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Plankton transfers and coastal front in the Dover Strait

Zooplankton
Front
Vertical migration
Recruitment
English Channel

Zooplancton
Front
Migration verticale
Recrutement
Manche orientale

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ABSTRACT

Zooplankton and current studies were carried out in the coastal front of the Dover Strait. We show that the maintenance of both offshore and inshore planktonic communities is due to two coupled phenomena: 1) the residual drift of water differs in the upper and in the deeper waters; and 2) the vertical distribution of plankton differs for inshore and offshore species. In the frontal area, the coastal species remain in the lower water layer where the residual drift is landward. Conversely, the offshore species remain in the upper water layer where the residual drift is seaward.

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RÉSUMÉ

Transferts planctoniques et front côtier du Pas de Calais

Une étude sur les courants et le zooplancton a été menée dans le front côtier du détroit du Pas de Calais. Les valeurs de biomasses spécifiques sont directement inféodées au cycle de la marée. Les espèces du large sont plus abondantes lorsque les eaux du large se rapprochent de la côte avec le montant. Inversement, les espèces côtières sont plus abondantes lorsque les eaux côtières s'éloignent de la côte avec le baissant. Nous montrons que le maintien des deux communautés zooplanctoniques, au large et à la côte, est rendu possible malgré ces déplacements importants grâce à deux phénomènes : 1) la répartition verticale, indépendante du cycle nycthéméral, est différente pour les espèces à préférendum côtier et pour celles qui préfèrent les eaux du large ; et 2) le courant résiduel est différent dans les eaux de surface et dans les eaux du fond. Ainsi, à la station frontale étudiée, les espèces côtières se maintiennent plutôt vers le fond, là où le courant résiduel porte vers la côte. A l'opposé, les espèces du large se trouvent plutôt en surface, là où la résiduelle de courant porte vers le large. L'étude sur les balanes (crustacés cirripèdes) montre qu'il existe une relation directe entre l'étagement des larves cypris dans la colonne d'eau et l'étagement des adultes sur le fond.

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INTRODUCTION

The English Channel has a "megatidal" regime. Tidal currents are alternating and mainly parallel to the coast (Anonyme, 1968). Because of the tidal residual and the dominant southwesterly winds, the residual circulation drifts northeastward, from the English Channel to the North Sea. Numerous multidisciplinary studies have been recently carried out on this longitudinal flux (this issue). Zooplankton studies demonstrate the long-term transit of larvae (Lagadeuc and Brylinski, 1987; Salomon, 1991) within the "fleuve côtier" (Brylinski *et al.*, 1991).

In the Dover Strait, the coastal water drifts nearshore, separated from the open sea by a complex frontal area [Fig.1 (Brylinski and Lagadeuc, 1990)]. Exchanges between inshore and offshore water masses (transverse flux) are favoured in neap tide by the larger extension of the coastal water seaward (Brylinski and Lagadeuc, 1990; Dupont *et al.*, 1992). Then, zooplanctonic transfers are maximum (Brylinski, 1986; Brylinski and Lagadeuc, 1988). Nevertheless, the transverse diffusion is ten times lower than the longitudinal one in the English Channel (Pingree *et al.*, 1975); the identity of the coastal water is actual and two ecosystems coexist, defined by different species dominance (Brylinski, 1986).

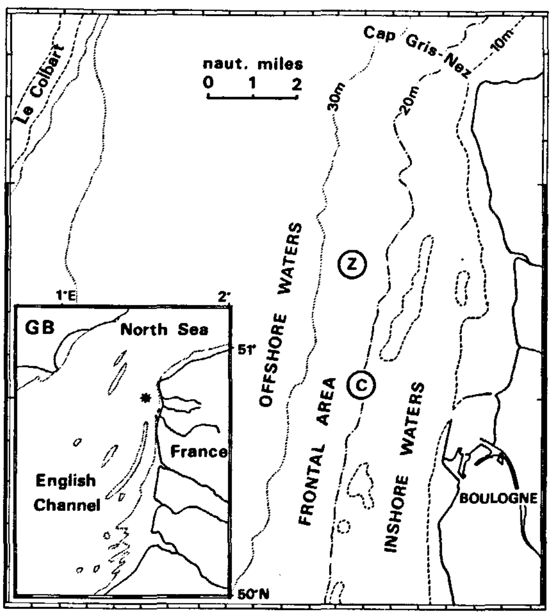

Figure 1

Location of zooplankton (Z) and current (C) stations in the Dover Strait (data from independent cruises).

Localisation des prélèvements de zooplancton (Z) et station de courantométrie (C).

The question is: how do both inshore and offshore planktonic communities succeed in coexisting, despite the exchanges? Do plankters act like passive particles (Hannan, 1984; de Wolf, 1974)? If so, does hydrodynamism alone create this biological structure? On the contrary (or concurrently), do plankters actively participate to the partition and maintenance of both offshore and inshore planktonic communities?

MATERIALS AND METHODS

Study area

In the Dover Strait, the tidal range varies between 3 and 9 metres during extreme neap and spring tides respectively. Also, the tide induces some large vertical and transverse movements of water and associated plankton. The water draws closely to the coast during the rising tide and recedes

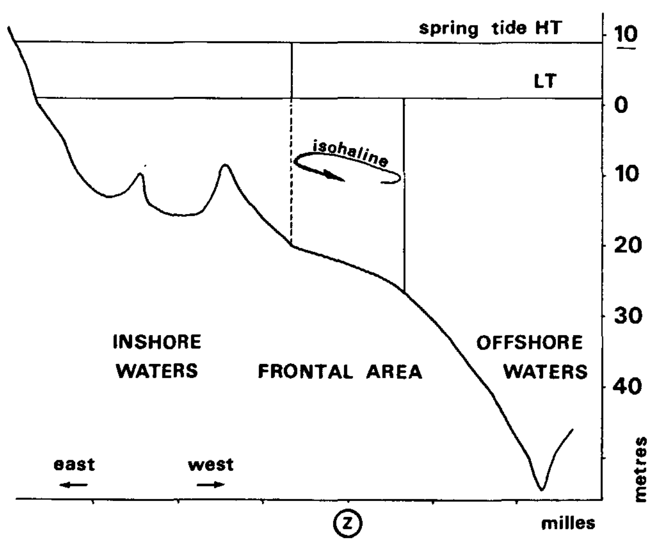

Figure 2

Vertical and inshore/offshore water movements during a tidal cycle of spring tide (HT = high tide, LT = low tide).

Mouvements verticaux et transversaux (côte/large) des eaux pendant un cycle de marée de vive eau (HT = pleine mer, LT = basse mer).

during the ebb tide. For example, during the present study, the tidal range was of 8 m and the 33.9 isohaline moved for 1.5 nautical miles (Fig. 2). The study was conducted during spring tide, the hydrological conditions (temperature and salinity) were vertically homogeneous (Brylinski and Lagadeuc, 1990).

Zooplankton sampling

The sampling station is located in the frontal area, 3.5 nautical miles off the French coast (Fig. 1), above the 25 m isobath. Nine vertical profiles were obtained on 15 and 16 April 1988, during two tidal cycles (25 hours) in an attempt to reveal possible diel migrations. Samples were taken every three hours, at different depths (Fig. 3) using a pump with a 10 cm diameter collection pipe. The pump delivery is 0.33

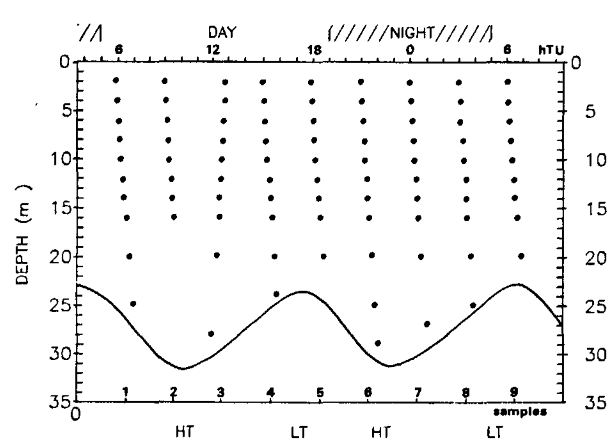

Figure 3

Location of zooplankton sampling levels. One vertical profile every three hours.

Échantillonnage zooplanctonique avec un profil vertical toutes les trois heures.

Table

Wind conditions during studies.

Conditions de vent au cours des études.

NUMBERS OF TIDAL CYCLES OF FIGURE 4	WIND DURING CURRENT MEASUREMENTS		WIND DURING PLANKTON SAMPLING	
	Direction	Knots	Direction	Knots
1	W	4		
2	SW	5	S-SW	5
3	SE	3	S	4
4	SE	7		
5	SE-S	10		
6	SW	8-5		

$m^3.min^{-1}$. Each sample of 1 m^3 was filtered through a 200 µm mesh net and preserved in a 5 % solution of formalin buffered with borax. Plankton counts were obtained from 1/10 subsampling or from the total sample for scarce species. Results are expressed as the number of animals m^{-3} at each depth, or are integrated through each vertical profile and expressed in percentage of variation during the total study.

Current measurements

Unfortunately no current measurements were available during the zooplankton sampling. Nevertheless, some data exist for another frontal station, 2.5 nautical miles to the south of the plankton station (Fig.1). Measurements were conducted with Suber currentmeters at 5 and 15 m. The total duration of measurements lasted one month and we chose some data corresponding to the conditions of wind and tide intensities that were present during plankton sampling (Table).

RESULTS

Hydrodynamic conditions

Data describing the Eulerian drift of water (Fig. 4) correspond to spring tide conditions prevailing during zooplankton sampling. These data present various conditions of wind direction (Table), but the wind direction during zooplankton sampling was similar to this one during the second and third current roses (Fig. 4).

The main axis of the current ellipsoids was parallel to the coast and to the frontal direction (Fig. 4), and the water globally drifted from the English Channel to the North Sea. Nevertheless, differences existed between data for the two prospected depths (5 and 15 m), particularly for the inshore/offshore components of the current. For the lower water layer, the residual current had a coastward component in comparison with the direction of the frontal axis (Fig. 4). In contrast, the residual current had a seaward component for the upper layer.

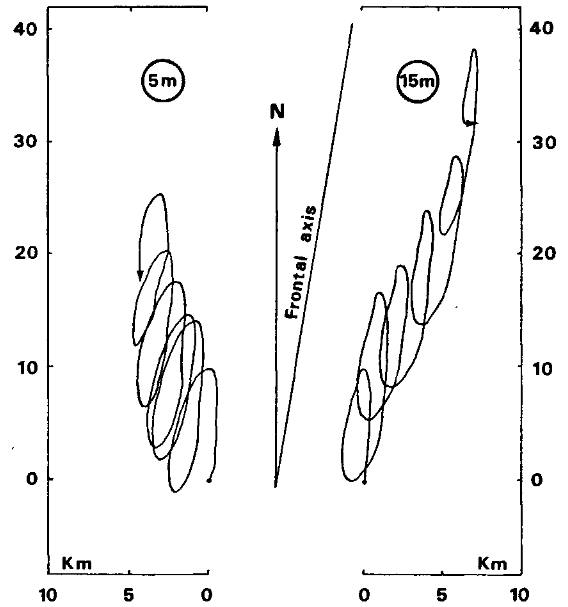

Figure 4

Eulerian residual drift at two depths (5 and 15 m) of a station in the coastal front during spring tide.

Hodographe intégré de la dérive eulérienne à deux niveaux de profondeur d'une station de la zone frontale, en période de vive eau.

Wind direction does not affect this divergence, even with higher wind (unpublished data), but can modify its amplitude.

Zooplankton data

For the intermediate (frontal) station, we verified that offshore species are more abundant when offshore waters draw near the coast during the rising tide. Conversely, coastal species are more abundant when the coastal waters recede during the ebb tide. For instance, the maxima of the coastal species *Acartia bifilosa* (copepod) alternated with the maxima of the offshore species *Oikopleura dioica* (tuniciate) [Fig. 5].

Variations of the abundances of each species were therefore cyclic with the same period as that of the tide. Nevertheless, we can observe a delay of about a quarter of a phase (Fig. 5) because there is a phase displacement between the tidal and the induced current cycles (Anonyme, 1968). In fact, maxima of abundance were observed near the time of the inversion of the western or eastern component of the current, *i.e.* when coastal waters were further away from the coastline, after low tide (coastal species), or when offshore waters were nearer to the coastline, after high tide (offshore species).

All species defined as coastal species (Brylinski, 1986) had an abundance cycle similar to that of *A. bifilosa* (Fig. 5). This was the case for holoplanktonic species such as *Temora longicornis* (copepod) and for meroplanktonic species such as the cyprid larvae of *Balanus crenatus* and *B. balanoides* (Barnacle) [Fig.6)]. Conversely, offshore species can be joined with *O. dioica*, *i.e. Arcatia clausi* (copepod), zoe larvae of crabs (indetermined) and cyprids of another barnacle *Verruca stroemia*.

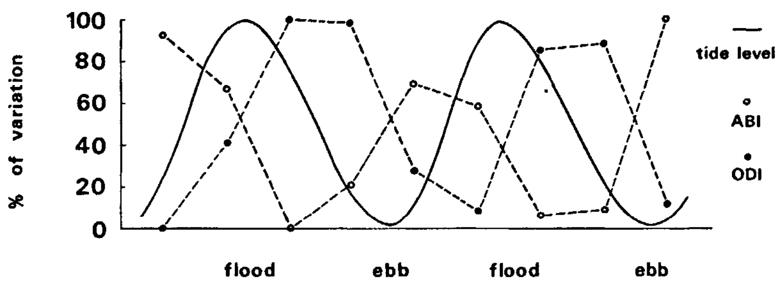

Figure 5

Cyclic changes of Acartia bifilosa *(ABI) and* Oikopleura dioica *(ODI) abundances (integrated data through vertical profiles) in the frontal station during two tidal cycles.*

Évolution cyclique des abondances, intégrées sur la verticale, de *Acartia bifilosa* (ABI) et *Oïkopleura dioica* (ODI) dans la zone frontale au cours de deux cycles de marée.

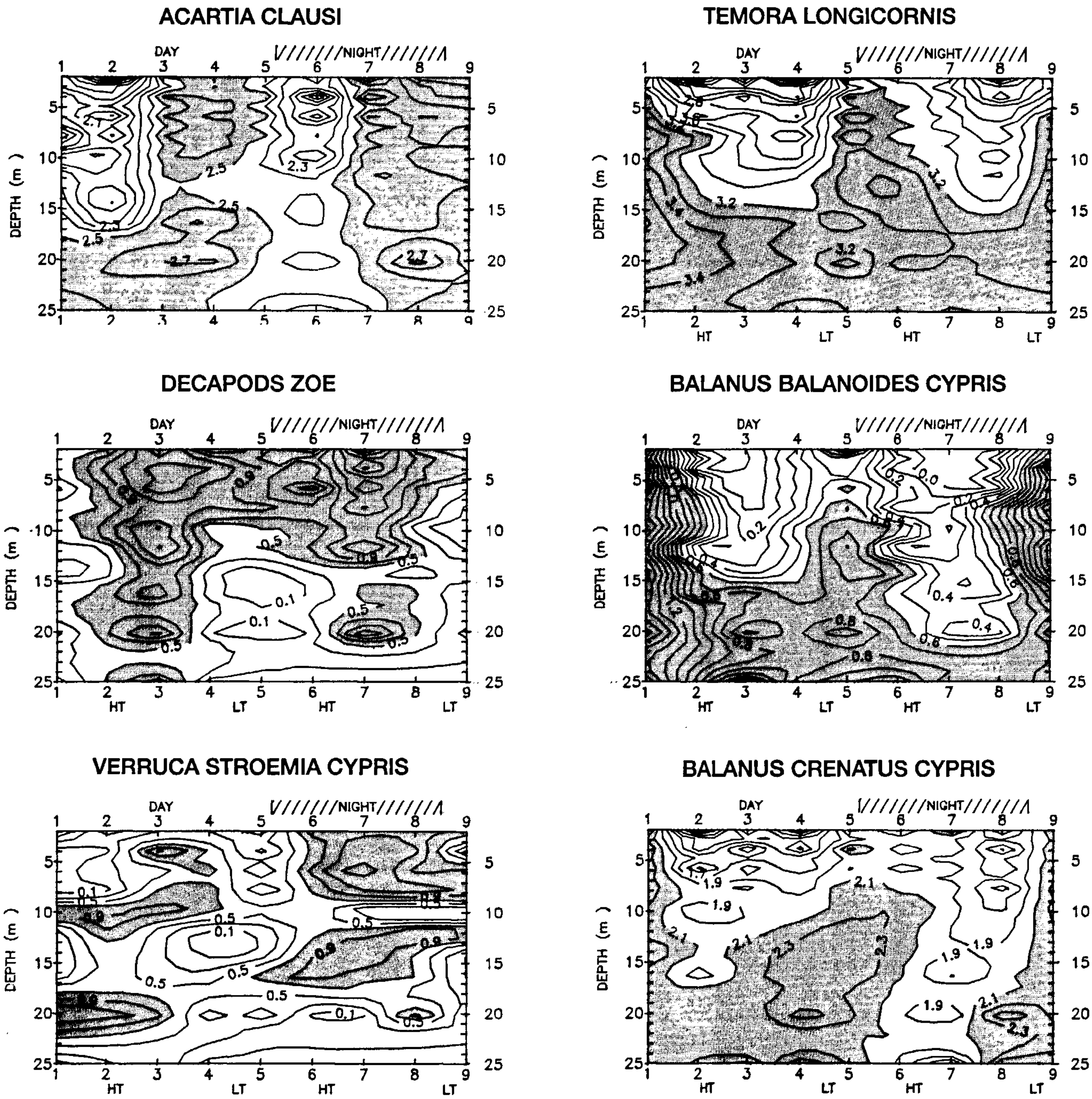

Figure 6

Vertical and temporal change of three offshore (A. clausi, *decapods zoes and* V. stoemia cypris) *and three inshore species* (T. longicornis, B. balanoides cypris, *and* B. crenatus cypris) *in the frontal station during two tidal cycles of spring tide.*

Évolution verticale et temporelle de l'abondance pour trois espèces du large (*A. clausi*, zoes de décapodes et *V. stoemia cypris*) et trois espèces côtières (*T. longicornis*, *B. balanoides cypris* et *B. crenatus cypris*) dans la zone frontale pendant deux cycles de marées de vive eau.

The analysis of vertical distribution (Fig. 6) showed an homogeneous distribution for *A. clausi*, but several species (most of them) had an oriented vertical distribution. Coastal species (*T. longicornis*, *Balanus* sp.) were more abundant in the lower water layer and offshore species (decapods, and less obviously *V. stroemia*) more abundant in the upper layer. This phenomenon was observed for both holoplanktonic and meroplanktonic species.

Species studied in this paper did not present any vertical migration coupled with the day/night cycle (Fig. 6).

DISCUSSION

Some studies exist on the variations of the biomass or composition of zooplankton during the tidal cycle. Data are mainly from studies on estuaries (Lee and McAlice, 1979; Fortier and Leggett, 1982; Laprise and Dodson, 1990), or bays in front of estuaries (Lagadeuc, 1992; Thiébaut *et al.*, 1992). Variations are directly correlated with the movement of the ingoing and outgoing seawater. There are few articles on regions outside freshwater influence (Sameoto, 1975) but results are similar. Because of the high tidal range and the low depth, and because of the large and alternating coastward/seaward movements of coastal waters, the nearshore area of this study could be considered as an estuary with a large breadth and a minute length.

The vertical distribution of zooplankton sometimes depends on the species' ability to migrate vertically during the day/night cycle. The animals can migrate in water masses that are circulating in different directions. Consequently, the horizontal transport of plankters is not necessarily the same as the transport of a water body (Dippner, 1987). Major differences exist in the residual transport according to whether or not the periodicity of the migration is synchronous with the tide periodicity (Hill, 1991).

The vertical distribution of presented zooplankters was constant and independent of the diel cycle (Fig.6). In this study, the species did not exhibit obvious vertical migration and we assume that horizontal transports of zooplankton correspond with water displacements. Coastal species remain in lower water layers and offshore species in upper layers (*cf.* after for *V. stroemia*). Consequently with the residual current in upper and lower layers (Fig. 4), the coastal species remain near the coast and the offshore species disperse seaward. This phenomenon explains the separation and the maintenance of two planktonic communities, inshore and offshore (Brylinski, 1986; Brylinski *et al.*, 1991). So, the dispersion of coastal larvae is restricted seaward, and the dominant transport is northward (Lagadeuc and Brylinski, 1987; Salomon, 1991) without excessive losses.

The behaviour of *Acartia clausi* is particular with regard to these trends. *A. clausi* is apparently an offshore species (Fig. 6) because its abundance is maximum between HT and LT, but it is also known as an ubiquitous species (Brylinski, 1986; Brylinski and Lagadeuc, 1988). Its vertical distribution is homogeneous and facilitates a broad horizontal distribution.

One of the main objectives of studies on vertical distribution of zooplankton in coastal waters is to determine the role of this distribution on both dispersion of meroplanktonic larvae and benthic recruitment. A heterogeneous vertical distribution can be controlled by ontogenic process (Lagadeuc, 1992; Thiébaut *et al.*, 1992). Young larvae are often in the upper layer and disperse; old larvae are often in the lower layer to come back to the coast and in the bottom layer for settlement. For example, larvae of barnacles progressively shift their preferred vertical distribution during ontogeny. The late naupliar and cyprid stages gradually select the deeper water layers (Bousfield, 1955).

In this study, cyprid stages have different behaviours according to species. Cyprids of *Balanus balanoides* (Fig. 6) are typically coastal planktonic species with maxima of abundance near the bottom; adults live in the upper part of mediolittoral level. In contrast, cyprids of *Verruca stroemia* are an example of offshore plankton and are more abundant during and after the high tide; the adult population settles exclusively in the infratidal area. But the vertical distribution of larvae is atypical: the maximum of abundance is not obviously located in the upper water layer (Fig. 6). Actually, the larvae' abundance in subsurface is certainly underestimated because the sampling is probably inadequate for this species. The upper samples are at 2 m and this species is a neustonic species living principally in the 1 m water layer (Le Fèvre and Bourget, 1991). Cyprids of the third species, *B. crenatus*, have a coastal behaviour, but the maxima of larvae occur in a higher water layer than the one of *B. balanoides*; adults live in the lower part of the mediolittoral level and in the infralittoral level. So, these results confirm that larvae of certain barnacles are capable of actively regulating their depths, even at the cyprid stage (Le Fèvre and Bourget, 1991), *i.e.* the final stage of planktonic life. Consequently, the planktonic zonation of barnacle larvae influences the vertical distribution of adults (Grosberg, 1982).

In conclusion, we show that the maintenance of both offshore and inshore plankton communities is due to two coupled phenomena: 1) a residual drift that is different in the upper and in the lower waters; and 2) a vertical distribution different for inshore and offshore species. In the intermediate station, in the frontal area, the coastal species remain in the lower water layers where the residual drift water is landward. Conversely, offshore species remain in the upper water layers where the residual drift is seaward. Nevertheless, further investigation should be conducted for detailing plankton distribution and currents. Firstly, because the timings of the different species are slightly asynchronized, *i.e.* there is practically a maximum of abundance of a species for each profile (data not shown); secondly, because attention was not given in this paper to the migrating species observed during the cruise.

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