The boundary circulation along the European continental slope as transport vehicle for two calanid copepods in the Bay of Biscay

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Abstract – The copepod fauna south-west of the British Isles includes a number of species which have their centre of distribution in the subtropical or tropical Atlantic. Among these, some species appear to be faunistically linked with the Iberian continental slope or slope waters even farther south along the NE Atlantic margin. It seems that these species reach their north-eastern range by means of poleward-flowing currents. For example, *Calanoides carinatus* has deep-living resting stages and ascends to surface waters only during its reproductive period, which is short at northern latitudes. Its main dwelling layers along the west Iberian continental slope cover the poleward-flowing undercurrent and the Mediterranean outflow water underneath. Part of the poleward flow regime tends to follow the slope bathymetry, i.e. it bends eastwards into the Bay of Biscay along northern Spain. Another part separates from the continental slope at Cape Finisterre and crosses the Bay of Biscay, approaching the continental slope at about 47° N, where it joins the north-westward flowing slope currents again. Because of its preference for the deeper layers during the long resting phase it is assumed that resting *C. carinatus* drifts mainly with the northward branch of the Mediterranean outflow water and penetrates only slightly into the inner Bay of Biscay. In contrast, *Calanus helgolandicus* has, on average, a shallower vertical distribution. Reproductively active individuals occur in the surface layers off western Iberia throughout the year. Here it drifts presumably northwards during late autumn and winter, but is recirculated southwards during late spring and summer. Due to advection with both the intermediate undercurrent and the variable near-surface currents, *Calanus helgolandicus* occurs more commonly in the inner Bay of Biscay than *C. carinatus*. © Elsevier, Paris

Bay of Biscay / continental slope current / Mediterranean water / salinity minimum / copepod transport

Résumé – Transport de copépodes par la circulation le long de la pente continentale du golfe de Gascogne. Au sud-ouest des îles Britanniques, la faune de copépodes comprend de nombreuses espèces originaires de l'Atlantique tropical ou sub-tropical. Certaines, liées à la faune de la pente continentale ibérique ou, plus au sud, à celle de la marge nord-est de l'Atlantique, arriveraient avec les courants dirigés vers le pôle. Ainsi, *Calanoides carinatus* se trouve en profondeur pendant ses périodes de repos et ne remonte dans les eaux de surface que pendant la période de reproduction, brève aux latitudes nord. Plongeant le long de la pente continentale à l'ouest de la péninsule ibérique, il atteint le sous-courant dirigé vers le pôle et les eaux sous-jacentes issues de la mer Méditerranée. Une partie du flux suit la bathymétrie en direction de l'est et entre dans le golfe de Gascogne au nord de l'Espagne. Une autre partie du flux quitte le talus continental au cap Finisterre et traverse le golfe de Gascogne pour retrouver, vers 47° N, la pente continentale et les courants orientés vers le

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nord-ouest. Par sa présence dans les eaux plus profondes pendant sa longue période de repos, *C. carinatus* pourrait dériver principalement avec la branche méditerranéenne orientée vers le nord et ne pénétrer que partiellement dans le golfe de Gascogne. Au contraire, *Calanus helgolandicus* se trouve en moyenne à la verticale des petits fonds. Les individus reproducteurs actifs restent tout au long de l'année dans les couches superficielles à l'ouest de la péninsule ibérique. Ils dérivent vers le nord à la fin de l'automne et en hiver, puis repartent vers le sud à la fin du printemps et en été. L'advection par le sous-courant intermédiaire et par les courants variables à proximité de la surface font que *C. helgolandicus* est plus commun à l'intérieur du golfe de Gascogne que *C. carinatus*.

golfe de Gascogne / courant de pente / eau méditerranéenne / minimum de salinité / transport de copépode

1. INTRODUCTION

Among some contrasting theories it has been discussed in the hydrographical literature that poleward-flowing undercurrents along the NE Atlantic continental slopes might be a continuous and consistent system from equatorial latitudes towards the British Isles. It was concluded that this hypothesis could only be corroborated by multidisciplinary studies, including biological indicator organisms as tracers ([3] and literature therein).

It was suggested that the seasonal appearance of diapausal copepodids (C5) of *Calanoides carinatus* "provides an excellent means of long-term dispersal and large-scale colonization of the species within its known global area of distribution" [30]. The life cycle of *C. carinatus* was thoroughly studied off tropical West Africa; see e.g. Binet and Suisse de Sainte-Claire [5] and Binet [4]. It occupies phytoplankton-rich shelf and slope waters from the surface (feeding, reproduction) to near or below 1 000 m (diapausing). Being primarily a subtropical species, it outlasts the hot, non-upwelling season in the tropics, or cold winters at higher latitudes, respectively, by diapausing. Diapausing copepodids may be recirculated by slope undercurrents to the habitat of the adults [4]. From many additional studies worldwide on the biology of *C. carinatus* as well as our own data from off Morocco and Portugal, Stöhr et al. [28] selectively discussed information on the along-slope, cross-slope and vertical distribution of resting C5s in relation to slope currents and the resulting large-scale distribution of this species.

The distribution of *C. carinatus* is restricted to the continental slopes, except for some stray individuals. Such slope-associated type of distribution is in ichthyology called 'pseudoceanic' [17]. The East Atlantic distribution covers the slope from the Cape of Good Hope to southwest of the British Isles (see *figure 1* for the NE Atlantic). Off NW Africa resting C5s of this species generally drift polewards within the intermediate slope undercurrent. This undercurrent originates at the equator and carries decreasing admixtures of South Atlantic central water (SACW). Off the western Iberian Peninsula the northward flow of Mediterranean outflow water (MOW) also forms a transport vehicle. Stöhr et al. [29] presumed that resting C5s also cross the Bay of Biscay by means of the above-mentioned currents.

Here we combine previously unpublished data obtained from 13 plankton stations by German *RV Heincke* in the Bay of Biscay with a review of the recent data obtained by Stöhr et al. off the Iberian Peninsula ([28] for *Calanus helgolandicus*; [29] for *C. carinatus*) as well as some of those accumulated during the Continuous Plankton Recorder (CPR) surveys [33]. We then analyse the biological information with respect to the spreading of water masses in the Bay of Biscay in order to exemplify the likely drift patterns of two copepod species in relation to their seasonal vertical distribution.

2. DATA BASES

2.1. Exemplifying distribution patterns of copepod species in the temperate NE Atlantic

Thirteen plankton stations covered by *RV Heincke* in the Bay of Biscay down to 1 000 m depth, made by the same multiple-opening-closing-net (although for other purposes and with partly deviating depth resolution) had not been dealt with by Stöhr et al. [29]. These stations are shown in *figure 2*. Three hauls taken during the spring in the Bay of Biscay yielded between > 29.6 and 100.8 adult *C. carinatus*/1 m^2 and 7.9 to 10.7 C5/1 m^2 (cruise *Heincke* 09). The sign > indicates potential underestimate due to loss of a stratum. At seven autumn stations, *C. carinatus* was missing in the upper 1 000 m (*Heincke* 17). Three winter stations yielded 3.8 adults/1 m^2 and > 7.9 to 42.0 C5/1 m^2 (*Heincke* 20). *Calanus helgolandicus* was abundant at all these stations, but not investigated

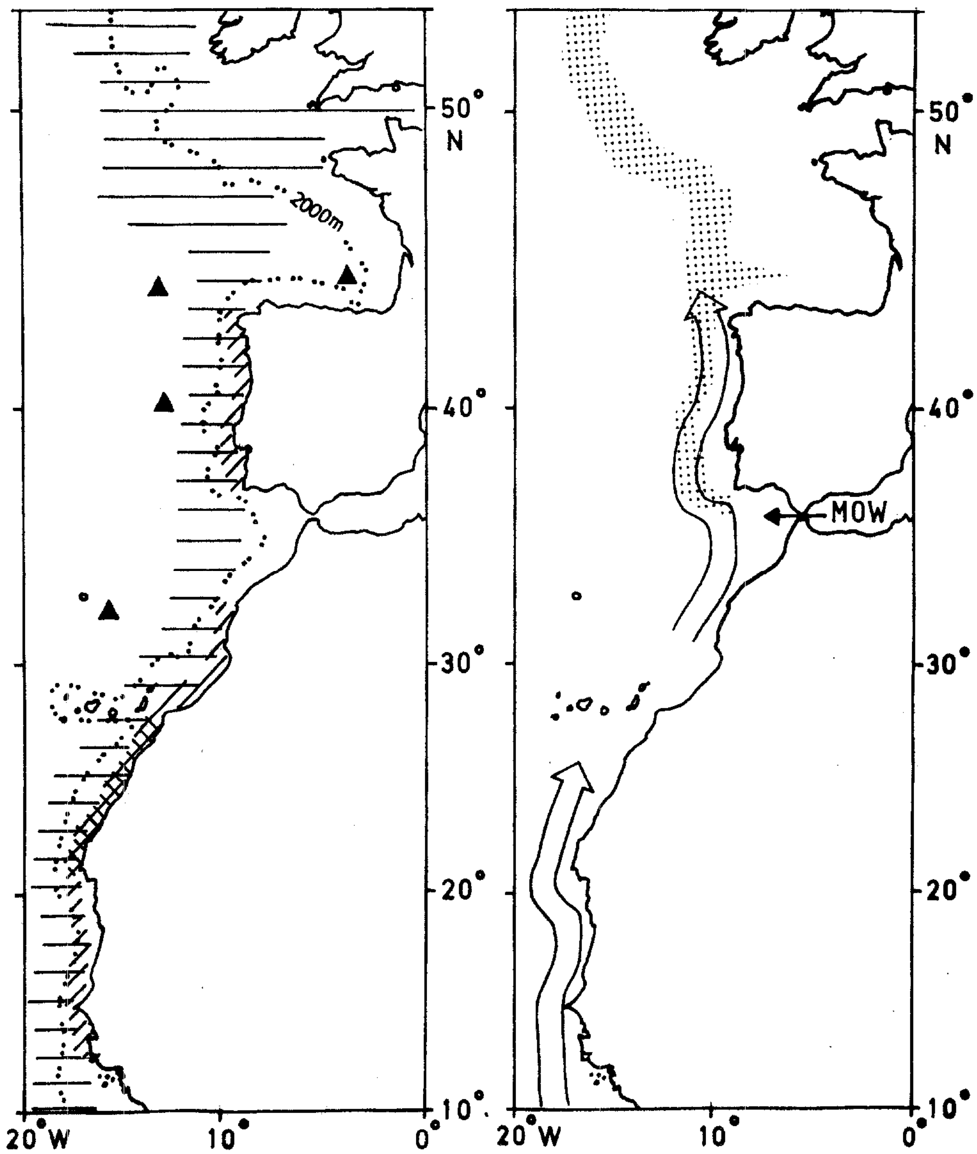

Figure 1. Distribution and northward transport of *Calanoides carinatus* along the NW African and European continental slope. Left: Distribution of reproductive populations (horizontal hatching) and single records (solid triangles) of *C. carinatus*. Diagonal and diagonal cross-hatching indicates seasonal and permanent coastal upwelling, respectively. Right: Drift of resting stage C5 of *C. carinatus* within the intermediate undercurrent at approximately 400–600 m depth (open arrows) and its entrainment within a part of the northward flowing Mediterranean outflow water below 600 m depth (MOW, shading). (From Stöhr et al. [29, figure 24]).

in detail. For details on the cruises and methods, see Stöhr et al. [28, 29].

Figure 3 presents four exemplifying distribution patterns from the long-term CPR-surface data. At a first glance those for *Calanus finmarchicus, Calanus helgolandicus* and *Neocalanus gracilis* appear to conform with the temperature fields both at the surface [33] and in the mesopelagic realm (see [2] and literature therein) and also with the North Atlantic Drift. *Calanus finmarchicus* is a boreal species and has affinities to subpolar waters [18], whilst *Calanus helgolandicus* occurs in the temperate waters of the North Atlantic and in the Mediterranean Sea [10, 18]. Both species inhabit shelf waters as well as the open ocean ('oceanic-neritic'). *Neocalanus gracilis* is widely

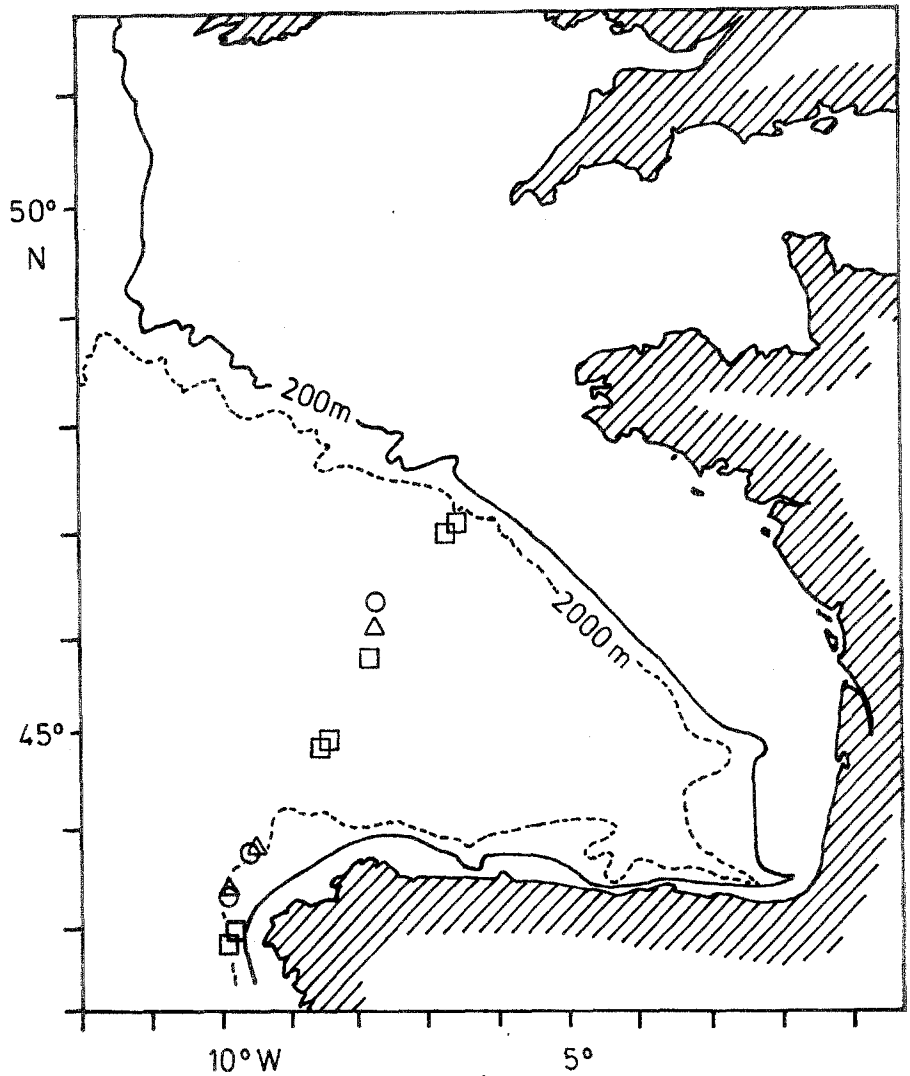

Figure 2. Previously unpublished plankton stations covered by German *RV Heincke* in the Bay of Biscay. Squares denote autumn stations (cruise H17, 1991), circles winter samples (H20, 1992) and triangles spring stations (H09, 1991).

distributed and common in the warm and temperate open oceans ('high oceanic') worldwide [31, 32].

Information on the fourth species, the pseudoceanic *C. carinatus*, has been summarised earlier. The data shown in *figure 3* provided the northernmost data for the summary given in *figure 1* and corroborated the affinity to the slope realm west of the Iberian Peninsula. A closer look at the patterns of the two more 'southern' (with respect to the boreal form *Calanus finmarchicus*) species *Calanus helgolandicus* and *Neocalanus gracilis* (compare as well *Nannocalanus minor* in [33]) suggests that the distribution pattern southwest of the British Isles shows a similar cluster to that of *C. carinatus*. There is a belt of lower frequency and abundance slanting from NW to SE, centred around 20° W, separating eastern and western clusters, and unexplainable by temperature or the North Atlantic Drift for any of these species. This might suggest that all respective north-eastern clusters are generally linked with the Iberian and the Moroccan slope. Stöhr et al. [28] had already concluded that *Calanus helgolandicus* off Morocco/Iberia forms a population independent of the Mediterranean and open ocean ones

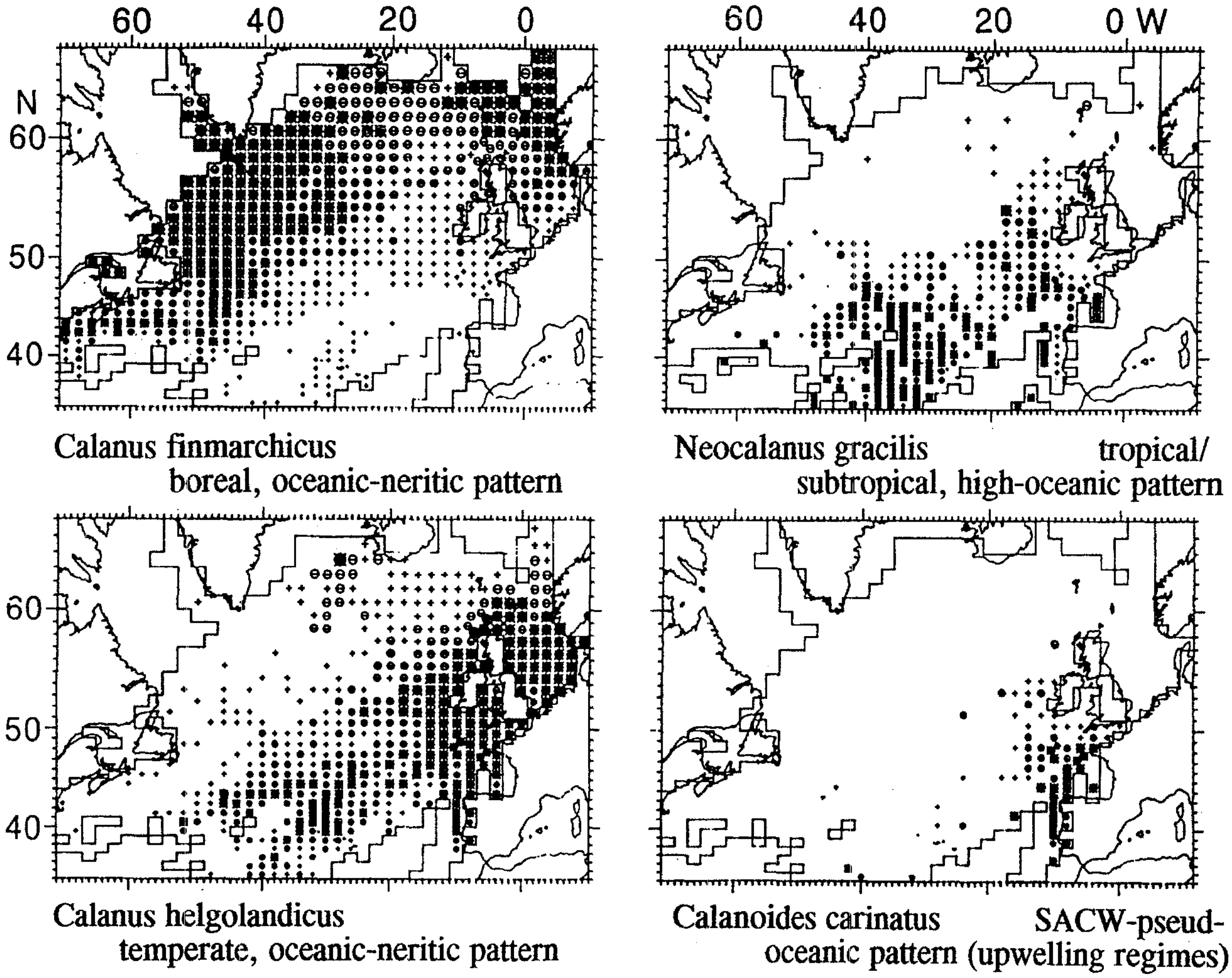

Figure 3. Exemplifying distribution patterns of four calanid species in the North Atlantic (CPR-10 m data extracted from Williams and Conway [33]). Rectangle means (1° latitude, 2° longitude) are represented by graded symbols, from absence of the species in CPR samples (open symbols) to abundant (closed symbols). The boundary of the sampled area is shown by straight lines. SACW: South Atlantic Central Water.

utilising the flow reversal between surface and intermediate layers as a maintenance system by means of ontogenetic vertical migration. Noteworthy is the apparent paucity of *C. carinatus* along the meridional transect in the inner Bay of Biscay where it appears to be restricted to the slope off northern Spain, whilst the other 'southern' species were frequent all along this transect.

2.2. The seasonal maturation cycle

The following information is mostly summarised from Conover [6], Williams and Conway [33] and Stöhr et al. [28, 29] and the respective literature cited therein:

Neocalanus gracilis occurs in the area in question in breeding conditions throughout the year.

Calanus helgolandicus is primarily at rest during autumn and winter off the British Isles. Off Iberia and in the Bay of Biscay mature individuals as well as C5s occur throughout the year and reproduction is intense during spring and summer throughout the area.

Calanoides carinatus off the British Isles reproduces only in summer, off Portugal during spring and summer. A rather early onset of maturation occurred off Portugal in the unusually warm winter 1992, but then adults still were distributed primarily at larger depths (*Heincke* 20 data, [29]). In the Bay of Biscay the species was either absent or distributed at depths of more than 1 000 m during autumn. During winter (perhaps unusually, see earlier) and spring, adult *C. carinatus* and their copepodids C5 were caught. By and large, this conforms with the cited results from off Portugal.

2.3. Vertical distribution of stages

All species show the ontogenetic pattern common to calanid copepods in that the resting stage (generally C5) dwells at larger depths than adults, feeding C5s or young offspring. These latter generally live in surface layers [6].

According to Williams and Conway [33] in the area in question the life cycle of *Neocalanus gracilis* is restricted to the upper 300 m only. Roe [25, 26] found off Morocco a much wider vertical range and a deep daytime distribution. Vervoort [31] considered deep occurrences as occasional.

Both *C. carinatus* and *Calanus helgolandicus* occupy wider vertical ranges. Mean seasonal vertical distributions off western Iberia (calculated from raw data by Stöhr et al. [28, 29]) are shown in *figure 4*. On average, resting *Calanus helgolandicus* lives up to 400 m shallower than *C. carinatus*, although these differences seem to be smaller off the British Isles [33]. However, for both species regional differences become apparent (*figure 5*). Off the British Isles and particularly off Portugal both reach deeper than off Morocco (compare also [25, 26]). Resting *C. carinatus* may occur even deeper than 1 000 m ([9] for off the Bay of Biscay). In our own above-mentioned samples from the Bay of Biscay they occurred below 600 m depth (perhaps below 1 000 m during autumn?), but the respective data on all species of interest for our study are scant.

3. CALANID COPEPODS AND CURRENTS

3.1. The surface layer

From the preceding it can be concluded that *Neocalanus gracilis* is affected during its entire life cycle primarily by surface currents. For the area in question surface currents affect part of the population of *Calanus helgolandicus* for most of the year, although least in winter. Only the biologically active stages of *Calanoides carinatus* are affected by surface currents and only during its reproductive period, which is restricted to spring and summer in the area in question.

At seasonal scales, northward surface currents prevail with velocities of 20 to 30 $cm \cdot s^{-1}$ off western Iberia during late autumn and winter, but southwards during spring and summer with velocities between 9 and < 15 nautical miles per day [12, 16 and literature therein; 8]. Calanid species, reproductive during spring and summer, thus are predominantly transported into southerly directions off western Iberia during this time.

The coastal surface circulation in the Bay of Biscay is clockwise (i.e. off northern Spain towards the west) during summer and counterclockwise during winter, with mean velocities of approximately 10 nautical miles per day [20, 23, 27]. In the central Bay of Biscay there are fluctuent surface currents throughout the year [21, 22]. The variable, mostly weak currents caused by winds and density gradients as well as by mesoscale eddies contribute to the more dispersed distribution patterns of the near-surface dwelling calanid species compared with *C. carinatus* dwelling at larger depths during most times of the year.

3.2. Deeper flows

Stöhr et al. [28] laid out in detail that off western Iberia planktonic organisms distributed at depths below 400 m, like *Calanus helgolandicus* (*figure 5*), drift northwards within the intermediate salinity minimum (*figure 6*). *Calanoides carinatus* drifts northwards also in the MOW located below approximately 600 m [29]. Both boundary currents are known to be permanent features along the continental slope of western Iberia [1, 7, 11, 19, 34 and literature therein], with velocities between 2 and > 20 $cm \cdot s^{-1}$ within the salinity minimum and 3 to 11 $cm \cdot s^{-1}$ in the MOW.

3.3. The Mediterranean outflow water

The MOW passes beyond Cape Finisterre (station 4 in *figure 6*). As visible from e.g. the French Phygas data [13], one branch bends eastwards along the northern Spanish slope. At about 7° W a consistent eastward flow was measured at the depth of the salinity maximum (1.5–3 $cm \cdot s^{-1}$ at 954 m depth [23]). The salinity characteristic diminishes at about 5° W [14]. All this conforms well with the rather isolated, easternmost occurrence of *C. carinatus* in the inner Bay of Biscay, when compared with the more widely spread shallower species (*figure 3*).

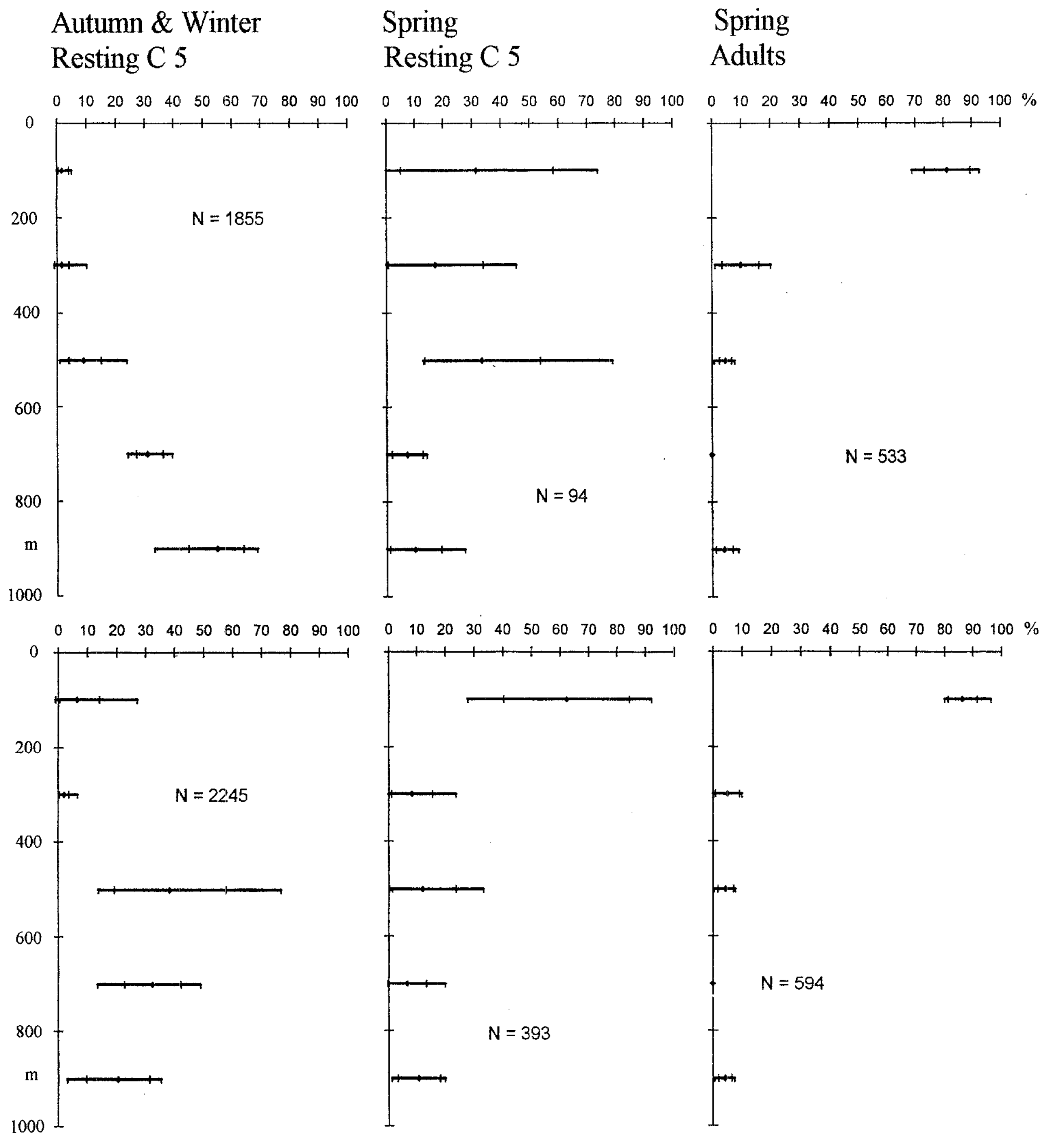

Figure 4. Seasonal relative vertical distributions of *Calanoides carinatus* (top) and *Calanus helgolandicus* (bottom) off the western Iberian Peninsula (mean, standard deviation, range and number of specimens). Calculated from the standard stations I 3 to I 17 by Stöhr et al. [28, 29]: 37° N–43.5° N; 12 stations during spring, 20 stations for autumn and winter.

The other branch of the MOW detaches from the continental slope and heads towards the British Isles, with a salinity maximum at depths of 900–1 100 m [13]. For these depths along the Celtic slope, Pingree and Le Cann

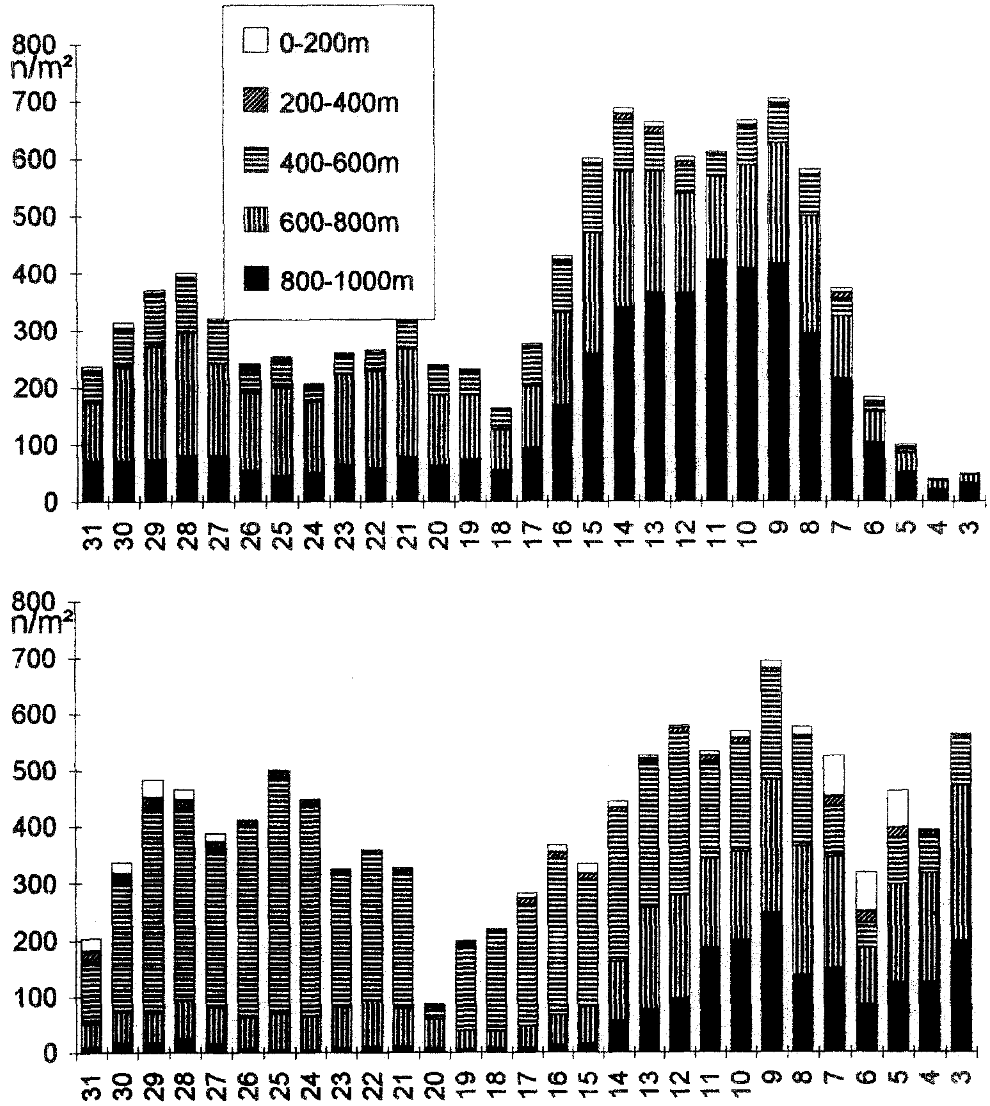

Figure 5. Meridional and vertical distribution of copepodite stage C5 of *Calanoides carinatus* (upper panel) and *Calanus helgolandicus* (lower panel) along the 2 000 m depth isobath between 32° N and 43.5° N (at the right) during winter 1992 in five plankton strata 1 000–0 m. The station numbers refer to standard station numbers I 3 to I 31. (From Stöhr et al. [28, 29]).

[22] listed mean poleward velocities between 2.7 and 5.7 cm·s^{-1}. Again this branch corresponds with the distribution patterns of 'southern' calanid species having deep-living resting stages (*C. carinatus*, partly *Calanus helgolandicus*). It transports the resting C5s towards the British Isles, where during the reproductive season the biologically active stages are advected partly by the surface currents into the Celtic Sea and the English Channel. A conceptual model of the entrainment of deep-living, resting C5s by the MOW is shown in *figure 7.*

3.4. The subsurface flow

Off western Iberia the poleward undercurrent within the layer between approximately 200 m and the salinity minimum (at about 500–600 m) extends northwards beyond Cape Finisterre [11, 15]. At Cape Finisterre a mean northward velocity of 2 cm·s^{-1} was measured at 435 m depth [15]. This salinity minimum has similar values of approximately 35.6 off western Iberia as well as in the Bay of Biscay, in contrast to decreasing values farther

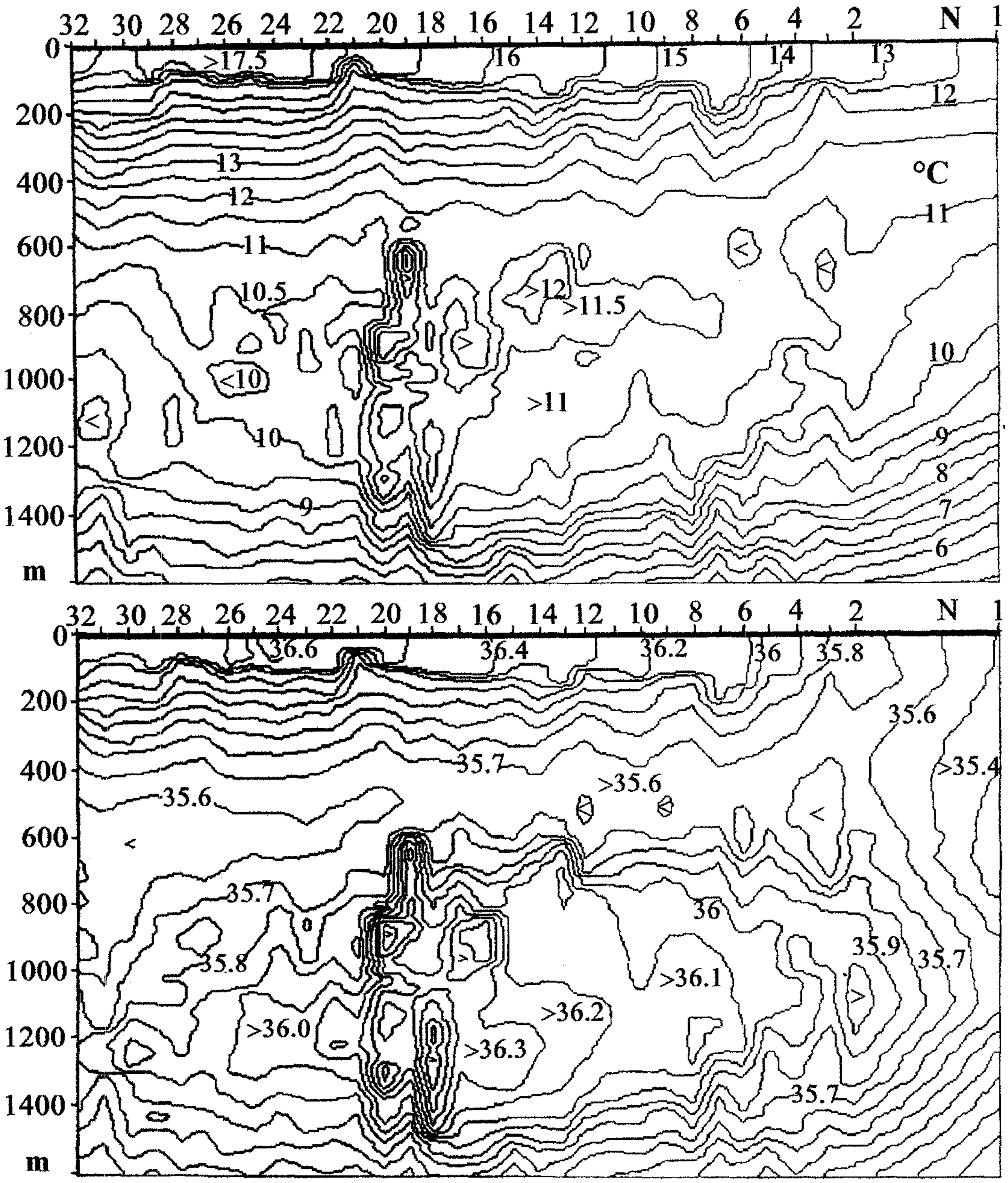

Figure 6. The hydrographical parameters temperature (top) and salinity (bottom) along the 2 000 m depth isobath off Morocco and western Iberia during winter 1992 (32° N–46° N, standard stations I 1 to I 32). North is towards the right. Cape Finisterre lies between stations 3 and 4, Cape St. Vincent at about station 17. (From Stöhr et al. [28]).

north-westwards [13, 14]. In the Bay of Biscay the minimum is found between 400 and 600 m depth. We interpret the distribution pattern of the salinity minimum as depicted by Fruchaud-Laparra et al. [13, 14] in horizontal and vertical sections also as evidence for a continuation of this subsurface flow beyond the north-western corner of Spain towards the Celtic slope. At the Celtic slope, Pingree and Le Cann [23] recorded a consistent poleward flow at the depths of the salinity minimum with mean velocities between 1.8 and 7.0 $cm \cdot s^{-1}$.

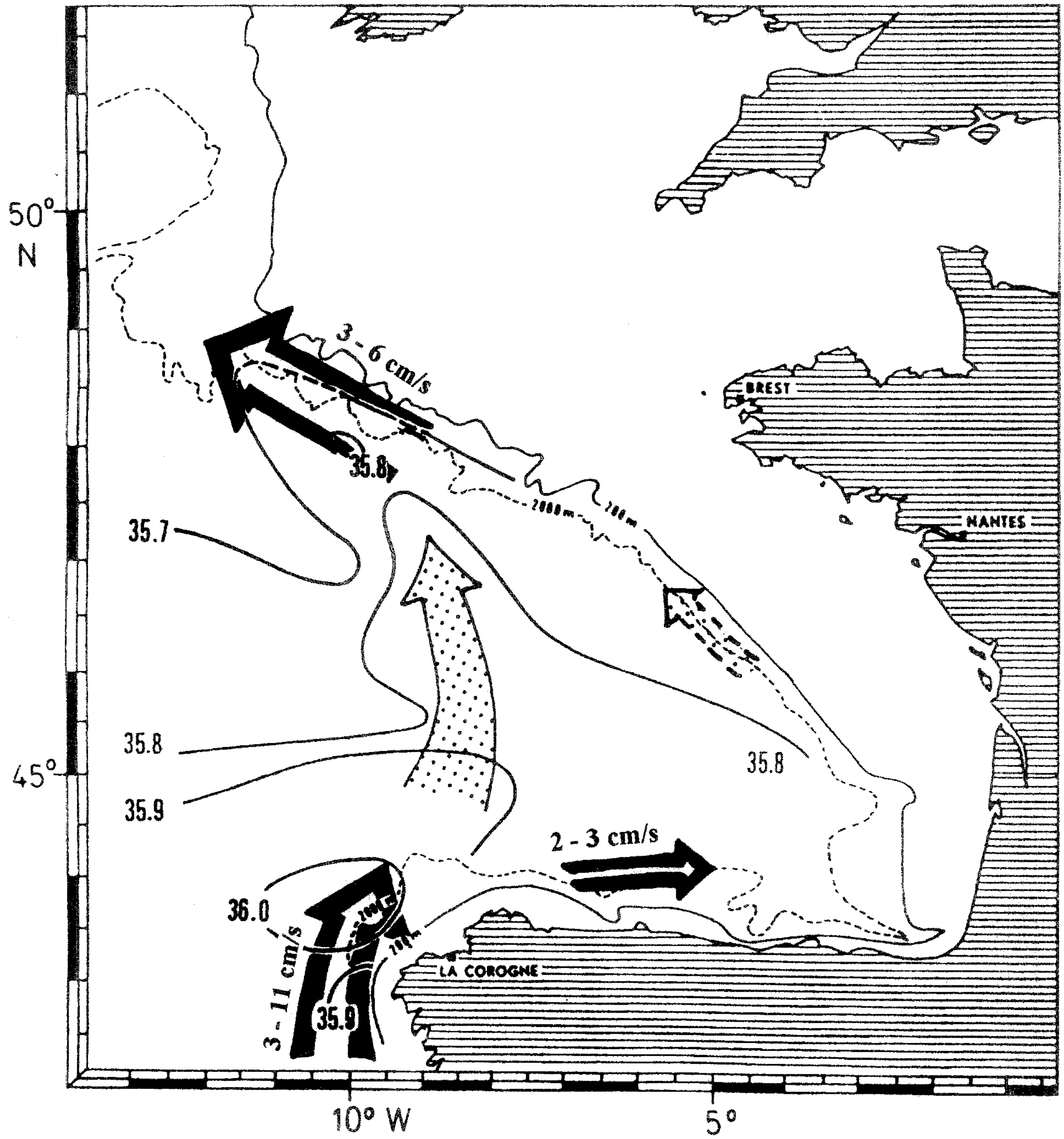

Figure 7. A conceptual model of the entrainment of deep-living, resting calanid copepods by the Mediterranean outflow water in the Bay of Biscay. The distribution of the salinity maximum (between approximately 900 and 1 100 m depth) is a simplified extract from Fruchaud-Laparra et al. [13, figure 26]. Solid arrows represent multidisciplinary evidence as e.g. from direct current-meter measurements (with mean velocities stated), water-mass analysis, geostrophy and biological tracers for that layer. The dotted or broken arrows represent interpretations from indirect evidence or a hypothetical flow.

It is likely that at Cape Finisterre parts of the northward subsurface flow follow the bathymetry and propagate into easterly directions along the northern Spanish slope. A geostrophical section across the Gulf of Biscay by Pingree [21] supports this idea as well as the spreading of the salinity minimum in the Phygas data [13, 14].

The assumption of a subsurface flow towards the east along the northern Spanish continental slope seemingly contrasts with the westward subsurface summer circulation supposed by Fraga et al. [11], or with stronger westward than eastward flow in direct current measurements near 7° W at about 500 m depth [23].

During autumn/winter a warm, narrow poleward surface slope current exists off western Iberia [1, 12, 16, 24]. It extends down to about 400 m, according to Haynes and Barton [16] or down to 500–600 m in our own data (e.g. *figure 6*). This surface current bends eastwards along the northern Spanish coast and presumably reinforces the subsurface flow seasonally. A corresponding signal for autumn and winter is generally visible in the previously mentioned current measurements from the two upper levels of observation by Pingree and Le Cann [23]. The subsurface flow reversed towards west in these data when the eastward surface flow relaxed, and may be generally westwards during summer due to the clockwise coastal surface circulation.

In general, the estimates of the geostrophic velocities in the Bay of Biscay [13, 14] indicate only sluggish and undefined flows at subsurface depths. A different reference level may entirely alter the resulting pattern of the geostrophic motions. At least on a short-term basis it seems that the subsurface flow in the Bay of Biscay is governed by variable currents steered among others by the wind and mesoscale eddies at the surface. Some of these eddies may influence the water column down to below the layer of the MOW [24].

4. CONCLUSIONS

The MOW spreads beyond Cape Finisterre. One branch heads northwards and approaches the Celtic slope at about 47 and 48° N and between 7–11° W. Another branch is guided by the slope bathymetry and propagates eastwards along the northern Spanish slope. This branch dimi-nishes at approximately 5° W.

This conclusion is based on congruent, although independently gained, multidisciplinary evidence from direct current measurements, the spreading of the salinity maximum, geostrophic calculations and the confined distribution pattern of the deep-living, biologically passive stage of the southern plankton organism *Calanoides carinatus*.

Above the MOW an intermediate layer of minimum salinities of 35.6–35.7 exists. In the Bay of Biscay the salinity minimum spreads generally as does the Mediterranean water beneath it, with an eastward and a northward branch. However, its pattern is far more diffuse, its propagation seems to be more sluggish and for any conclusion concerning the Bay of Biscay proper there exists less and partly contradictory evidence. The salinity minimum coincides with the subsurface poleward boundary current being well documented off western Iberia as well as along the Celtic continental slope. Along the northern Spanish slope, however, the boundary undercurrent is variable due to a prevalent seasonal signal superimposed by the surface layer. The resting stages of *Calanus helgolandicus* conform vertically and in their horizontal distribution with the distribution of this salinity minimum.

Highly variable surface flows on seasonal as well as shorter time scales in the Bay of Biscay cause the highly disperse distribution patterns of surface-living species like *Neocalanus gracilis*, or *Calanus helgolandicus* in the adult stage.

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