < 0.01$ ;  $p^{***} < 0.001$ ). We show the seven kinds of models studied (E, T, W, S, E+S, T+S, W+S). See Table 1 for the acronyms of the variables and models.

Taxa	Variable	E	T	W	S	E+S	T+S	W+S
Spionids	OR0.5 -	9.3***	9.3***			9.3***	9.3***	
	OR20 -	5.2*	5.2*			5.2*	5.2*	
	FR5 -	10**	10**			10**	10**	
	DF -			6.1*				6.1*
	Total	24.5	24.5	6.1	0	24.5	24.5	6.1
<i>Nephtys</i> sp.	OR0.5 -	8***	8***			8***	8***	
	FR2 -	9**	9**			9**	9**	
	D -	10.3**	10.3***			10.3**	10.3***	
	SI -	5.2*		6.1*		5.2*		6.1*
	Total	32.5	27.6	6.1	0	32.5	27.6	6.1
Littorinids	CO0.5 +	10.6**	9.5**			9.9**		
	CO2+						4.3*	
	FR 20 -		5.1*					
	SST +	11.7***		11.7***			7.9*	
	CHLA<5 -	4.8*		5*		5.2*		5.2*
	UPW +					6.8**		6.3*
	Space X) +				13.7**	13.7***		13.7***
	Space Y) -						12.3***	
Total	27.1	14.6	16.7	13.7	35.6	24.5	25.2	
<i>Hiatella</i> spp..	OR0.5-		6*				3.0*	
	FR20 -		10.9***				2.0*	
	D+	15***	13.3***			16.9***	16.9***	
	SST +	30.1***		30.1***				
	CHLA							3.4*
	UPW +					6.1**		7.5**
	Space X) +				32.4***	32.4***	32.4***	32.4***
Total	45.1	43.8	30.1	32.4	55.4	54.3	44.3	
<i>Amphiura</i> spp.	OR2 -	6.5*	7.9**			6.7**	6.7**	
	FR20 -	21.1***	21.1***			10.4**	10.4**	
	SST +			17.8***				
	CHLA<5 +	8.2**						
	UPW +							6.6*
	Space X) +				22.6***	22.6***	22.6***	22.6***
Total	35.8	29.0	17.8	22.6	39.7	39.7	29.2	
<i>Paracentrotus lividus</i>	OR05 -	6.4**	7.7**			4.0*	4.0*	
	FR20 -	6.9***	20.8***			6.3***	6.3***	
	SST+	36.2***		36.2***				
	UPW +							3.6*
	Space X) +				44.8***	44.8***	44.8***	44.8***
Total	41.5	28.5	36.2	44.8	55.1	55.1	48.4	

Table II.6. Variance explained by the environmental variables for all the taxa, except for *Chthamalus* spp. late nauplii whose abundances were not fitted by any of them. Note that significance is indicated p\* < 0.05; p\*\* < 0.01; p\*\*\* < 0.001). We show the seven kinds of models studied (E, T, W, S, E+S, T+S, W+S). See Table 1 for the acronyms of the variables and models.

Taxa	Variable	E	T	W	S	E+S	T+S	W+S
<i>Chthamalus</i> spp. early nauplii	OR2 +	5.8**	5.8**			5.8		
	CO0.5 +	7.5**	7.5**			7.5	4.1*	
	SST -	26.9***		31.7***		26.9***		31.7***
	Space X) -				26.3***		26.3***	
	Total	40.2	13.3	31.7	26.3	40.2	30.4	31.7
<i>Chthamalus</i> spp. cyprids	CO2 -	4.3*	4.3*			5.5**	5.5**	
	D -	23***	23***			19.4***	19.4***	
	SST +	20***						
	CHLA < 5 +			22.4***				
	Space X) +				24.5***	24.5***	24.5***	24.5***
Total	47.3	27.3	22.4	24.5	49.4	49.4	24.5	
<i>Balanus</i> <i>perforatus</i> early nauplii	FR20 +	2.7*	16.1***			3.8*	9.2**	
	BS +						3.2*	
	SST -	50.4***		50.4***		50.4**		50.4**
	DF -	2.7*						
	Space X) -				5.5**			
Space Y) +				43.6**	5.7**	43.6***	5.7**	
Total	55.8	16.1	50.4	49.1	59.9	56.0	56.1	
<i>Balanus</i> <i>Perforatus</i> late nauplii	OR20 +		10.2**			4.7***		
	CO5 +		7.5*					
	CO20 +	2.8*						
	FR20 +					3.7*		
	D +	4.7*	9.8***			5.6**	9.5***	
	BS +						5.4***	
	SST -	20.1***		20.1***				3.2**
	SI +	13.2***		13.2***		2.7*		3.4***
	DF -	7.2***		7.2***		3.5**		7.3**
	UPW +	3.9*		3.4*				
	Space X) +							0.5*
Space Y) +				35.0***	35.0***	35.0***	35.0***	
Total	51.9	27.5	43.9	35.0	55.2	49.9	49.4	
<i>Balanus</i> <i>perforatus</i> cyprids	OR5 -	11.9**	11.9**			11.9**	11.9**	
	CHLA -			8*				8*
	Total	11.9	11.9	8		11.9	11.9	8
<i>Liocarcinus</i> spp. zoeae	OR0.5 -	6*				6*		
	CO5 +		7*				7*	
	CHLA +	6.8*		6.8*		6.8*		6.8*
	Total	12.8	7	6.8	0	12.8	7	6.8

## Species-specific analyses: variance partitioning

The components of the variation were of different importance depending on the taxa and the stage (Fig. II.11). The interaction between water column properties and space ( $wxs$ ) explained an average of 11.74% (range from 35.8 to 0%) of the total variance in distributions of meroplankton taxa, followed by the pure topographic component ( $t$ ; mean=11.45%, range=24.9-3.8%), the interaction between topographic and water column predictors ( $txw$ ; mean=4.17%, range=9.8-0%), the three-way interaction ( $txwxs$ ; mean=4.07%, range=11.6-0%), the spatial component ( $S$ ; mean=3.15%, range=10.3-0%), the water column component ( $w$ ; mean=3.02%, range=11.1-0%) and the interaction between topography and space ( $txs$ ; mean= 1.73%, range=7.5-0%).

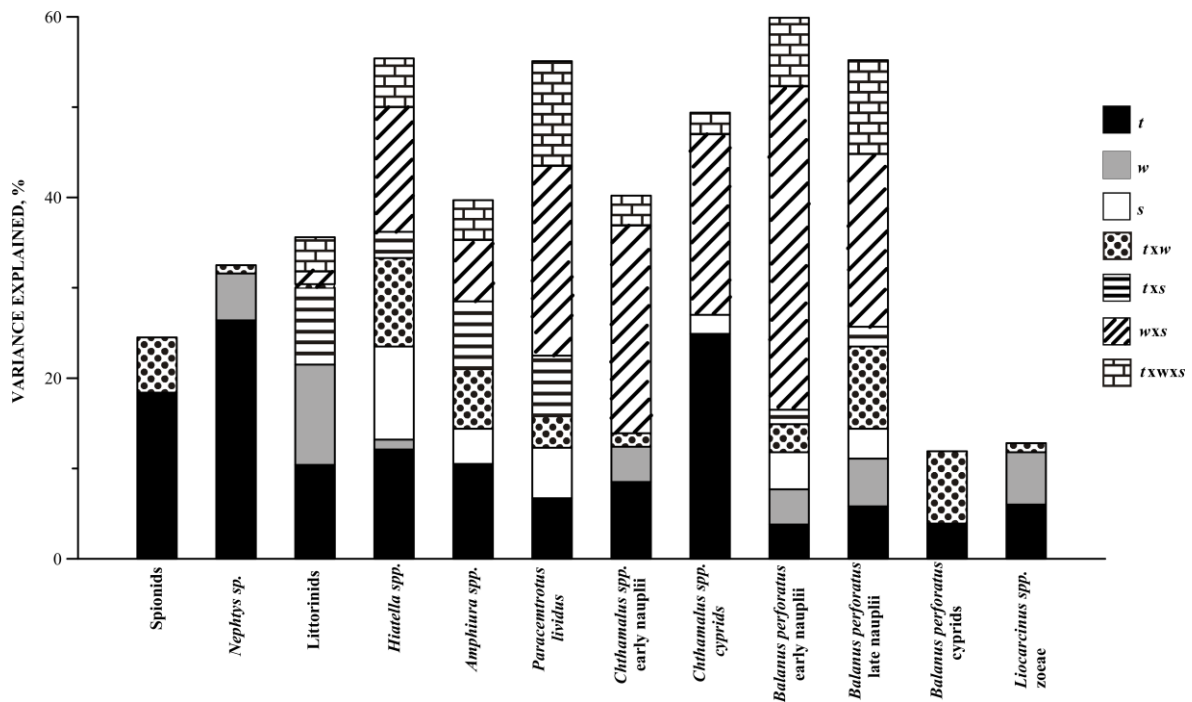


Figure II.11. Variance partitioning for the main larval taxa obtained from the GLS, with the exception of *Chthamalus* spp. late nauplii whose abundances were not fitted by any model. Pure components and their interactions are shown.

### Trends with larval age

We found a significant power law fit between larval abundances and larval age ( $p=0.0027$ , Fig. II.12). Thus, the higher the number of larvae, the older the larvae, which points to long water residence time as the main cause of accumulations. Larval age, as reported in the literature (Table II.4), was significantly correlated with both the variance explained by  $wxs$  and that by  $t$  ( $p=0.02$  and  $p=0.03$  respectively; Fig. II.13), but not with the rest of components of the variation ( $p>0.05$  for all of them, data not shown). The sign of the correlations suggests that, as larvae grow older, their distribution becomes more dependent on coastline topography and less dependent on the spatial structure of water column properties, or else, that younger larvae depend more on *in situ* properties of the water column and less on coast configuration.

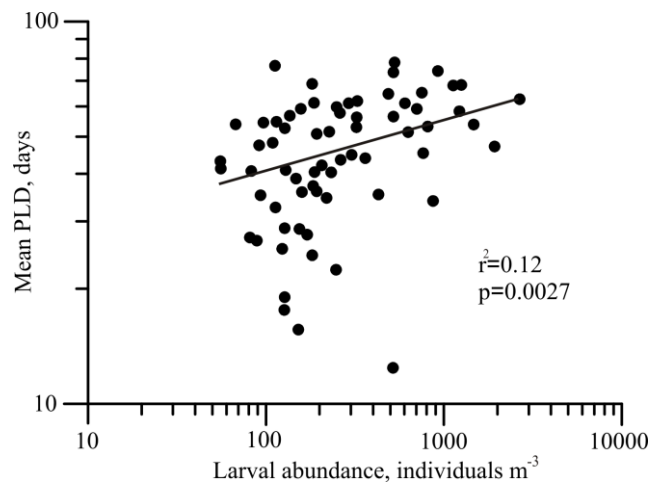


Figure II.12. Mean planktonic larval duration (PLD) as a function of larval abundance. Both variables are represented in a logarithmic scale. The dark line shows the power law fit together with its respective  $r^2$  and P value.

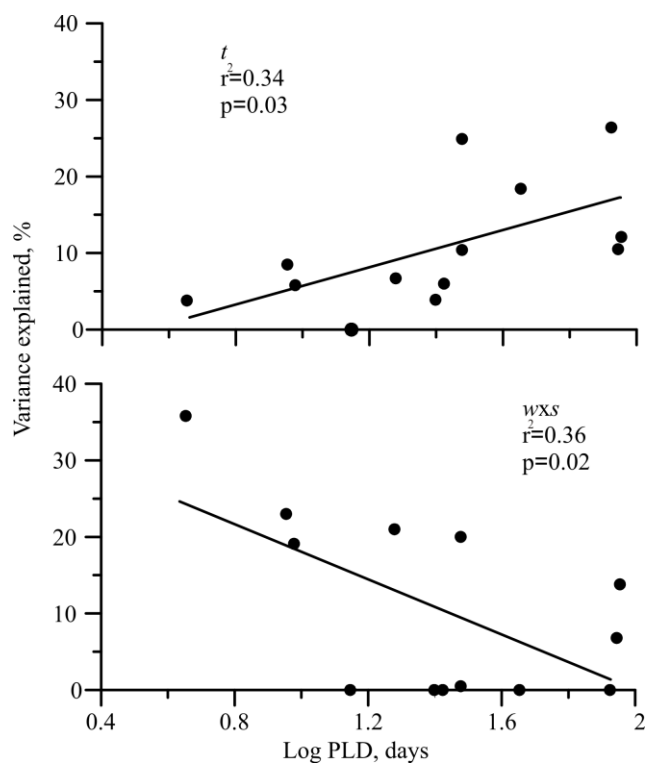


Figure II.13. Variance explained by  $t$  and  $wxs$  (see material and methods for the acronyms) as a function of planktonic larval duration (PLD) in logarithm. Dark lines show the linear fits together with their respective  $r^2$  and  $p$  value.

## Discussion

### *The importance of topography*

Several studies have revealed the role of singular coastline features like headlands (Roughan et al. 2005, Mace and Morgan 2006, Morgan et al. 2011), capes (St John 1958) or embayments (Byrne 1995, Archambault and Bourget 1998) on plankton distribution. This study takes a different, generalized approach based on the quantification of those features at different points along a 200 km coastal stripe. Quantitative variables describing coastline shape are then submitted to regression models to detect the strength and scale of association of coastal features with plankton distributions. Using this typically landscape approach, we have found that the spatial structure of the water column properties ( $wxs$ ) is of the same importance as topography ( $t$ ) in defining the spatial distribution of meroplankton taxa. This means that different meroplankton assemblages are associated to different water masses, probably because they respond to their physicochemical properties which are spatially structured. Similar results were found for the distributions of annelid larvae in the Northern Bay of Biscay

(Ayata et al. 2011), meroplankton in the North Sea (Belgrano et al. 1995) and barnacle recruitment patterns in Chile (Lagos et al. 2008). In Ayata et al. (2011), the spatial coordinates explain large amounts of variability, what they interpreted as a consequence of spatially structured characteristics of the populations. For example, a population of spawning adults occupying a certain, localized stripe of the coast, may give rise to a restricted larval distribution which will be closely tied to the spatial coordinates. Topography, which Ayata et al. (2011) did not consider in their study, may have explained part of this variability in our regression models, leading to a lower contribution of  $s$ . Accordingly, it is possible that their annelid distributions could have been explained to a large extent by coastal convexity, because most adult polychaetes live and spawn inside embayments (Ayata et al. 2011). Likewise, adult populations of *Balanus perforatus* are located in exposed coasts (Connor et al. 2004) a characteristic which may explain our observation of a significant association between larval abundance and coastal orientation and convexity, and a relatively minor role of the purely spatial component in this species (Table II.6).

#### *Cape Peñas as a natural breakpoint*

Our meroplankton observations are consistent with the role of Cape Peñas as a physical and biogeographical boundary. We have observed a clear west-east gradient of physicochemical water properties (Fig. II.4, Fig. II.7), which is consistent with the typically warmer summer conditions towards the inner Bay of Biscay (Fischer-Piette 1957; Koutsikopoulos et al. 1998; Alcock 2003) and which is related to a concomitant shift in the structure of larval assemblages along the coast, with veligers increasing and barnacle nauplii decreasing towards the east (Fig. II.7). This gradient is more marked at Cape Peñas, leading to detection of patches 90 km in length in spatial autocorrelation analyses (Fig. II.8), that is, half the extent of our sampling study (ca. 200 km). Cape Peñas has been found to be a boundary for the distribution of wave energy (Iglesias and Carballo 2010), macroalgal species (Anadon and Niell 1981, Lobón et al. 2010), frequency and intensity of the West Iberia coastal upwelling (Botas et al. 1990, Varela et al. 2005) and fuel deposition patterns following an oil spill (Acuña et al. 2010).

*Accummulation biotopes*

In our study, larvae accumulated and were in general older in east facing coasts, both at the large spatial scale of Cape Peñas (20 km; e.g. post-trochophore veligers of *Hiatella* spp. and littorinids, cyprids and plutei, all close to 1 month; Tables II.5 and II.6, Fig. II.5, Fig. II.6) and at smaller spatial scales (0.5 km, veligers of *Hiatella*, segmented larvae of spionids and sea urchins; 2 km, *Amphiura* spp.; Tables II.5 and II.6). This pattern is consistent with other studies revealing a tendency for meroplankton to accumulate at the lee of headlands, where alongshore currents are forced to recirculate (e.g. Roughan et al. 2005, Mace and Morgan 2006). However, the prevailing currents during our study period were weak and mostly westwards ( $-2.89 \pm 6.27$  cm/s, Rayo moored buoy, Puertos del Estado, 15 km off Cape Peñas, 44 N 6W, Fig. II.1), thus eastern sides of the capes during our study period were windward, rather than leeward, and an alternative mechanism of larval accumulation must have been operating. Plankton and larvae have certainly been shown to be confined to the coastal area of Villaviciosa by meanders of the Iberian slope Poleward current (González-Quiros et al. 2004), but this is a typically winter-spring phenomenon not common during the month of July (Pingree and LeCann 1990). More likely, our observations are consistent with topographically driven changes in the tidal flows. Rosenfeld and Beardsley 1987 showed that short-scale variations in the nearshore velocity field may arise by propagation of Kelvin waves along irregular coasts ("bumpy boundaries") and model simulations show tidal ellipses shifting from predominantly alongshore at Cape Peñas to predominantly across-shore east of Cape Peñas (Alvarez-Fanjul et al. 1997). We hypothesize that the predicted reduction of the alongshore flow at coasts oriented to the east would enhance water residence time and retention, leading to older larval assemblages closer to the coast. This explanation is consistent with the positive relationship between larval age and abundance (Fig. II.12), which points to time dependent dynamics as the cause of the accumulations. Our regression models suggest that this mechanism is pervasive across spatial scales, and ground-truthed, model simulations have shown that a mid-sized cape modifies the tidal flow structure in a coastal stripe ten times longer (Rosenfeld and Beardsley 1987). Since Cape Peñas protrudes 17 km, it may likely affect tidal currents in the whole eastern portion of our study area, as suggested by model simulations showing altered tidal ellipses spanning from Cape Peñas to Llanes ( $\approx 70$ km, Alvarez-Fanjul et al. 1997).



Larvae were also more abundant and older at simpler coasts, at scales of 2 km (*Nephtys sp.*), 5 km (spionid annelids) and 20 km (littorinids, *Hiatella* spp. and echinoderms), but not at 0.5 km (Table II.5). All of these taxa presented maximum abundances around Villaviciosa (Fig. II.5), a region with a very simple coastline especially at the 20km spatial scale (Fig. II.3). Wolanski and Spagnol (2000) found that the tidal currents at the Great Barrier were "steered away" in areas of densely packed, complex coral reefs as compared to simpler ones. We hypothesize that the width and the strength of the coastal boundary layer separating the inshore, "sticky water" (*sensu* Wolanski 1994), from the offshore, shelf waters, is reduced at simpler coastlines, leading to enhanced permeability to cross-shore larval transport. Accordingly, both eastward orientation and low complexity would favour accumulation of older, competent larvae at the Villaviciosa coastal region, which would therefore be a sink biotope (Bode et al. 2006).

*Age-dependent larval distribution patterns: landscape vs. water column control*

A salient feature of our results was a significant increase in the variance explained by landscape descriptors ( $t$ ) with increasing larval duration, both in general or when only stages of the same species are considered (e.g. *Balanus perforatus* early nauplii, late nauplii and cyprids, Fig. II.11 , Fig. II.13). This pattern was associated with a concomitant decrease in the variance explained by  $wxs$ . If we tentatively translate correlations into causation, this result can be interpreted in three ways. The first one is that larval distributions became more sensitive to topographic features as the larvae approach competence, thus leaving less variance to be explained by spatially structured water column properties. This is consistent with the idea of larval accumulation taking place at coastal sites where water residence time and permeability to offshore larvae increase as a consequence of particular topographic peculiarities (east orientation and simple coastline respectively). Longer water residence times will lead to an older, competent larval pool at those sites. Another possibility is that older larvae were less dependent on spatially structured water column properties, leaving more variance to be explained by topography. This is also consistent with a shift in the importance of growth and survival for newly released larvae, to recruitment to the benthic habitat for older larvae. Moreover, due to functional compromises between feeding and swimming and limitations to follow the correct chemical cues to settle, there could be a trade-off between feeding abilities and the capacity of larvae to pick favourable sites (Strathmann 1985, Strathmann and Grünbaum 2005). For example, early barnacle nauplii usually appear in the

plankton during periods of active growth of their phytoplankton food (Starr et al. 1990), but late cyprid larvae are fast, non-feeding swimmers specialized in the process of settlement (Anderson 1994). This would explain a tighter dependence on growth factors-water column temperature, quantity and quality of potential food- in early than in competent larvae. Finally, the third possibility implies that both trends would be operating independently on the spatial distributions of larvae.

In conclusion, topography explains significant portions of the variance in meroplankton abundances. In studies where topography was not taken into account, much of that variability may have been attributed to spatially structured characteristics of the species. In our study, larvae accumulated at east facing coastal sites both at small scales and at the scale of Cape Peñas, probably because of topographically mediated changes in the tidal currents. Coast complexity also influences the distribution of meroplankton, which tended to accumulate in simpler coasts. In general terms, our work points to the need of incorporating coastal shape properties along with ocean dynamics to understand the spatial distribution and recruitment of the planktonic larvae of coastal organisms.



### Chapter III: Larval distributions across coastal fronts





### **Introduction**

Meroplankton distributions in space and time have been shown to be of great importance in the dynamics of coastal populations (Sandifer 1975; Gaines & Roughgarden 1985; Shanks et al. 2002, Largier 2002, Largier 2003, Becker et al. 2007, Pineda et al. 2007, Pineda et al. 2009). However, many studies have inferred patterns in abundance and recruitment from samplings carried out in offshore waters. Only recently, researchers have focused their attention on the very nearshore waters (McCulloch & Shanks 2003, Shanks et al. 2003, Pineda et al. 2007), which are the beginning and end of the whole dispersal process. Although local, the dynamics occurring in this narrow coastal layer can rule larval spawning and recruitment (Guichard & Bourget 1998, Archambault & Bourget 1999).

One of the most evident hydrographic features on this small spatial scale is the presence of foam lines or slicks. Usually, they mark the limit between different water types, thus being characterized by surface horizontal gradients of the physicochemical properties (Le Fevre 1986, Longhurst 1998). Their origin may depend on the interaction between hydrography, meteorological conditions (Romano 1995) and local topography. For example, flow patterns of alongshore currents or onshore propagation of internal waves depend in great extent of site-specific topographic features (McCulloch & Shanks 2003, Leichter et al. 1998). Despite their physical origin, they give rise to frontal structures characterized by a convergent flow where upward- swimming or floating organisms and objects may accumulate, provided that their upward velocity is faster than the downwards movement of water (Franks 1992; Pineda 1999; Helfrich & Pineda 2003, Shanks & Brink 2005, Scotti & Pineda 2007). The effect of slicks has been studied in many groups of organisms (e.g. Kingsford & Choat 1986, Young & Adams 2010) but rarely on meroplankton (but see Shanks 1995, Pineda 1999). Here, the swimming abilities of the different larval taxa define the strength with which they accumulate, although even very slow swimming larvae like gastropod veligers, that roughly reach speeds of few  $\text{mms}^{-1}$ , can resist typical vertical flows at downwelling-upwelling areas (Poulin et al. 2002, Shanks & Brink 2005). Moreover, in these sites, swimming against the vertical flow has been proved to be the usual behaviour for the whole zooplankton community (Genin et al. 2005). However, before resisting the downwards current and thus being concentrated, larvae have to reach the front. Here, the way larvae face the horizontal currents that converge to the slick is a key feature and little is known about it. Traditionally, medium size zooplankters have been considered passive tracers of surface frontal circulation (Mann 1988) but some studies point

that larvae could control its own position even in the horizontal plane (Luckenbach & Orth 1992, Abelson 1997, Metaxas 2001).

For population dynamics, it is not only the presence of fronts what matters, but also their frequency, the strength of convergent flow, its persistence or characteristic time scale, its cross-shore displacement and the age, size and swimming behaviour of the larvae (Largier 1993). Here we report detailed observations of the structure and dynamics of 4 slicks at the coast of Cudillero, N. Spain, along with the distribution of meroplanktonic taxa in the vicinity of these fronts at a sampling scale of tens of meters. The resolution of our study has allowed us to quantify the magnitude of convergent circulation, of onshore frontal excursions and their impact on larval distributions.

### **Materials and Methods**

During a period of 10 days before the survey, we monitored Cudillero from the top of the surrounding cliffs in search for a suitable study site. Finally, we selected a site within 1km from the shore and close to the Cudillero port where slicks were frequently detected (Fig. III.1). The survey was then conducted from 14 June to 24 June 2009. We took into account the water level time series obtained from the Aviles Port records, wind speed and direction observed from the “Nueva Asturias” during each sampling and calculated the upwelling index with the hourly alongshore wind data (Bakun 1973) obtained from Peñas Buoy (Fig. 2). For each front, we first looked from the boat for foam lines or linear, oily patches at the surface. If more than one were present, we selected the most conspicuous. CTD and net sampling was done aboard the 9 m boat "Nueva Asturias". Simultaneously, a drifter experiment was done using an inflatable, 4.5 m Zodiac boat. CTD and nets were deployed at each of 9 stations for each front. We first sampled 3 stations at the front, 3 stations landward at different distances from the front and last 3 stations at different distances from the front to the open sea (Fig. III.1). We did not intersperse the stations because slicks could disappear (and sometimes they actually did) in a matter of minutes. As the foam lines moved and were sinuous and not strictly parallel to the coastline, the 3 frontal stations were located at different distances from the shore. Even more, offshore stations could be located closer to the coast than onshore ones in some cases. At each station, we deployed either a SBE 25 or SBE 19 CTD to obtain vertical profiles of salinity, temperature, density and fluorescence. With the data obtained, we made

cross shore contour profiles of the variables measured to describe the local hydrography using Surfer 8 software package.

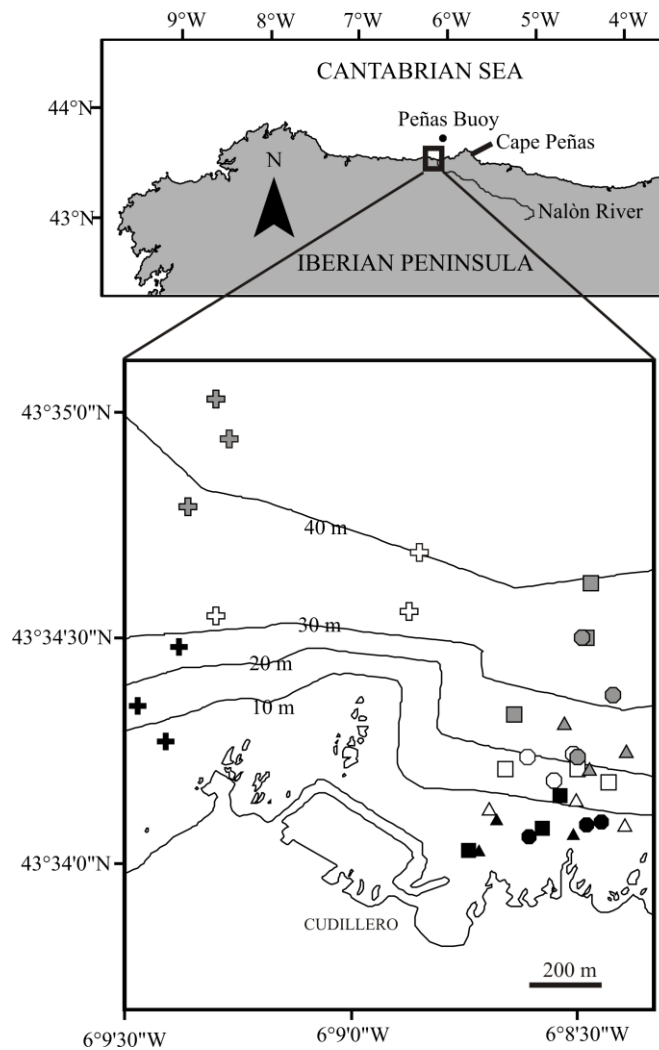


Figure III.1 Geographical location of the samplings. Circles, crosses, squares and triangles represent stations sampled on June 15, 21, 23 and 24, respectively. The colour of the symbols show the relative position respect to the front: dark, white and grey for onshore, frontal and offshore stations, respectively. Isobaths every ten meters are also shown.



### Drifter experiments

To measure surface currents during each slick, we used a Zodiac motorboat to deploy a set of 15 GPS-tracked surface drifters based on the design by Magome et al. 2007 (Fig III.2). It consisted of a square styrofoam float with a wooden board which was hung at 0.45 m depth from a rope and kept taut by a weight, to anchor the buoy to the surface currents. Each drifter was marked with a colour flag to identify those deployed in a linear pattern at the front, between the front and the coast, and offshore of the front ( $n=5$  at each location). Every drifter was equipped with a BT-Q1000X QSTARZ GPS unit located inside a waterproof plastic box, which recorded the position every 3 seconds. Drifter experiments lasted 15 to 90 minutes depending on the proximity to the coast, the persistence of the front and the weather conditions. Drifter trajectories were plotted using software ArcGis 9. We approximated the shape of the front to the line formed by the initial position of the 5 drifters that were deployed in the front, at the beginning of each drifter experiment. We then drew a line perpendicular to the front, which we used as reference for calculation of the absolute velocity component perpendicular to the front of offshore ( $\mu_{\text{off}}$ ), onshore ( $\mu_{\text{on}}$ ) and front drifters ( $\mu_{\text{f}}$ ) (Table III.1). We paid special attention to which drifters entered the front from both sides and which ones did not remain inside the front, according to observations logged during the survey.

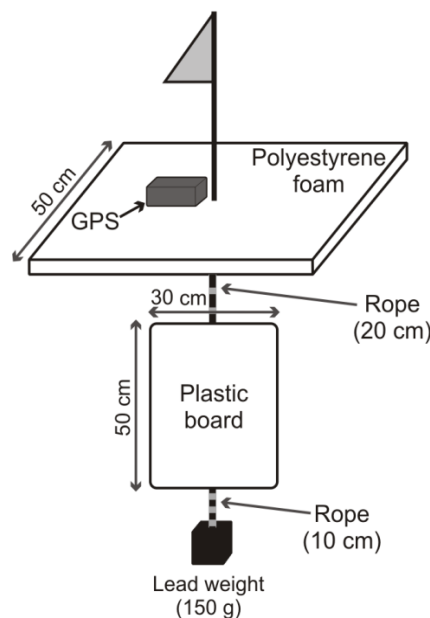


Figure III.2 Drifter structure.

### **Meroplankton sampling**

We used a 100  $\mu\text{m}$ , 20 cm radius bongo net equipped with flowmeters and floats that kept sampling within the upper 20 cm of the water column. It was specifically designed to avoid clogging in green coastal waters (Sameoto et al. 2000). The net was deployed after each CTD cast, by pulling it at 2-3 knots during 3 minutes around every station. Thus, we had 9 tows per front, 3 at each inshore, offshore and frontal waters respectively. It was usually difficult to steer the boat so that the net remained within the meandering geometry of the front continuously, thus larval densities may be underestimated at the front. Samples were preserved in 4% formalin with sea water in 250 ml bottles. We took 5% or 10% aliquots depending on the organic matter in the sample. We counted and identified all the meroplankters to the most accurate taxonomic category that we were able to reach, species in most of the cases.

### **Data analysis**

*Detection of accumulation patterns.*- Our survey fits an ANOVA design with one fixed factor (location with respect to the front), with three levels (positions of the samples with respect to the front: offshore, inshore or at the front). As dependent variables we used the larval abundances, with  $L_{\text{off}}$ ,  $L_{\text{on}}$  and  $L_{\text{f}}$  standing for larval abundances offshore of the front, onshore and at the front, respectively. To avoid heterogeneity of variances, we used log-transformed abundances. For analysis, we only used those taxa reaching at least  $10 \text{ ind. m}^{-3}$  in one of the stations within each front. If there was a significant effect of the fixed factor, we conducted post hoc Fisher contrasts. Three cases are possible: frontal accumulation in the case of higher abundances in the front respect to both sides; onshore retention if onshore or both onshore and frontal abundances were higher respect to offshore ones; offshore retention if offshore or both offshore and frontal abundances were higher respect to onshore ones.

In addition to ANOVA, to obtain a continuous description of larval distributions, linear ( $L=a+b*D$ ), power law ( $L=a*D^b$ ), logarithm ( $L=a+b*\ln D$ ) and exponential ( $\ln L=a+b*D$ ) regressions were used, where  $D$  is distance from the coast in meters, as measured using ESRI ArcGIS software and  $L$  is larval density in  $\text{ind m}^{-3}$ . A  $b<0$  points to a decreasing offshore

trend, consistent with a diffusive process not altered by frontal dynamics and, as such, it serves as null hypothesis of no front effects.

**Sources of accumulation.**- To infer which side of the front was supplying larval accumulation at the front, we followed a modification of calculations in Pineda 1999, originally developed for internal wave fronts, but which can also be used for other structures. We depart from a situation where the front, the offshore surface waters and the onshore surface waters move toward the coast at velocities  $\mu_f$ ,  $\mu_{off}$ ,  $\mu_{on}$  respectively, with negative values indicating departure from the coast.  $\mu_{on}$  was not considered by Pineda 1999 but the displacement of our drifters shows that there is a surface current ahead the fronts. Water speed toward the front can be calculated as

$$\Delta\mu_{off} = \mu_{off} - \mu_f \text{ and } \Delta\mu_{on} = \mu_f - \mu_{on} \quad (1)$$

where  $\Delta\mu_{off}$  and  $\Delta\mu_{on}$  denote the velocities of offshore and onshore surface waters towards the front (Table III.1). Larval supply rates from each side of the front (larvae  $m^{-2} h^{-1}$ ) can be thus be calculated as

$$S_{off} = \Delta\mu_{off} L_{off} \text{ and } S_{on} = \Delta\mu_{on} L_{on} \quad (2)$$

where  $L_{of}$  and  $L_{on}$  are larval densities at the offshore and the onshore sides of the front, respectively. Comparison between  $S_{off}$  and  $S_{on}$  provides an indication of the source of the larvae accumulating at a front. When the supply rate from one side of the front is markedly superior to that from the other side, a simple accumulation factor can be calculated based on Pineda's (1999)

$$A = L_f / L_s \quad (3)$$

where  $L_s$  is the larvae concentration at the source, i.e.  $L_s = L_{off}$  or  $L_s = L_{on}$ , depending on whether the source is the offshore or the onshore side of the front.

To infer larval source from these supply rates has obvious limitations: if both relative speeds  $\Delta\mu_{off}$  and  $\Delta\mu_{on}$  are positive and larvae do not concentrate significantly at the front, it is feasible that larvae could sink in the convergence and cross the front, especially toward the stratified

side. In this case, larval abundances in one side could be dependent of the supply rate from the other, so it does not make sense to make any comparison.

We hypothesize that the accumulation factor for a given larvae will depend:

1) On the larval supply rate, directly related with the strength of the convergence flow at the source of the larvae. More zooplankters would reach the slick with higher surface currents, especially if there is no effective resistance in the horizontal plane.

2) On the vertical water velocity in the convergence, also presumably proportional to the horizontal velocity at the larval source. The ability to withstand the vertical flow and remain in the front will decrease dramatically if this downwards flow exceeds larval speeds.

Then if we follow both 1) and 2) conditions, the potential of accumulation at the slick can be characterized by a quotient

$$Q = \mu_l / \Delta\mu_s \quad (4)$$

where  $\mu_l$  is the swimming velocity as reported in the literature (Table III.2) and  $\Delta\mu_s$  is the water velocity at the source of the larvae, i.e.  $\Delta\mu_s = \Delta\mu_{\text{off}}$  or  $\Delta\mu_s = \Delta\mu_{\text{on}}$  depending on the source of larvae being at the offshore or the onshore side of the front.

## **Results**

### **June 15**

***Structure of the water-column.***- There was an evident foam line at ca. 500 m off the coast. Wind was weak and variable during the sampling, like the three previous days, with brief and weak episodes of positive Ekman transport (Fig. III.3). The tide was at 1.56 m above LAT (Lowest Astronomic Tide) and rising to a full, neap tide of 3.45 m above LAT. The foam line coincided with a clear hydrographic cross shore gradient, with salinity and density decreasing seawards from 35.6 to 32 psu and from 26.6 to 22.8 kg m<sup>-3</sup> respectively, while fluorescence increased from 1 to 9 arbitrary units (a.u. hereafter, Fig. III.4). This marked gradient is consistent with offshore waters originating at the Nalón river outflow 3 km east, a situation

which has been previously observed during monthly monitoring surveys (Spanish IEO project RADIALES) or by satellite SeaWifs imagery. Thermal stratification was well marked only offshore of the front, with a surface-bottom difference of 2.9 C° and a thermocline located between 0-10m depth which almost outcropped at the front (Fig. III.4)

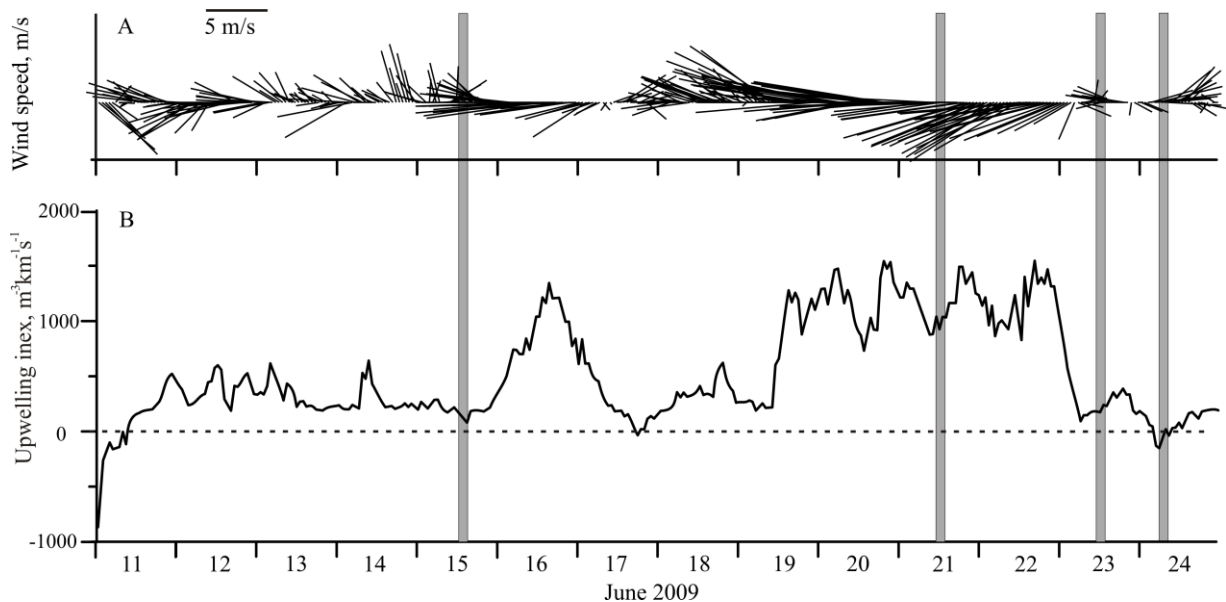


Figure III.3. Hourly time series of wind vectors and upwelling index during June 11-24, 2009. Grey rectangles point to the timing of the four cruises. Wind vectors (m/s) are disposed clockwise with upwards vectors pointing to winds coming from the south. The discontinuous line marks null Ekman transport.

**Drifters.-** This was the most complex front in terms of water circulation. The experiment lasted 80 minutes approximately. 4 out of the 5 drifters deployed at the front followed its southeast onshore displacement (Fig. III.5) at an average speed  $\mu_f=3.8 \text{ cm s}^{-1}$  (Table III.1). At this velocity, the front should have reached the coast in 3.65 h. and actually it did so in approximately 3 hours but, while the front moved onshore, the foam progressively dissipated and the front line became less clear. All the onshore drifters moved north at  $\mu_{on}=-4.8 \text{ cm s}^{-1}$  (Fig. III.5; Table III.1). When they reached the front, we observed a clear change in their trajectories, which followed the foam line to the southeast. Convergence velocity at the onshore side was  $\Delta\mu_{on}=8.6 \text{ cm s}^{-1}$ , the highest observed in our study (Table III.1), while the trajectories of the offshore drifters were more variable (Fig. III.5), and none of them reached the front, with  $\Delta\mu_{off} < 0 \text{ cm s}^{-1}$  (Table III.1). In summary, we observed quite strong onshore convergence, but circulation offshore was quite complex. We achieve offshore flow variability to the formation of a weaker foam line at 600 m off the coast approximately. This new structure may change the divergent pattern experienced by the offshore drifters during the first 20 minutes.

**Meroplankton.**- Only zoeae of *Pachygrapsus marmoratus* zoeae and *Chthamalus* spp. cyprids showed a clear accumulation pattern ( $L_{on}=L_{off}<L_f$ , Fig. III.5), with a likely origin at the onshore side because  $\Delta\mu_{off}$  was negative (Table III.1). Chrysopetalid annelid segmented larvae and *Chthamalus* spp. early and late nauplii showed offshore retention ( $L_{on}=L_f<L_{off}$ , Fig. III.6). Their abundances peaked at 100-200 m offshore of the front and both nauplii stages followed power law fits increasing their abundances with distance ( $b>0$ , Fig. III.7). No significant pattern was found for litorinid veligers, although their abundances peaked 100m offshore of the front (Fig. III.7).

### June 21

**Structure of the water-column.**- During the morning of June 21 we observed a succession of slicks very close to the coast. We chose the furthest one, at a distance of 500m. It was linear and the only one that presented some algae and debris. Sampling was initiated with strong northeasterly winds around  $8 \text{ m s}^{-1}$ , like the previous two days, when positive Ekman transport reached more than  $1000 \text{ m}^{-3} \text{ km}^{-1} \text{ s}^{-1}$  (Fig. III.3) following daily patterns due to thermal sea breezes (personal observations). Tidal height was 0.91 m above LAT, rising to a maximum neap tide of 4.03 m. The front started to disintegrate 20 minutes after the beginning of the sampling, and coincided with the point where a slight thermocline and its associated fluorescence maximum intercepted the bottom, while the  $15 \text{ C}^\circ$  isotherm outcropped at the surface (Fig. III.4). In general, the cross shore gradient was not as marked as the 15<sup>th</sup> June.

**Drifters.**- All drifters moved toward the coast at very similar and low speeds, although onshore drifters were a bit slower than those deployed in the front ( $2 \text{ cm s}^{-1}$  and  $2,5 \text{ cm s}^{-1}$  respectively, Table III.1, Fig. III.5), pointing to a slight onshore convergent flow  $\Delta\mu_{on}=0,5 \text{ cm s}^{-1}$ , Table III.1). Although the front was visually undetectable after 20 min, drifter trajectories did not change appreciably.

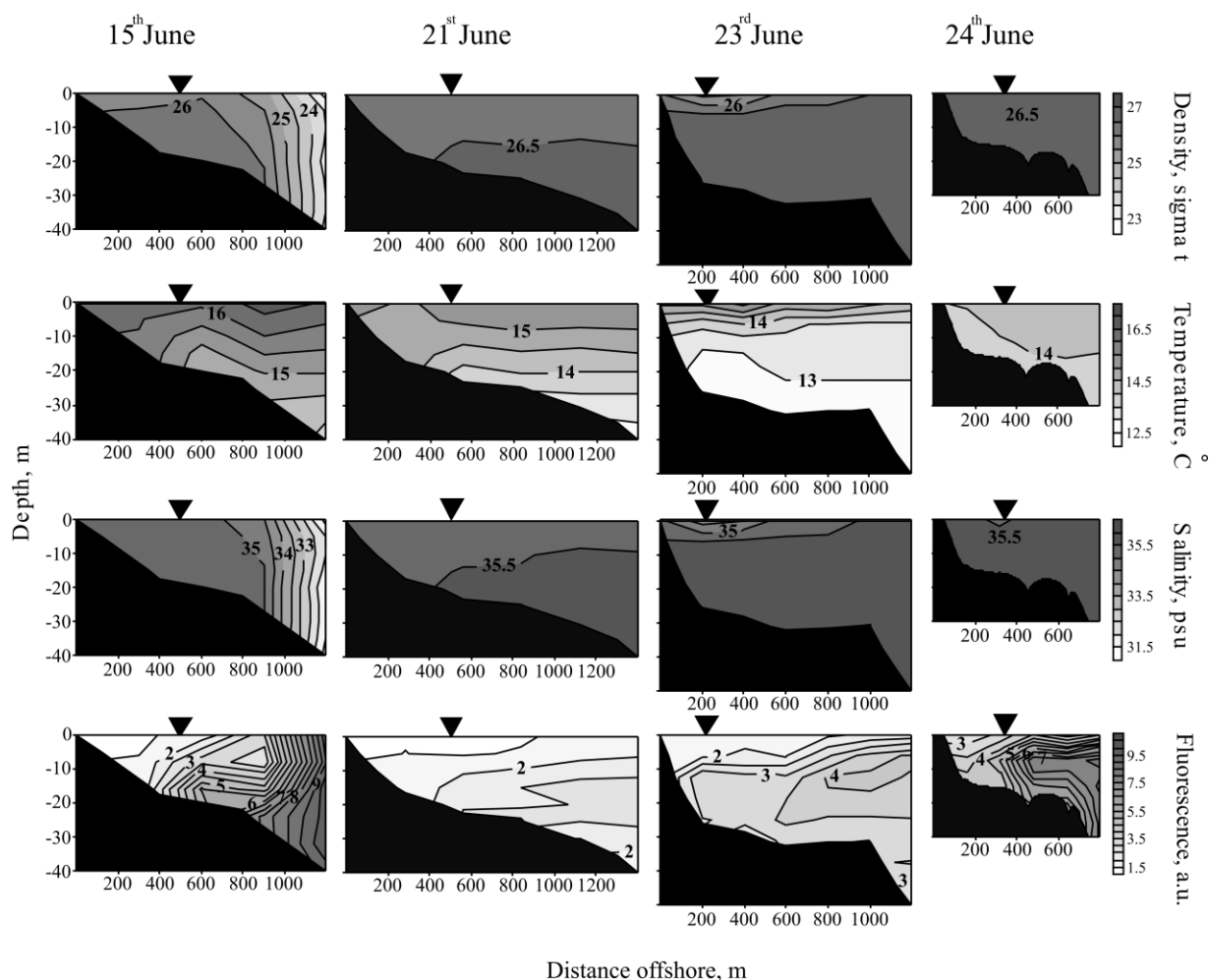


Figure III.4 CTD countour profiles of density, temperature, salinity and fluorescence for each event. Dark triangles mark the initial mean position of the front.

**Meroplankton.**- The front had little effect on larval distributions (i.e.  $L_{on}=L_f=L_{off}$  with "=" standing for non-significant differences, with  $p>0.05$ ; Fig. III.6). Ascidian tadpole larvae and *Chthamalus* spp. early nauplii reached maximum abundances at the front and 1000 m offshore, respectively (Fig. III.7). The density of *Chthamalus* spp. cyprids and *Balanus perforatus* decreased offshore according to power and logarithmic laws, respectively (Fig. III.7).

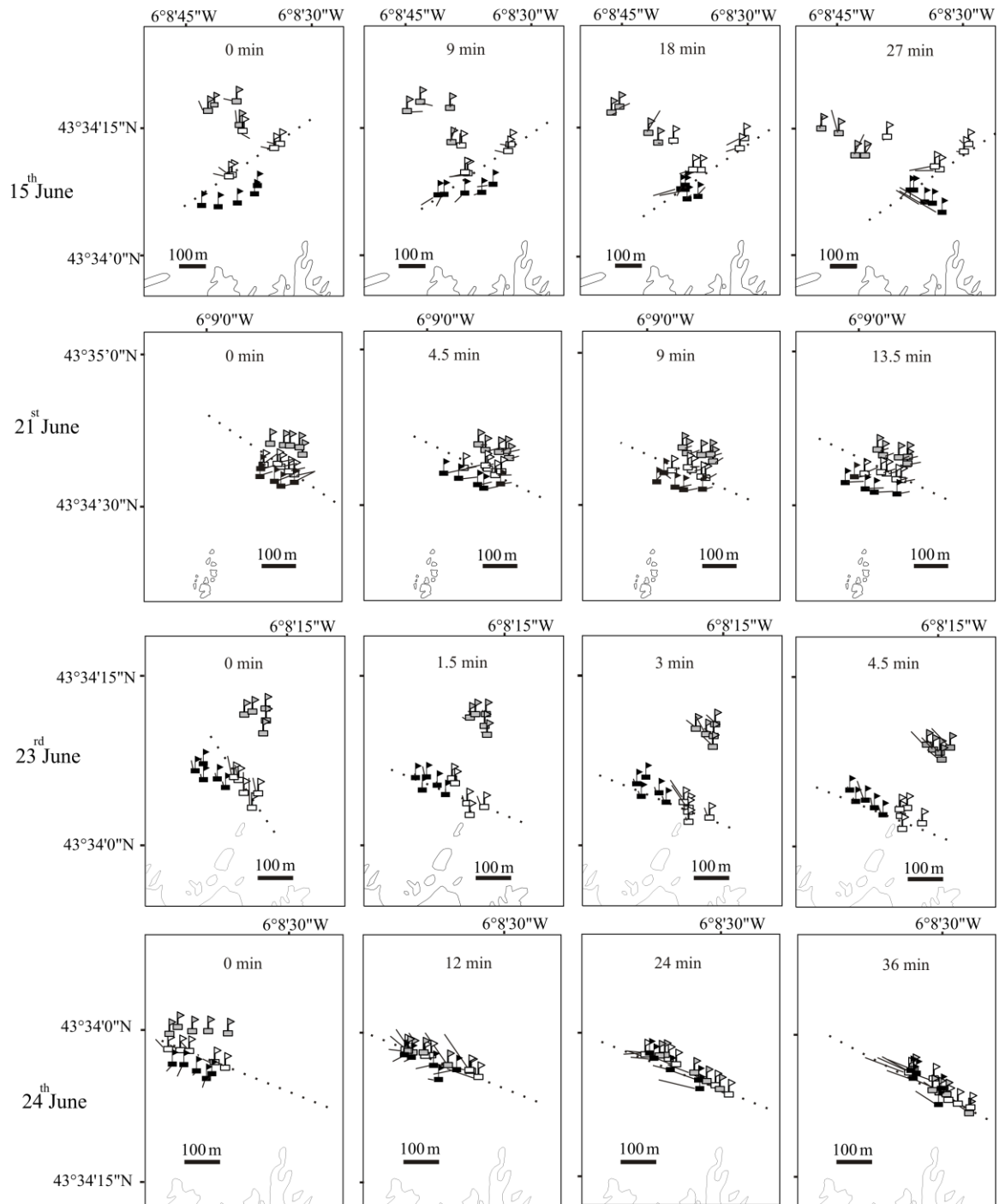


Figure III.5 Drifter trajectories. Black, grey and white drifter drawings show the position of onshore, frontal and offshore drifters, respectively. Time intervals of 9, 4.5, 1.5 and 12 minutes were used to represent drifter movements for June 15, 21, 23 and 24, respectively. Initial time was set when all the drifters have been already deployed, while final time corresponds to the moment when they were beginning to be recovered. Dark lines beside each drifter represent the distance covered between intervals. Dotted lines mark the approximated position of the front. Note that on time 0, frontal and onshore drifters for June 21, 23 and 24 and frontal and offshore ones for June 15 presented a distance already covered as they were the first to be deployed.



### June 23

**Structure of the water-column.-** This slick was ca. 250 m offshore. Weak winds (around  $2\text{ m s}^{-1}$ ) were blowing from the southwest after four days of relatively strong upwelling (Fig. III.3). The tide was 0.63 m above LAT and rising to a maximum spring tide of 4.41 m above LAT (Fig. 4A). CTD profiles (Fig. III.4) showed surface water lenses at the front which were warmer ( $15.5\text{ C}^\circ$ ) and fresher (34.5 psu) than the surrounding waters ( $14.5\text{ C}^\circ$  and 35.5 psu, Fig. III.4). A  $3.3\text{ C}^\circ$  thermocline was located between 0 and 10m depth and it reached the coast well onshore of the front, with a fluorescence maximum of 4 a.u. located behind the front at a depth of 10-15m (Fig. III.4). It slightly shallowed shorewards, especially the  $13\text{ C}^\circ$  isotherm. These characteristics and the presence of  $13\text{ C}^\circ$  water at the bottom point to a situation of upwelling.

**Drifters.-** This was the most active front in terms of drifter velocities (Fig. III.5). All of them moved rapidly eastwards and to the coast, although  $\mu_{\text{off}} < \mu_{\text{f}}$  (Table III.1), thus the onshore drifters never reached the front (Fig. III.5). Our observations of the slick line indicated that only one of the drifters deployed on the slick caught up with the fast displacement of the slick with  $\mu_{\text{f}} = 10.9\text{ cm s}^{-1}$ . The rest of them were slowly left behind, while the onshore drifters, moving at  $9.4\text{ cm s}^{-1}$  (Table III.1), were almost reached by the front upon impact on the coast (Fig. III.5). This points to a slow convergent flow at the onshore side of the front ( $\Delta\mu_{\text{on}} = 1.5\text{ cm s}^{-1}$ , Table III.1).

**Meroplankton.-** Cyprids of both *Chthamalus* spp. and *Balanus perforatus* were most abundant at onshore and frontal waters ( $L_{\text{on}} = L_{\text{f}} > L_{\text{off}}$ , Fig. III.6). These taxa together with *Membranipora* spp. cyphonauts followed exponential trends in abundance decreasing offshore (Fig. III.7). Chrysopetalid segmented larvae and especially littorinid veligers were more abundant at the front ( $L_{\text{on}} \approx L_{\text{off}} < L_{\text{f}}$  and  $L_{\text{off}} < L_{\text{on}} < L_{\text{f}}$ , Fig. III.6) Frontal accumulation was supplied from the onshore side of the front in all these cases, since offshore velocity with respect to the front was negative ( $\Delta\mu_{\text{off}} < 0$ ) and offshore larval supply rates were consequently negative as well (Table III.3)

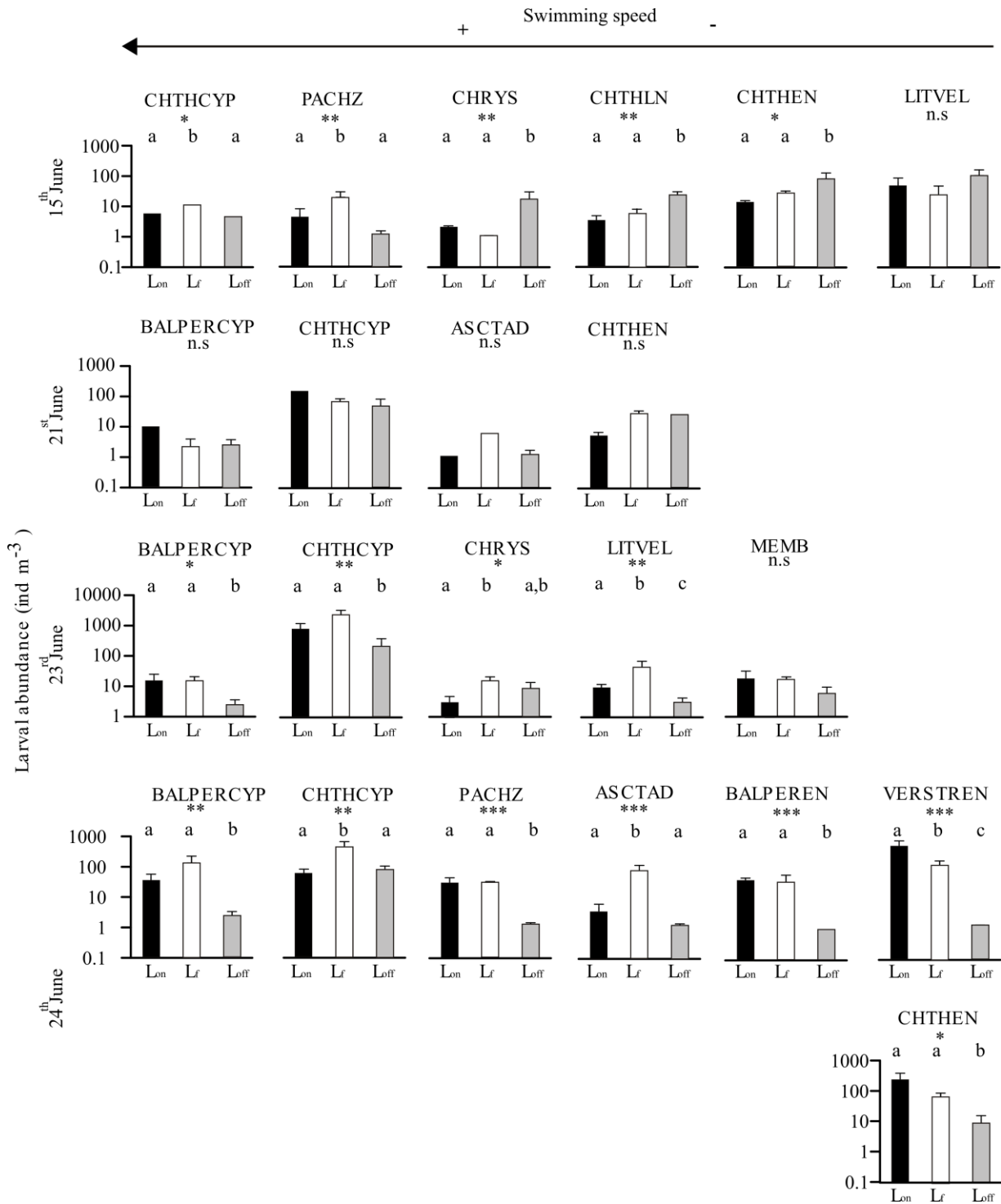


Figure III.6 Meroplankton distributions: analysis of variance. Taxa are ordered following increasing theoretical swimming speeds,  $\mu_1$  (see Table III.2 for acronyms). Each plot represents larval abundances using a logarithmic scale. Dark, white and grey bars represent larval mean abundances onshore, inside and offshore of the front, respectively, and standard deviations are shown with thin bars. The significance level of ANOVAs is shown for each plot (n.s.-non significant;  $p^* < 0.05$ ;  $p^{**} < 0.01$ ;  $p^{***} < 0.001$ ). The nomenclature “a-b-c” is used to group mean larval abundances following the results of Fisher’s post hoc tests.

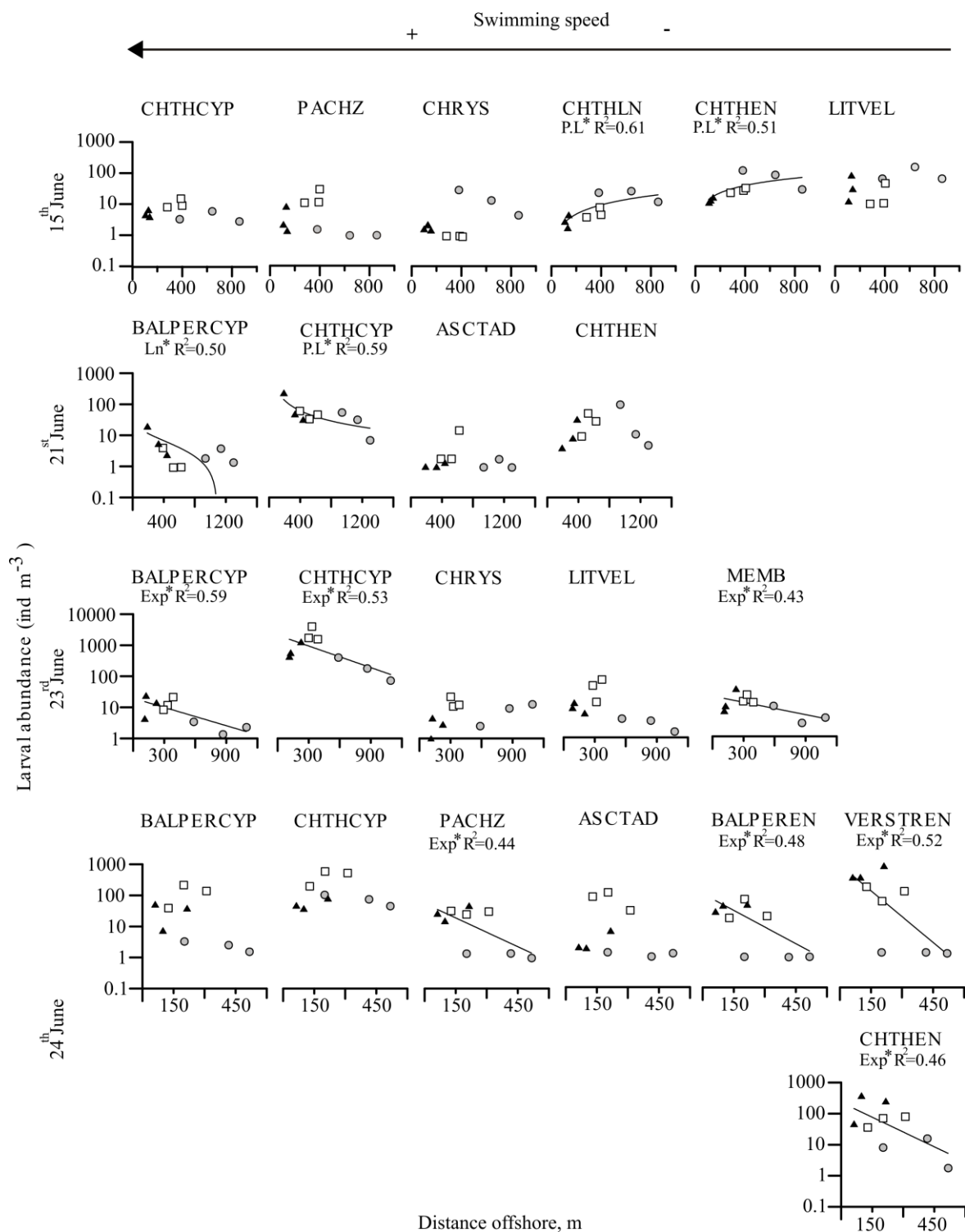


Figure III.7. Meroplankton distributions: continuous trends with distance. Taxa are ordered following increasing theoretical swimming speeds,  $\mu_1$  (see Table III.2 for acronyms). Each plot represents larval abundances using a logarithmic scale versus distance offshore. Dark triangles, white squares and grey circles represent larval abundances at every station onshore, inside and offshore of the front, respectively. Fits to continuous functions were shown if they are significant (Exp: exponential; Log: logarithmic; P.L: power law) showing also the significance level ( $p^* < 0.05$ ;  $p^{**} < 0.01$ ;  $p^{***} < 0.001$ ) and the determination coefficient.

Table III.1. Values of current speeds: surface onshore ( $\mu_{on}$ ) surface offshore ( $\mu_{off}$ ), frontal ( $\mu_f$ ), accumulation onshore ( $\mu_{on}^*$ ), accumulation offshore ( $\mu_{off}^*$ ) in cm/s calculated for each event. For the first three current speeds, standard deviation values are also shown.

Event	$\mu_{on}$	$\mu_f$	$\mu_{off}$	$\Delta\mu_{on}$	$\Delta\mu_{off}$
<b>June 15 2009</b>	$-4.8 \pm 1.4$	$3.8 \pm 0.6$	$1.5 \pm 0.6$	8.6	-2.3
<b>June 21 2009</b>	$2.0 \pm 0.5$	$2.5 \pm 1.5$	$1.8 \pm 0.4$	0.5	-0.7
<b>June 23 2009</b>	$9.4 \pm 0.9$	$10.9 \pm 0.1$	$6.4 \pm 0.6$	1.5	-4.5
<b>June 24 2009</b>	$-3.5 \pm 0.2$	$2.0 \pm 0.4$	$8.3 \pm 0.4$	5.5	6.3

### June 24

**Structure of the water-column.-** This was the most visually evident and active front, with a wide foam line 350m off the coast which accumulated all kinds of floating debris, attracting feeding fish and seagulls. Weak westerly winds (around  $4\text{ m s}^{-1}$ ) were blowing during the sampling, following a typical upwelling relaxation after the 19-22 June upwelling episode (Fig. III.3). The spring tide was 4.21m above LAT and going down to a minimum of 0.57 m above LAT. There was evidence of fresher surface lenses on the front (35 to 35.5 psu), which were less marked than that observed on June 23 (Fig. III.3). Temperature differences were less than ca.  $0.5\text{ }^\circ\text{C}$  approximately (Fig. III.4). The most evident gradient was found in fluorescence, rapidly increasing seawards in the whole water column from 3 to 7.5 a.u. and quite similar to that one on 15<sup>th</sup> June.

**Drifters.-** Offshore and onshore drifters rapidly converged to the front at velocities of  $\mu_{off}=8.3\text{ cm s}^{-1}$  and  $\mu_{off}=-3.5\text{ cm s}^{-1}$  respectively, while the front approached the coast at  $\mu_{off}=2\text{ cm s}^{-1}$  (Fig. III.5, Table III.1). This was the only event with positive net convergence speeds from offshore waters ( $\Delta\mu_{off}>0$ , Table 1). Drifter trajectories reveal a prevailing eastward flow which was more intense at the front.

**Meroplankton.-** There was a clear frontal accumulation of ascidian tadpole larvae ( $L_{on}=L_{of}<L_{fr}$ , Table III.4, Fig. III.6), with a higher supply rate from the onshore ( $S_{on}=0.13\text{ larvae m}^{-2}\text{ h}^{-1}$ ) than the offshore side ( $S_{off}=0.01\text{ larvae m}^{-2}\text{ h}^{-1}$ ). *Chthamalus* spp. cyprids exhibited also a frontal accumulation ( $L_{on}=L_{of}<L_{fr}$ , Table III.4, Fig. III.6), but this time their origin was probably offshore of the front, with  $S_{on}=3.11\text{ larvae m}^{-2}\text{ h}^{-1}$  and  $S_{off}=4.79\text{ larvae m}^{-2}\text{ h}^{-1}$ .

$^2 \text{ h}^{-1}$  (Table III.4). *Balanus perforatus* cyprids were more abundant onshore and at the front ( $L_{\text{on}}=L_{\text{f}}>L_{\text{off}}$ , Fig. III.6). *Pachygrapsus marmoratus* zoeae and early nauplii of *Balanus perforatus*, *Verruca stroemia* and *Chthamalus* spp. were also similarly retained onshore and their abundances followed exponential functions decreasing seawards (Fig. III.6, Fig. III.7).

### *General results*

For a given front, it makes sense to expect accumulation of those taxa attracted to the slick but also able to swim against the vertical currents characteristic of convergent flow. To test this idea, we first searched for published measurements of swimming velocities for those taxa appearing in our study (Table III.2). We then assumed that the vertical velocity perceived by a larva at the front resembles the velocity of the source water, and calculated the quotient  $Q$  between larval and environmental velocities.  $Q$  indicates whether the larva is faster ( $Q>1$ ), as fast ( $Q=1$ ) or slower ( $Q<1$ ) than the velocity of the convergent flow. We also characterized frontal aggregation using the term  $A$ . Large  $A$  values indicate intense accumulation at the front (Table III.3, Table III.4). To calculate both  $Q$  and  $A$ , estimations of relative water speed  $\Delta\mu_s$  and larval abundances  $L_s$  at the source have to be known. The source of accumulating larvae could be clearly identified at onshore waters during 3 out of four fronts because  $\Delta\mu_{\text{off}} < 0$  (Table III.1, Table III.3). The situation was less clear on June 24, where both  $\Delta\mu_{\text{off}}$  and  $\Delta\mu_{\text{on}}$  were positive (Table III.1, Table III.4). In this case, we only consider the comparison between supply rates in those taxa that significantly accumulated in the front, as transport across it by sinking in the convergence is not probable. Thus, ascidian tadpole larvae had a higher contribution from onshore waters, while in *Chthamalus* spp. cyprids an offshore origin prevailed.

Table III.2 Larval speeds  $\mu_L$  taken from literature for every species. *Chthamalus* spp. early nauplii (CHTHEN), *Chthamalus* spp. late nauplii (CHTHLN), *Chthamalus* spp. cyprids (CHTHCYP), *Balanus perforatus* early nauplii (BALPEREN), *Balanus perforatus* cyprids (BALPERCYP), *Verruca stroemia* early nauplii (VERSTREN), *Pachygrapsus marmoratus* zoea (PACHZ), chrysopetalid annelid (CHRYS), *Membranipora* spp cyphonaut (MEMB), ascidian tadpole larvae (ASCTAD), litorinid veliger (LITVEL)

Taxa	$\mu_L$ (cm*s <sup>-1</sup> )	References
BALPERCYP	6.7	Anderson (1992)
CHTHCYP	5.7	Anderson (1992)
PACHZ	2.2	Knudsenj (1960), Chia et al. (1984)
CHRYS	0.7	Nozais (1997)
CHTHLN	0.4	Williams (1994), Walker (2004)
ASCTAD	0.3	McHenry (2005)
BALPEREN	0.3	Williams (1994), Walker (2004)
VERSTREN	0.3	Williams (1994), Walker (2004)
CHTHEN	0.3	Williams (1994), Walker (2004)
LITVEL	0.13	Mileikovsky (1973), Chia et al. (1984)
MEMB	0.11	Abelson (1997)

Table III.3 Resume of parameters which characterize larval distributions on June 15, 21, and 23. Taxa were ordered following increasing larval speeds. For each event and taxa, supply rates  $S$  in individuals  $m^{-2}s^{-1}$  are shown. Note that we only consider onshore supply rates and probable larval origin was set onshore of the front because offshore accumulation speeds  $\Delta\mu_{off}$  were negative in these three cases. We also represent the accumulation factor  $A$ . See Table III.2 for the acronyms of the taxa.

Event	Taxa	$S_{on}$	A
<b>June 15 2009</b>	CHTHCYP	0.41	2.27
	CHRYC	0.08	0.1
	PACHZ	0.26	5.39
	CHTHLN	0.19	2.06
	CHTHEN	1.10	2.12
	LITVEL	3.85	0.52
<b>June 21 2009</b>	BALPERCYP	0.04	0.13
	CHTHCYP	0.78	0.44
	CHTHEN	0.02	6.49
	ASCTAD	0	43.37
<b>June 23 2009</b>	BALPERCYP	0.20	0.97
	CHTHCYP	11.69	2.95
	CHRYC	0.02	7.75
	LITVEL	0.11	5.15
	MEMB	0.23	0.95

Table III.4 Resume of parameters which characterize larval distributions on June 24. Taxa were ordered following increasing larval speeds. For each event and taxa, supply rates  $S$  in individuals  $m^{-2}s^{-1}$  are shown. Both onshore and offshore supply rates are considered because both accumulation speeds  $\mu^*$  were positive. However, we could only set the origin of larvae for *Chthamalus* spp. cyprids and ascidian tadpoles as they show a significant frontal accumulation pattern. We also represent the accumulation factor  $A$ . See table 2 for the acronyms of the taxa.

Event	Taxa	$S_{on}$	$S_{off}$	Origin	A
<b>June 24 2009</b>	PACHZ	1.55	0.01	-----	-----
	BALPERCYP	1.78	0.09	-----	-----
	CHTHCYP	3.11	4.79	Offshore	0.23
	CHTHEN	12.67	0.49	-----	-----
	BALPEREN	2.18	0	-----	-----
	VERSTREN	29.03	0.02	-----	-----
	ASCTAD	0.13	0.01	Onshore	30.26

Our dynamic observations in 4 fronts along with the literature data on swimming velocities allow us to regress  $A$  against  $Q$  for different larvae at each event. Largest accumulations ( $A > 10$ ) were reached by larvae which swam at velocities which do not even reach the velocity of the convergent flow ( $0.1 < Q < 1$ , Fig. III.8). Relatively faster or slower larvae showed lower accumulation ratios, according to a unimodal response curve which best fits the quadratic equation

$$\text{Log } A = -0.5968(\pm 0.2002) (\log Q)^2 - 0.4927(\pm 0.2040) \log Q + 0.7035(\pm 0.2134)$$

with  $R^2 = 0.40$ ,  $p = 0.025$  and  $n = 17$  (Fig. III.8).

Solving the equation for theoretical maximum  $A$  values, that is, when the first derivate of the function equals 0, we obtain  $A = 6.38$  when  $Q = 0.38$  (flow in the source is 2.63 higher than larval speeds). If we get  $Q$  values which brings to  $A = 1$ , we are defining a theoretical range of relationships between larval and environmental speeds (from  $Q = 0.02$  to  $Q = 5.60$ ) that lead to frontal accumulations. Then we represented this  $Q$  accumulation range for different taxa as a function of the possible magnitude of the flow in our coasts (Fig. III.8D).



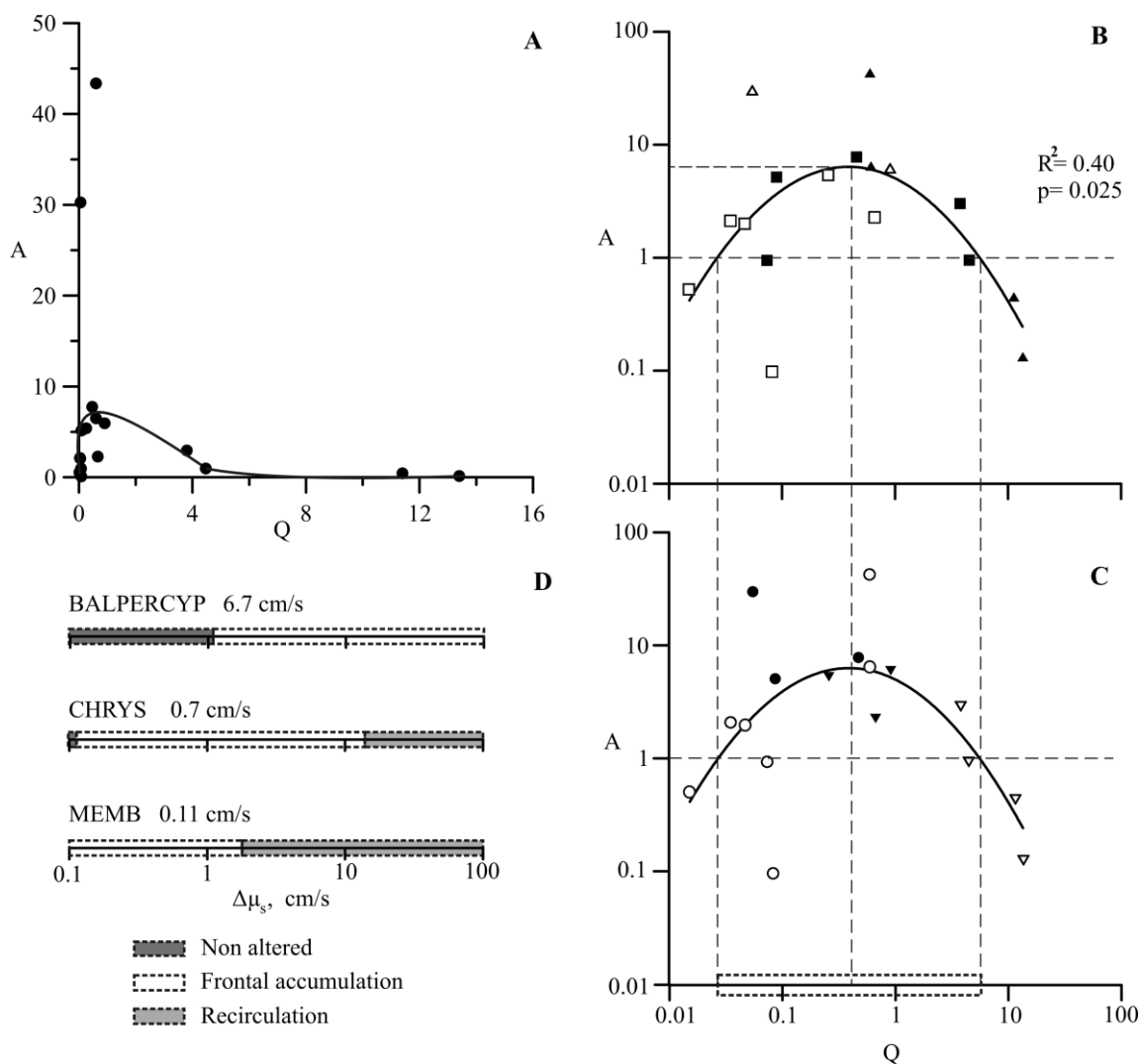


Figure III.7 Accumulation factor (A) versus velocity quotient (Q) plots (n=17). The significant quadratic fit for both variables logarithmic transformed is represented with a dark curve line in the three plots. A) Plot with both variables represented with a linear scale; B) Plot with both variables represented with a logarithmic scale and data split by event: white squares, dark squares, dark triangles and white triangles represent data from June 15, 21, 23 and 24, respectively. C) Plot with both variables represented with a logarithmic scale with data split by larval speed: circles show values for slow larvae ( $\mu_1 < 1 \text{ cm/s}$ ) while inverted triangles represent values for fast larvae ( $\mu_1 > 1 \text{ cm/s}$ ) (see Table III.2 for both kinds of taxa). Black symbols show which larval distributions presented significant frontal accumulations as result of the analyses of variance. Discontinuous lines mark the theoretical Q values when  $A=1$  and when A reaches the maximum given by the function. D) Ranges of current velocities ( $\Delta\mu_s$ ) which lead to non altered, frontal accumulation and recirculation patterns for three different taxa (see Table III.2 for the acronyms) according to the A-Q unimodal peaking curve. All possible current magnitudes are considered (from 0.1 to 100 cm/s) and  $\mu_1$  for every taxa is also shown.

## **Discussion**

### *Physical origin of the fronts*

Our meteorological (Fig. III.3), hydrographical (Fig. III.4) and drifter data (Fig. III.5) point to two different processes causing the fronts: internal waves (June 15, 21 and 23) and topographic fronts (June 24). The study site is located close to the Avilés Canyon, with an abrupt topography and a shelf break only 15 km offshore where intense tidal motions in the thermocline and the consequent internal waves are most likely generated (Shea & Broenkow 1982; Kunze et al. 2002). The thermocline may approach the surface due to upwelling conditions (Botas et al. 1990) what surely enables short amplitude internal waves to reach the surface and form trains or series of slicks or foam lines. Elevations of the thermocline in the proximity of the foam line were observed in these 3 first events (Fig. III.4) and the consecutive parallel structures observed on June 15 and 21 point to wave packets propagating onshore. Internal tidal motions have been linked with the shallowing of the thermocline in the coast of California by Pineda & Lopez 2002. They found that these low frequency cooling events respond to upwelling events and their propagation by coastal trapped waves. Upwelling wind conditions are set in summer in our region due to the usual seasonal evolution of both the Azores High and the Iceland Low (Varela et al. 2005). Eastward transmission of these emerging waters from upwelling hotspots in Galicia could also take place as Kelvin waves, especially active in the Cantabrian Sea (Alvarez-Fanjul et al. 1997). Another key factor performing upwelling dynamics are sea-land breezes. During our samplings, their effects were clear on June 21 (Fig. III.4), when water temperature dropped respect to June 15 and northeasterly winds were blowing. These winds seemed to follow daily cycles that we interpret as thermal sea breezes: note how positive increments in upwelling index coincide with the afternoons from June 19 to June 22. Thermal breezes have been show to drive upwelling on Monterey Bay (Woodson et al. 2007) but also in West Iberia (Vitorino et al. 2002). Moreover, even the duration of the whole upwelling episode (4 days) remains the typical breeze variability time scale (Varela et al. 2005). After this upwelling episode, the thermocline shallows on June 23 to 10 m depth (Fig. III.4). On June 15, however, it is the displacement of the Nalón river plume what may also generate internal waves. Convergence at

the plume front can trigger the release of individual internal waves seawards, similar to those topographically generated (Nash & Moum 2005).

Alternatively, we think that the presence of a strong eastwards coastal current was associated with the formation of only one structure off the Cudillero harbour on June 24. This situation corresponds to the most frequent, downwelling phase in the Central Cantabrian Sea, and is driven by SW winds (Gil 2003). Again, the position of both high and low pressure atmospheric systems determines the westerly direction of these winds (Varela et al. 2005). Our study area is located in the lee of the Cudillero harbour and nearby rocks (Fig. III.1) which possibly deflect the eastwards main flow offshore and then, at a certain distance to the east, onshore, conforming a meander in the pattern of the currents. On the other hand, a recirculation feature is expected in the lee of these coastal bumps, characterized by a reversal of the flow, that is, mainly offshore. The result may be a well developed and strong convergence attached to the topographic feature which may not imply any physicochemical surface gradient across the front.

*Effect of nearshore fronts on larval distributions: accumulation*

Our results confirm other studies showing plankton accumulation at nearshore fronts and slicks, including crustacean, polychaeta and gastropods (Zeldis & Jillet 1982, Shanks 1995, Pineda 1999, Molinet et al. 2006), and describe previously unknown frontal aggregations for ascidian larvae. Our maximum accumulation rates  $A$  in the slicks given by the quadratic function ( $A \approx 7$ ) are clearly higher than those suggested by models that predict maximum increases in concentration less than twice the local background concentration (Lennert-Cody & Franks 1999). However, our highest  $A$  values exceed 30 for ascidian tadpole larvae, maybe because they are buoyant, a property which we observed in the laboratory and was already studied for their eggs (Vázquez & Young 1996). Thus, tadpole larvae would keep on floating in the front and accumulating even when the vertical flow exceeds their swimming abilities. In fact, part of the variability observed in the peaking accumulation curve (Fig. III.8) could be due to the different buoyancies of the taxa.

Accumulation seems to peak at some intermediate ratio of larval swimming speed to surface convergence velocity (Fig. III.8), what makes hydrodynamic and biological sense. We may safely assume that swimming is undirected in the horizontal plane or at least it opposes that flow inefficiently. It seems that there is some kind of horizontal resistance against the convergence in the case of barnacle cyprids, whose cross shore distributions are diffusive decreasing trends from the coast on June 21 and 23, while much slower larvae were concentrated in the front or located offshore (Fig. III.6, Fig. III.7). However, in general, our results show how accumulation arises ( $A > 1$ ) when  $\mu_1$  is still much higher than the convergence velocity ( $Q = 5.60$ , Fig. 7). This means that, even when larvae could theoretically face the horizontal currents, they are starting to be transported towards the slick. In agreement with these observations, Genin et al. 2005 shows how larvae behave passively in the horizontal axis, but not in the vertical. Upward motion against the vertical convergence current could be activated upon arrival at the front and guided by the light field (Wendt et al. 1999) or pressure gradients (Mann & Wolf 1983). This behaviour determines the aggregation because animals arriving to the front from the surrounding waters will remain vertically stationary and accumulate (Franks 1992, Pineda 1999). If the convergence flow increases and the vertical flow exceeds the locomotion abilities of the larvae, then they sink in the convergence and the aggregation decreases. The frontier between the influence of vertical and horizontal water motions on the accumulation pattern would be set at  $Q = 0.38$ , when  $A$  is maximum. Thus, at  $Q > 0.38$  meroplankton distributions around the convergence would be driven by changes in the horizontal currents, while at  $Q < 0.38$  vertical motions in the front would govern these distributions. As the magnitude and variability in the horizontal currents are much greater than those characterizing the vertical flow, the ranges of  $Q$  affected by each component differ, being the distribution strongly skewed (Fig. III.8A)

As we did not get direct measurements, we can only hypothesize the magnitude of the vertical flow ( $\mu_v$ ) from the unimodal curve. We can suppose that between  $Q = 5.60$  and  $Q = 0.38$ , larvae are much faster than the downwards currents and it is below  $Q = 0.38$  when  $\mu_v > \mu_1$  and larvae start to sink so  $A$  decreases (Fig. III.8). It is a dramatic decrease in relative frontal concentrations if we consider again the skewed untransformed relationship between  $A$  and  $Q$  (Fig. III.8A), showing how larvae are rapidly swept away by the downward flow. Then, when  $Q = 0.38$  the velocity of the zooplankton matches the vertical flow velocity, so at this point when  $A$  is maximum,  $\mu_v = \mu_1$ . If we also accept that the velocity of the vertical flow is

proportional to the velocity of the horizontal, convergent flow ( $\Delta\mu_s$ ), such that  $\Delta\mu_s = x\mu_v$ , then  $Q=0.38 = \mu_i/\Delta\mu_s = \mu_v/x\mu_v$ . Solving for  $x$ ,  $x=1/0.38=2.63$ , which means that horizontal currents would be 2.63 higher than the vertical ones for a given slick. In his model, Franks 1992 considered that the proportion between vertical and horizontal scales of motion is 1:100. Some direct measurements confirm this ratio in the ocean (Rodríguez et al. 2001) while others points to 1:10 (Manasrah et al. 2006), which brings to vertical speeds of  $m^{-4} s^{-1}$  or  $mm s^{-1}$ , respectively. However, in convergent systems, as water is forced downwards, the proportion varies between 1:10 for termohaline fronts (Yanagui et al. 1995) to 1:1 for the Columbia river plume front with vertical currents up to  $0.5m s^{-1}$  (Kilcher & Nash 2010). Concretely, for internal waves of some metres of amplitude, like the ones we recorded on June 15, 21 and 23, downwelling rates are in the order of several  $mm s^{-1}$  or even  $cm s^{-1}$  (Zeldis & Jillet 1982) which seems to be in reasonable agreement with our ratio (1:2.63). We think that this concordance is lending support to our explanation for the peaking accumulation curve but it is only a rough approach given the variability in both the estimates of larval and current speeds.

Our hypothesis about the origin of the quadratic function response are also supported if we examine larval distributions for each point considered in the A vs Q regression analysis (Fig. III.8A). Note that frontal accumulations that were found significant in the analyses of variance are located between  $Q=0.02$  and  $Q=5.60$  where theoretically  $A>1$ . In addition, we hypothesize that when  $Q>0.38$  larvae starts to be independent from the environmental flow. Actually, all decreasing offshore cross shore trends ( $b<0$ ), characteristic of spatial distributions not altered by the slick, took place when  $Q>0.38$ . In general, zooplankters presenting such distributions are relatively fast swimmers (barnacle cyprids, *Pachygrapsus marmoratus* zoea, Table III.2). Contrarily, at  $Q<0.38$  larvae are expected to sink in the convergence following passively the circulation patterns. Franks 1992 showed that weaker swimmers accumulate is lesser extent and follow the streamlines along the pycnocline, i.e, to the stratified side that tends to be offshore. In agreement with his model, we do find increasing offshore cross shore trends ( $b>0$ ) and offshore retention patterns when  $Q<0.38$ . Zooplankters in this case are slower swimmers, especially litorinid veligers and *Chthamalus* spp. nauplii (Table III.2). Thus, the peaking curve is characterized by slow and fast swimmers at low and high Q values, respectively (Fig. III.8C). This observation is suggesting that, given the diversity in locomotion capacities among meroplankters, a given organism cannot present Q values along all the range defined by the quadratic function. We reflect this constraint representing the possible larval

distributions along the whole range of convergence currents  $\Delta\mu_s$  for 3 different taxa (Fig. III.8D). This range of convergence velocities is imposed by the magnitude of the currents in the study area: data from Peñas Buoy points to maximum surface flows of  $100 \text{ cm s}^{-1}$ , far above mean values around few  $\text{cm s}^{-1}$ . On the other hand, values below  $0.1 \text{ cm s}^{-1}$  are considered virtually 0. Consequently, strong swimmers like barnacle cyprids ( $\mu_i > 5 \text{ cm s}^{-1}$ ), cannot present Q values typical of recirculation patterns, as that would require currents above the natural limit (even higher than  $2 \text{ m s}^{-1}$ ). In the other end, weak, slow swimmers like ascidian tadpole larvae, barnacle nauplii, littorinid veligers and bryozoan cyphonauts, which swim at speeds of few  $\text{mm s}^{-1}$  (Table III.2), may not keep a non altered pattern because even a very weak convergence flow around  $0.1 \text{ cm s}^{-1}$  would bring them to the front. Only when  $0.7 < \mu_i < 3 \text{ cm s}^{-1}$ , approximately, (i.e, chrysopetalid annelids and *Pachygrapsus marmoratus* zoea, Table III.2) all the spatial patterns around the slick are theoretically possible (Fig. III.8D). In this way we are defining spatial distributions as a function of potential behaviour, which emphasizes the role of larval morphology and hydrodynamics.

*Effect of nearshore fronts on larval distributions: retention and dispersal*

A consistent result of our cruises is that the origin of larvae that presented higher abundances inside the fronts was probably shorewards from them (Table III.3, Table III.4). Only on June 24,  $\Delta\mu_{\text{off}}$  was positive (Table III.1) and the ratio of abundances in the case of *Chthamalus* spp. cyprids pointed to an offshore origin (Table III.4). From these observations, we can suggest that local onshore retention was the prevailing effect of the fronts in our site, an effect suggested by other studies (Cowen et al. 2000; Mace & Morgan 2006). We describe this process as a “broom effect”, pushing organisms located onshore towards the coast, repeatedly in the case of consecutive internal waves. However, the frontal accumulation of offshore larvae, although less probable, cannot be rejected at all, since maximum negative values of  $\Delta\mu_{\text{off}}$  were only  $-4.5 \text{ cm s}^{-1}$  on June 23 (Table III.1). These speeds could be faced by strong swimmers as barnacle cyprids and crab megalopae if we suppose that these species could be active in the horizontal axis and could swim against the flow. Shanks (1995) suggested the possibility of an active swimming behaviour towards internal wave fronts from offshore waters in the case of fast crab megalopae. Note, however, that for slow swimmers the negative values of  $\Delta\mu_{\text{off}}$  are still too high, thus to reach the front from the offshore side would not be

possible for them. Frontal aggregation and transport of larvae coming from distant locations would not be a common feature in the internal wave fronts that we have observed.

Frontal dynamics may be of relevance for cross shore spatial patterns even if they do not lead to retention or accumulation. We found evidence that offshore dispersal can be enhanced by the motions of the slicks. We explain drastic offshore increases in *Chthamalus* spp. nauplii, chrysopetalid annelids and littorinid abundances especially on June 15 in these terms (Fig. III.6, Fig. III.7). It is unlikely that during this event the slick was acting as a barrier for the shorewards displacement of larvae from the offshore side because  $\Delta\mu_{\text{off}}$  was negative (Table III.1). Consequently, hypothetical offshore larvae, weak swimmers in this case, would not even reach that barrier. Inversely, we interpret that convergent circulation is acting like a “vacuum cleaner”, attracting onshore larvae due to a quite strong  $\Delta\mu_{\text{on}}$  ( $8.6 \text{ cm s}^{-1}$ , Table III.1) and forcing them to sink and to follow the pycnocline away from the front till upward swimming counteracts downwelling flow and larvae reaches the surface again. In this particular feature, differences in the stratification regime between both sides of the slick were well marked, with an offshore surface layer influenced by the river plume (Fig. III.4). A similar scenario but at a greater spatial scale was studied by Shanks et al 2000 with surface accumulation of relatively slow larvae in the stratified offshore side of an upwelling front. These classical frontal structures, with offshore stratified waters and clear circulation patterns, may potentially segregate the planktonic communities by their swimming abilities across the front, what Franks 1992 described as spatial dislocations of populations. If we consider only one taxa like *Chthamalus* spp., the front may have a stage-specific effect on June 15. For cyprids, aggregation at the slick is the result arising from the interaction between strong onshore convergence and fast locomotion, but the same physical process may cause offshore recirculation for weaker nauplii (Fig. III.6, Fig. III.7). The same event may accumulate and transport onshore the cyprid competent stage and disperse offshore early nauplii ones, what can be determinant for this particular species in both recruitment and spawning processes, respectively. However, in convergences arising just from topographically driven currents like the one on June 24, when both sides were characterized by a mixed water column (Fig. III.4), current circulation patterns are not clear. Thus, weak barnacle nauplii did not present offshore distributions on June 24 (Fig. III.6, Fig. III.7) suggesting that these kind of fronts only alter larval distributions if the organisms accumulate just in the foam line.

*Effect of nearshore fronts on larval distributions: transport and potential recruitment*

We have evidences to support that fronts are common features in our coastal site. In a 10 days period we recorded at least four different structures. This frequency together with their origin, previously discussed, suggest that both downwelling and intermittent upwelling seasonal phases can set up the conditions required for frontal development. In addition, we consider that both types of convergence structures are not mutually exclusive, especially in a scenario of rapid upwelling-downwelling transitions typical of summer months. For example, on June 23 we found downwelling eastwards circulation (Fig. III.5) that would originate a single foam line that we would interpret as a topographically driven flow deflection. However, taking into account the vertical deformation of the thermocline and its shallowing after the upwelling episode during 19-22 June (Fig. III.4), on June 23 the slick observed may respond to internal wave dynamics.

About frontal movements and persistence, all the structures moved onshore (Table III.1) till they reach the coast with the exception of the front on June 21 which disaggregated before that. Moreover, on June 15 and 24 the fronts seemed to accumulate competent cyprids of barnacles and old litorinid veligers on June 23 (Fig. III.6). This has an important ecological significance: in a period of 10 days, three different fronts advanced towards the coast with high abundances of strong (cyprids) but also slow (veliger) swimming larvae in what we consider potential recruitment events. On June 24, drifter trajectories show that, together with a perpendicular transport respect to the front, there was a strong slick-parallel circulation just inside the foam line to the east (Fig. III.5). This kind of processes has been defined as larval conduits for some taxa, like crab megalopae (Eggleston et al. 1998). Along frontal circulation may be the consequence of a deflected incidence flow to the front (Largier 1993). Moreover, this study suggested that, if the structure is “anchored” to a given topographic feature (i.e, Cudillero harbour rocks, Fig III.1), larval transport would be driven to a single point in the coastline where the frontline intersects the shore. In the case of the event recorded on June 24, the front was not strictly fixed in the space as we recorded axial displacement of the foam line (Table III.1) but the flow along the front seemed to be much greater (Fig. III.5). Thus, organisms concentrated in the foam line would be recurrently transported not to a single



location, but probably to a few hundred meters of coastline just eastwards respect to our study area.

We have shown how fronts accumulate and transport some competent larval stages of intertidal invertebrates just to their parental habitats in the rocky shore. However, to infer from our observations the real importance of these features in terms of adult population dynamics could be too risky (Largier 1993). Post settlement processes entailing high mortality rates may impact these dynamics in great extent, thus concealing potential inputs of new recruits provided by the slicks. Nevertheless, mesoscale studies along Chilean coasts (Lagos et al. 2008) successfully link slick occurrence with high recruitment rates for barnacles. New studies that complete very nearshore frontal samplings with recruitment estimates in the intertidal are the next step to know the final relevance of these events.





## General Discussion





## Passive tracers or active swimmers?

According to the data presented in this thesis, many meroplanktonic organisms had a very nearshore distribution (e.g. Fig. I.5) which was uncorrelated with the time-averaged upwelling index (Table I.2, Fig. I.7). This is commonly explained by an active swimming behaviour of the larva. The mechanism is simple and has been demonstrated in zooplankton: swimming against the vertical currents determines both accumulation at fronts and coastal retention (Genin et al. 2005). However, an active swimming behaviour is not strictly necessary to explain nearshore accumulation. For example, the presence of a coastal boundary layer (CBL) would also favour nearshore retention by reducing nearshore Ekman transport due to frictional effects (Largier 2003). In our study area, this second mechanism is fully consistent with data from offshore (Peñas) and onshore (Cudillero) moored current meters (Fig. 1). Ekman transport calculated from wind velocities measured at the offshore buoy is positively correlated with cross shore surface currents (i.e. positive upwelling leads to northwards flow) both at the offshore and the onshore sites (Fig. 1). Moreover, bottom currents were negatively correlated with Ekman transport in the onshore site (i.e. positive upwelling leads to southwards flow), indicating that water movements at depth were opposite to those at the surface, a pattern which resembles the classical picture of a coastal upwelling (Mann & Lazier 1996). The opposite applies to downwelling situations, with offshore transport of the surface layer and onshore transport of the deep layer. However, the upwelling index explained less variance in current velocities and the slope of the regression line was markedly lower at the onshore location, indicating slower water currents which were more loosely coupled to Ekman transport ( $R^2=0.18$  and  $R^2=0.13$ , in the offshore and onshore sites, respectively; Fig. 1). Note how the range of surface cross shore currents decreases by a factor of 2 (40 to  $-40\text{ cm s}^{-1}$  and 20 to  $-20\text{ cm s}^{-1}$ , approximately; Fig. 1) and the slope of the linear fit with the upwelling index by a factor of almost 3 (0.00467 and 0.00192; Fig. 1). This is consistent with the idea of a stagnant coastal boundary layer, bound to some extent to the coast by frictional effects.

As a kind of null hypothesis, we can estimate how far a passive larva located at the surface can be carried offshore by Ekman transport during upwelling (as in Roughgarden et al. 1988). We can estimate the surface flow at Cudillero for the period of our monthly field survey (2007-2008) from wind data using relationships in Figure 1. During upwelling situations lasting 1 week, that is, the approximate duration of an early barnacle nauplii, the average upwelling

index is of only  $137.28 \text{ m}^3 \text{ km}^{-1} \text{ s}^{-1}$  and the surface offshore current velocity is  $0.26 \text{ cm s}^{-1}$ . Such slow current velocity times larval duration yields a maximum transport distance of 1527 m. Alternatively, we can estimate how far a passive larva located at the bottom can be carried offshore by Ekman transport during downwelling (as in Grantham 1997). For downwelling situations lasting 1 week the average upwelling index is of  $-191.22 \text{ m}^3 \text{ km}^{-1} \text{ s}^{-1}$  and the surface offshore current velocity is  $0.11 \text{ cm s}^{-1}$ , even slower than that reached at the surface. The resultant distance is 693 m. These two estimated distances envelope our measured average distances of ca. 1200 m offshore for *Verruca stroemia* early nauplii (Table I.2). It is interesting to note that such reduced transport distances are only possible close to the coast, since cross shore Ekman transport decreases markedly shorewards. For example, during a typical 1-week upwelling episode, offshore velocity of the surface layer at the Peñas buoy is  $0.64 \text{ cm s}^{-1}$ , and the corresponding distance, 3877 m, is notably larger than the estimated advection distances at the coastal site (1527 and 693 m). These observations indicate that a potential inhibition of crossshore transport associated to frictional effects at the coastal boundary layer cannot be ruled out as a potential explanation for the observed larval distribution patterns.

Our monthly coastal survey was designed with a descriptive purpose, and cannot be used to decipher whether a given larval distribution can be explained by larval behaviour, by hydrodynamic nearshore processes or both acting together. However, our study of larval distribution around very nearshore frontal features (Chapter III) may give more insight on the role of active vertical movements against the flow. In our study, faster larvae accumulated at the front, while slower larvae seemed to be at the offshore side of the front (see June 15, when the measured currents were faster, Figs. III.6 and III.7, Table III.1). This resembles the theoretical predictions by Franks (1992), who suggested that faster organisms accumulate at the fronts by swimming against the downwards current, while slower ones would be transported offshore following the streamlines. Moreover, in our study of 4 fronts, larvae tended to accumulate at the fronts when the velocity of the horizontal currents was nearly 3 times the swimming velocity of the larva. Given typical ratios of horizontal to vertical velocities at oceanic fronts, this suggests that accumulation took place at flow velocities which were fast enough to carry larvae to the front but slow enough to allow the larvae to remain at the surface (Fig. III.8). In any case these results are hard to explain without an active swimming behavior.

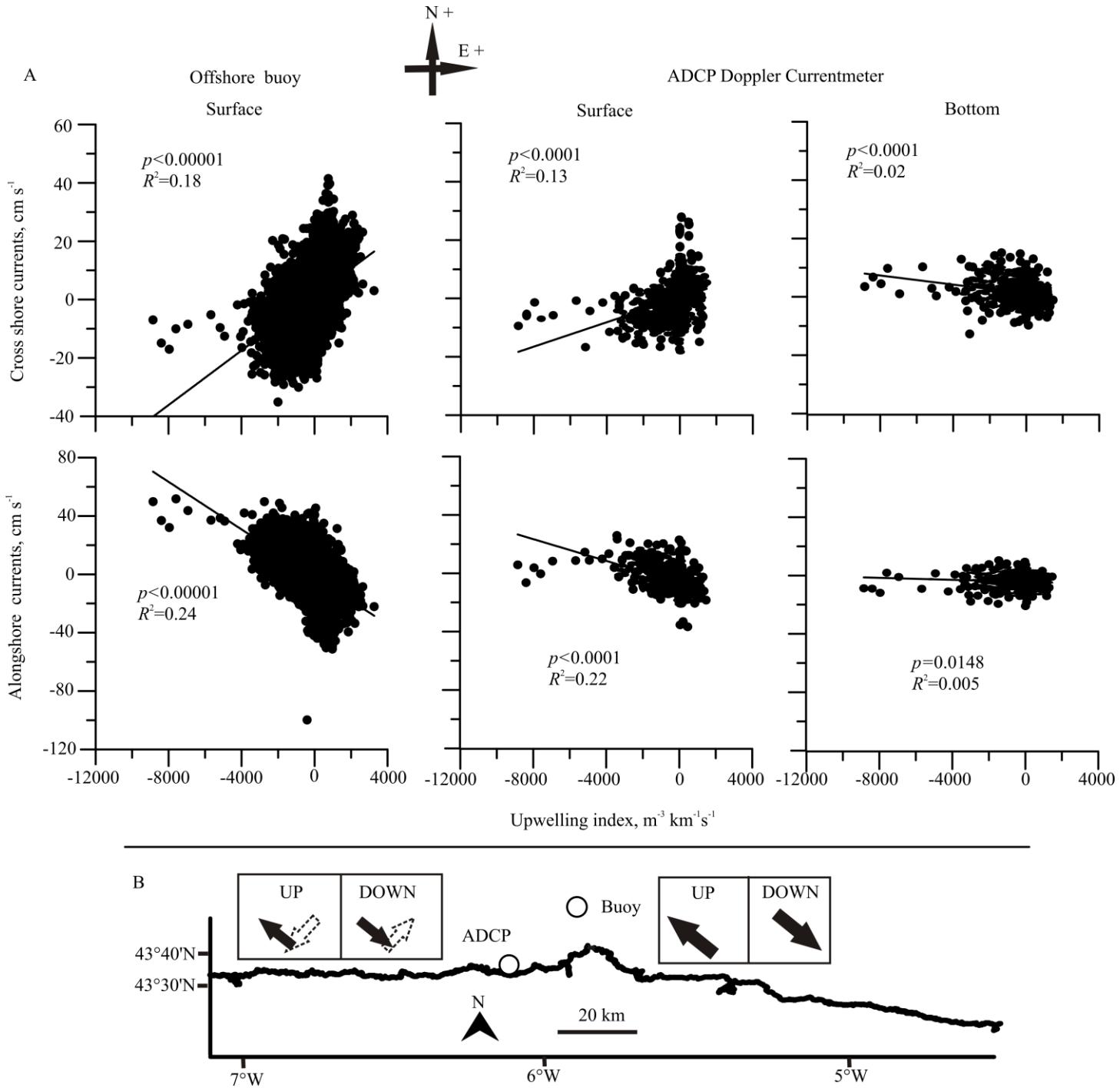


Figure 1. A) Alongshore and cross shore components of the currents vs upwelling index at the offshore and inshore sites during 2008-09. Currents have been measured hourly throughout the water column (20 m) by an ADCP acoustic Doppler currentmeter from October 08 to April 09 ( $n=1062$ , 400m off Cudillero, 43° 34.18'N 6° 8.43'W) and compared with hourly wind and surface currents data from a buoy farther offshore during 2009 ( $n=7123$ , Rayo moored buoy, Puertos del Estado, 15 km off Cape Peñas, 44° N 6°W, Fig.1). Northwards and eastwards currents are considered positive. Equations for each linear fit: Surface cross shore currents offshore= $0.00467 \cdot \text{upwelling index}$ ; Surface alongshore currents offshore= $-0.00814 \cdot \text{upwelling index}$ ; Surface cross shore currents onshore= $0.00192 \cdot \text{upwelling index}$ ; Surface alongshore currents onshore= $-0.0031 \cdot \text{upwelling index}$ ; Bottom cross shore currents onshore= $-0.00066 \cdot \text{upwelling index}$ ; Bottom alongshore currents onshore= $-0.00019 \cdot \text{upwelling index}$ . B) Location of the sites in the Central Cantabrian Sea and direction of the currents in light of the regression analyses in upwelling (UP) and downwelling (DOWN) regimes. Dark and discontinuous arrows show the direction of surface and bottom currents, respectively. Their magnitude is represented by the size of the arrow, approximately.



Active larval positioning in the water column may also contribute to remain in the coastal “sticky” water layer, thus shortening alongshore dispersal and favouring accumulation and transport in internal wave fronts. Woodson & McManus (2007) point to feeding performance as another adaptive advantage of swimming against the vertical currents: both coastal waters during upwelling or internal wave fronts are areas of enhanced phytoplankton biomass. The presence of fast cyprids shorewards from the fronts when the convergence currents were weaker (Table III.1, Fig. III.6, Fig. III.7) points to some kind of resistance to the horizontal flow. Leis (2006) found that the horizontal swimming capabilities of fish larvae were much more relevant than previously thought, enough to consider them to be nekton and not plankton. Note that some marine invertebrate meroplankters, especially crustacean late stages, are almost as fast as demersal fish larvae.

Apparently, the great influence of active behaviour on the patterns of larval distribution across the shelf and at coastal fronts is not reflected in the alongshore distributions. Indeed, some of our results point to a passive behaviour of larvae as they are displaced along the coast: accumulations at east facing coasts sheltered from tidal currents, higher abundances at simpler shorelines and, in general, an increase in the amount of variance explained in spatial distribution with increasing planktonic larval duration (Table II.5, Table II.6, Fig. II.13). However, we contend here that active control of larval position within relatively small distances in the cross-shore direction may severely influence passive alongshore dispersal. Note that the alongshore component is much faster (from 60 to  $-60 \text{ ms}^{-1}$ ; Fig. 1) and more strongly coupled to Ekman transport ( $R^2=0.24$ ; slope= $-0.0081$ , that is, positive transport leads to westwards flow; Fig. 1) at the offshore site than at the inshore currentmeter location in Cudillero ( $30$  to  $-30 \text{ ms}^{-1}$ ;  $R^2=0.22$ , slope= $-0.0031$ ; Fig. 1), where weaker flows are probably due to frictional effects linked to the CBL. In contrast with the cross-shelf direction, bottom alongshore currents are not opposed to surface currents, although their negative fit to Ekman transport is worse (Fig. 1). This means that, at least close to the coast, the water column is not stratified for the alongshore currents so there are not opposite flows at different depths. This is consistent with the known flow structure in upwelling regions: stratification respect to cross shore currents is usually shallower than that for the alongshore component, with alongshore countercurrents at 50m depth or more for the systems off Peru and Northwest Africa (Mann & Lazier 1996, Colling 2001).

In the above hydrodynamic scenario, we may speculate on the effect that active, vertical positioning of the larvae may have on alongshore advection. First, the absence of a differentiation between bottom and surface alongshore currents means that larvae are going to be displaced in the same direction along the coast irrespective of their vertical position: eastwards during downwelling and westwards during upwelling. However, it is likely that, by actively choosing their vertical position may cause non-symmetrical alongshore transport. For example, during upwelling, a larva swimming against the vertical flow should stay close to the bottom, otherwise it would be carried offshore by the stronger horizontal flows (Shanks & Brink 2005). There, the larva will be carried by the prevailing alongshore flow, which is westwards like the surface flow, but much weaker (Fig. 1). The situation is inverted during downwelling, where the larvae would resist the vertical flow at the surface, where the alongshore flow is eastwards and more intense than the bottom alongshore flow. In other words, eastwards transport during downwelling should be faster than westwards transport during upwelling. Assuming an upwelling situation lasting 1 week and using again wind data from our monthly surveys during 2007-2008, a newly released *Verruca stroemia* nauplii staying at the bottom would be carried at an average velocity of  $0.02 \text{ cm s}^{-1}$  (calculated from Fig. 1), covering a distance of only 157 m westwards. During a downwelling situation, the same larvae would be carried by surface alongshore currents flowing at  $0.59 \text{ cm s}^{-1}$ , covering a distance of 3585 m eastwards. This theoretical asymmetry in the direction of the alongshore transport due to active vertical positioning may explain why larvae accumulated in east facing coasts: these sites are in the lee of capes when eastwards, passive surface advection is driven by downwelling, thus being potential retention zones (Fig. 2). The opposite situation, accumulation at west facing coasts during upwelling, would be much weaker as it would be driven by much weaker and more variable bottom currents (Fig. 2). Similarly, higher up-stream than down-stream transport in estuaries of crab megalopae during flood and ebb tides, respectively, has been shown to be determined by active depth regulation (González-Gordillo et al. 2003). This asymmetry of larval alongshore advection may be complementary to topographical accumulation effects described in Chapter II, where it was not proposed because current velocities are not available for that particular dataset. Thus, the active behaviour in the vertical axis inferred from our observations across coastal fronts may also explain in some extent alongshore distributions.

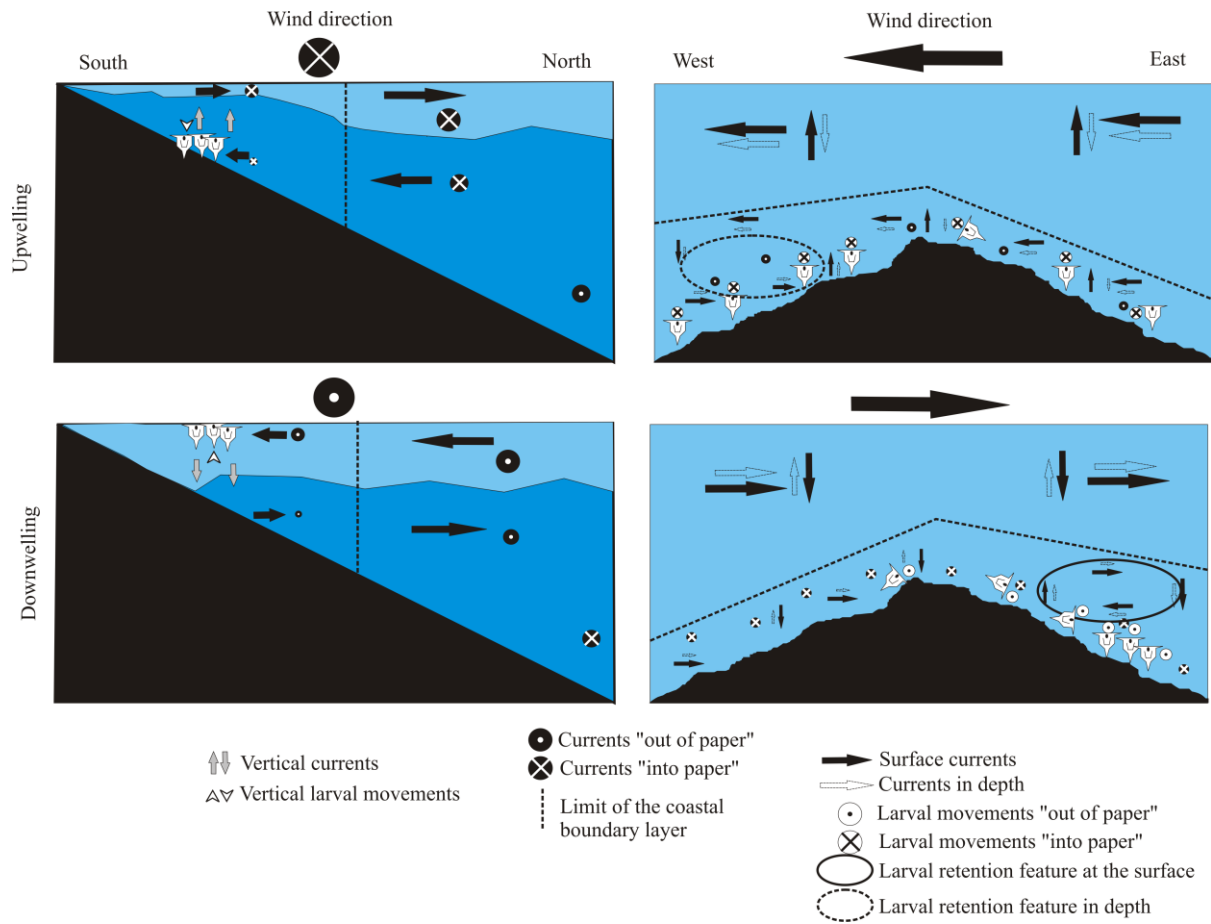


Figure 2. Asymmetric alongshore distributions driven by active larval behaviour in the water column. Passive transport to the east and retention patterns at east facing coasts would prevail because they are driven by surface currents. Changes in the magnitude and direction of the currents are represented as a function of depth and the proximity to the coast.

The presence of a CBL is crucial in this context. During a 1-week downwelling situation with an unimpeded flow comparable to that at the surface in the Peñas Buoy ( $1.55 \text{ cm s}^{-1}$ , Fig. 1), larval alongshore transport distance would amount to 9414 m eastwards, much larger than the meagre 3585 m that are obtained when applying the weaker flow velocity at the onshore site, potentially influenced by the CBL. Thus, confinement to very coastal waters seems a suitable strategy to reduce alongshore dispersal.

## Relevant scales in larval distributions and potential recruitment

Short dispersal distances may not only be due to active behaviour and/or passive interaction with the CBL, but also to the stochastic nature of winds and currents. Weather variability is said to be "shifted to red", i.e., with more power in the low frequency variations (Balmforth et al. 1998). Accordingly, the velocity of upwelling currents decreases when averaged over increasing time intervals (Largier 2003), or else, larger integration periods lead to decreased means and increased variances. In littorinids and *Verruca stroemia* cyprids the correlation between their average distance from the coast and the upwelling index peaked for integration intervals of 13 and 52 days, respectively (Fig I.7). During our observation period (2007-2008), the instantaneous peak Ekman transport reached  $1000 \text{ m}^3\text{km}^{-1} \text{ s}^{-1}$  (Fig. I.3), but only few hundreds when time-averaged (Fig. I.7). Such attenuation of the dispersal velocity with time spent in the plankton is a counterintuitive and important consequence of this property.

From our results, it is possible to infer time and spatial scales which are relevant to the biology of meroplankton and compare them with those of the most important oceanographic processes (Fig. 3). Although accumulation and transport of larvae by fronts may depend on active behaviour, the scales of these processes are strictly tied to those of their hydrographical origin, mainly internal waves (Fig. 3). Note, however, that for time scales corresponding with the time spent in the pelagic environment, cross shore spatial scales are much shorter than alongshore ones (Fig. 3). This observation points to the great importance of very coastal retention patterns influenced in great extent by active behaviour. While alongshore relevant scales fall into those typical of some oceanographic processes, like coastal upwelling, eddies and fronts, cross shelf distribution patterns are more shifted to the scales at which physico-biological coupled processes may occur (Fig. 3). Nevertheless, these irregularities in the coupling between space and time in larval distributions are inside the expected range for the ocean, where the spatiotemporal overlap between physics and biota is much greater than that in terrestrial systems (Steele & Henderson 1994).

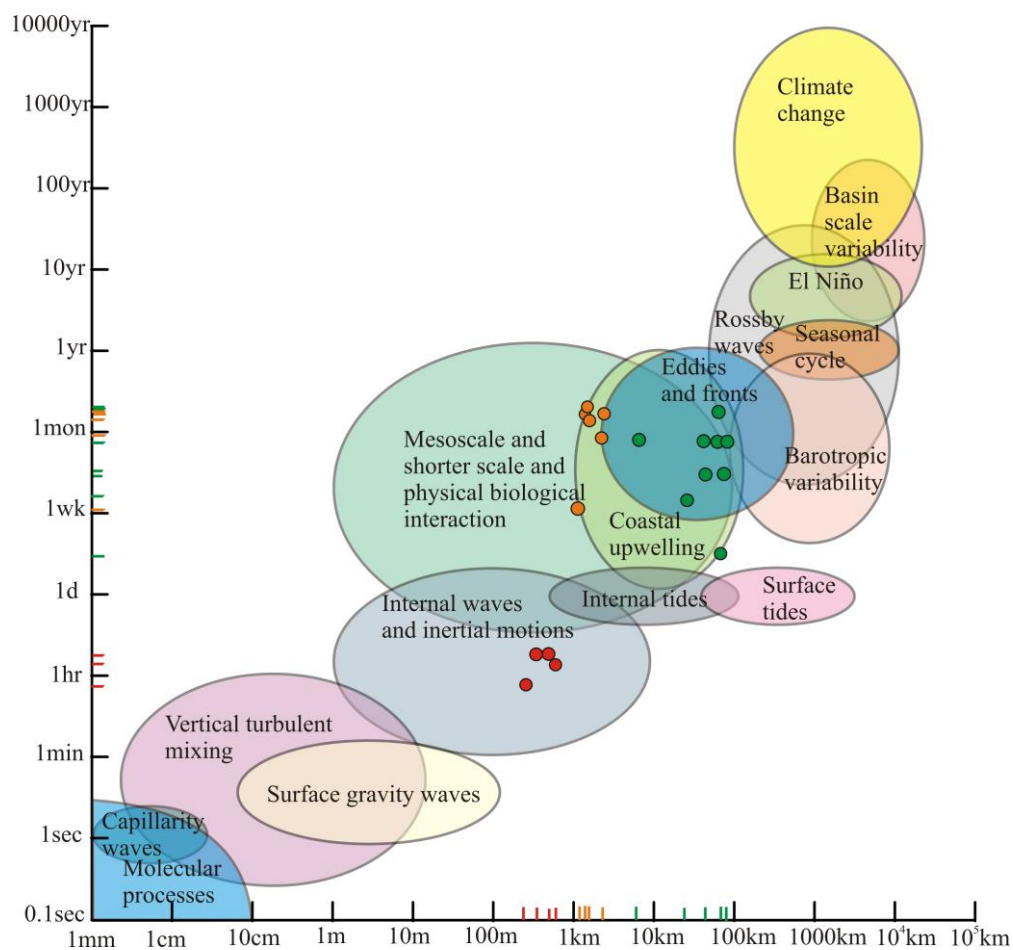


Figure 3. Time and space overlapping scales of the main physical processes in the ocean, adapted from D. Chelton, University of Oregon. From the monthly coastal cruises, mean distances offshore and planktonic larval durations, or very similar periods in the case of significant correlations with time averaged Ekman transport, were taken into account for the most abundant taxa (Table I.2, Fig. I.7). From the coastal survey along the Central Cantabrian Sea, abundance patch sizes inferred from the species-specific autocorrelation analyses (Fig. II.8, Fig. II.10) were compared with the planktonic larval durations (Table II.4). In addition, a mean period in the plankton for all the larvae (25 days) was compared with the typical patch size of the larval community. It was also related to the mean spatial scale at which topography seemed to affect larval distributions (6.4km) calculated as:  $\sum (\text{Spatial scale} (0.5; 2; 5; 20\text{km}) * \text{Variance explained}) / \text{Total variance explained}$ , given the results of the multiple regression analyses with all the environmental variables plus spatial coordinates (E+S models, Table II.5, Table II.6). About the surveys around very coastal fronts, the spatial scale of their action was approximated to the distance offshore at which they became visually conspicuous (few hundreds of meters, see results Chapter III) while the time they took to reach the coast or disappear may be a proxy of their relevant temporal scales (few hours given their speeds, Table III.1). Dots represent significant scales extracted from our results respect to meroplanktonic distributions around coastal fronts (red), across the inner shelf (orange) and along the coast (green), respectively. These scales are shown with marks in both axis with the same colour code.

We have identified the important scales influencing larval distributions, but which are the ones that define the patterns of recruitment? We hypothesized that the timing and spatial patterns of the processes accumulating and transporting larvae towards the coast, that is, hours and hundreds of meters, are those at which recruitment may significantly vary. Cross shelf and alongshore distributions may set the initial concentrations of competent larvae nearshore but coastal fronts may act as selective filters to the final destination. Local persistent variations in settlement have been studied in our coasts for *Chthamalus montagui* and they were supposed to be topographically driven (Suárez & Arrontes 2008). The distribution of *Perna perna* juvenile mussels may also vary considerably at very small spatial scales (McQuaid & Lawrie 2005). Extremely high spatial variability in the coastline configuration may drive frontogenesis leading to very specific, *quasi* unique conditions for larval aggregation and transport at each site (Shanks et al. 2003). This would explain why Rilov et al. (2008) failed to correlate larval abundances and onshore recruitment at large spatial scales. Moreover, Navarrete et al. 2005 did not find any significant relationship between mussel and barnacle recruitment in their data along a 200 km coastal swath of the Chilean coast. However, once site to site variation was removed from their data, the resulting regional recruitment rates of both species were correlated. In other words, once the large scale trend was removed, the residuals of the recruitment -i.e. the site-specific variability- was uncorrelated among mussels and barnacles. This is strong indication of scale-dependence and is fully consistent with the findings in this Thesis. Regional trends may be similar for both taxa as they may respond primarily to alongshore distribution patterns driven passively and characterized by homogeneous patches at scales of tens of kilometres (Fig II.10); however, locally, high recruitment sites are not the same for both species, probably because at this scale behaviour interacts with very coastal, site-specific frontal structures. For example, veligers are much slower than barnacle cyprids (Table III.2), thus they require much weaker frontal flows for accumulation (Fig. III.8). Thus, fronts of a given intensity will concentrate and transport veliger larvae, but not cyprid larvae, thus counteracting any superimposed regional trends, and raising interspecific differences in recruitment rates. Even at this small scale, the temporal persistence of the recruitment pattern suggests that very nearshore hydrography is highly predictable in time and in space (Suárez & Arrontes 2008, Navarrete et al. 2008). This predictability agrees with our observations of fronts in Cudillero: the known seasonality of the upwelling may define the kind of convergence structure off our site, with internal waves or topographically deflected convergence currents at upwelling and downwelling conditions, each one with its own characteristic flow ( Table III.1, see also Discussion Chapter III). In

general our results point to the convenience of new studies with high spatial and temporal resolution to explain the recruitment patterns of coastal species.







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## Conclusiones





- 1- La estacionalidad en la comunidad meroplanctónica es marcada. Durante el periodo de desestratificación, la abundancia de larvas es baja. El periodo de estratificación temprana se caracteriza por altas abundancias de las nauplius del cirrípedo *Verruca stroemia*; en verano y otoño predominan las larvas veliger de molusco. Estas transiciones estacionales podrían deberse a adaptaciones al tamaño del alimento, de naturaleza también estacional.
- 2- Las distribuciones de los taxones más abundantes son independientes del transporte de Ekman. La exportación hacia el mar podría ser evitada por mecanismos activos de natación contra la corriente vertical o de forma pasiva por influencia de la *Franja Límite Costera* (FLC; traducción libre de Coastal Boundary Layer, o zona de aguas marinas cuyo hidrodinamismo se ve ralentizado por fenómenos de fricción contra la costa).
- 3- Las larvas veliger de litorinidos y las cyprid de *Verruca stroemia* responden al transporte de Ekman. Sus distribuciones son más costeras durante el afloramiento, lo que indica que se sitúan en las capas profundas de la columna de agua. Esta distribución podría deberse a migraciones verticales durante el desarrollo larvario muy cerca de costa. Las distribuciones responden a la actividad del afloramiento en escalas temporales que reflejan el periodo larvario.
- 4- A lo largo de la costa del Cantábrico Central en verano, las distribuciones de las larvas coinciden con un gradiente longitudinal en temperatura y clorofila especialmente marcado en Cabo Peñas. Este gradiente define los patrones de autocorrelación espacial que presentan tamaños de parche en torno a los 80 km.
- 5- Las características topográficas explican gran parte de la variabilidad en la distribución espacial del meroplancton a lo largo de la costa. El efecto más importante es la acumulación larvaria al Este de los cabos y en costas simples a distintas escalas espaciales. Esto probablemente se debe a la mayor magnitud y capacidad de penetración de las corrientes mareales en costas con estas características.

- 6- La variabilidad en las distribuciones larvarias explicada por la topografía aumenta con el periodo larvario, mientras que la importancia de la estructura de las variables hidrográficas decrece con el mismo. Estas tendencias se explican bien porque el efecto de las corrientes inducidas por la topografía es acumulativo en el tiempo o bien porque la edad de la larva influye en su adaptación al ambiente pelágico.
  
- 7- Los frentes de convergencia muy costeros en el área de Cudillero parecen deberse a la propagación de ondas internas y alteran la distribución del meroplancton. Las corrientes son asimétricas a los lados del frente, siendo favorecida la retención costera. Sin embargo, también se observa una estructura frontal cuyo origen es topográfico en el que las corrientes acumulan larvas provenientes de ambos lados del frente.
  
- 8- La acumulación de las larvas en la línea del frente es función de su capacidad para oponerse a las corrientes de convergencia. Es a valores intermedios de la velocidad del organismo respecto a la corriente (casi 3 veces menor) cuando la acumulación frontal se hace máxima. En esta situación la magnitud de la corriente es suficiente para transportar a los organismos hacia la convergencia pero no para que se hundan en ella.
  
- 9- El equilibrio entre la velocidad del organismo y la magnitud de las corrientes que maximiza la acumulación es único para cada taxón dada su capacidad de natación. Tanto los nadadores rápidos como los lentos son susceptibles a la agregación en frentes pero no a otros patrones de distribución. Por lo tanto, la velocidad de la larva define por si misma las distribuciones que puede presentar a través de un frente de convergencia.
  
- 10- Los frentes costeros presentan un desplazamiento claro hacia la costa y pueden acumular estadios larvarios competentes para el reclutamiento. Su llegada a la costa podría corresponderse con abruptos eventos de asentamiento.











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