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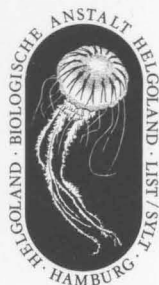
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## No. 12

S. STÖHR, E. HAGEN, H.-CH. JOHN, E. MITTELSTAEDT,  
K. SCHULZ, M. VANICEK & H. WEIKERT

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# Poleward plankton transport along the Moroccan and Iberian continental slope

S. Stöhr<sup>1</sup>, E. Hagen<sup>2</sup>, H.-Ch. John<sup>1</sup>, E. Mittelstaedt<sup>3</sup>, K. Schulz<sup>1</sup>, M.  
Vanicek<sup>4</sup> & H. Weikert<sup>5</sup>

- 1 Taxonomische Arbeitsgruppe (TAG) der Biologischen Anstalt Helgoland  
c/o Zoologisches Institut und Museum, Martin-Luther-King-Platz 3,  
20146 Hamburg, Germany (address for reprints)
- 2 Institut für Ostseeforschung, Seestraße 15, 18119 Warnemünde, Germany
- 3 Bundesamt für Seeschifffahrt und Hydrographie, Postfach 301220, 20305 Hamburg
- 4 Institut für Meereskunde, Düsternbrooker Weg 20, 24104 Kiel, Germany
- 5 Institut für Hydrobiologie und Fischereiwissenschaft, Zeiseweg 9, 22765 Hamburg

Hamburg

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## 1. Introduction

Poleward flowing undercurrents along the continental slope are typical features of Eastern Boundary Current upwelling systems (e.g. Clarke 1989). The model by Clarke (1989) implies that the undercurrents of the upwelling regimes are largely independent of each other. Voituriez and Herbland (1982) presented a conceptual model, suggesting that the undercurrent off NW-Africa originates in the tropics and is associated with the system of equatorial undercurrents. Once it hits the upper continental margin it becomes trapped by bottom topography and moves towards the north in the NE-Atlantic (Mittelstaedt 1982). It undergoes seasonal fluctuations and varies in depth (Barton 1989; Hagen et al. 1993, 1994).

It is suggested in this study that an interconnection exists between the undercurrents of the Portuguese and the Northwest African upwelling systems even in areas of permanent non-upwelling (as in the Gulf of Cadiz) or where upwelling is seasonal as off Morocco and Portugal (Wooster et al. 1976).

To investigate the questions of variability of this undercurrent in space and time, multidisciplinary studies have been carried out in slope areas off the Iberian Peninsula and off Morocco (Hagen et al. 1992). These studies included CTD-O<sub>2</sub> casts, current-meter moorings and biological sampling of the target copepod species *Calanoides carinatus*, anticipating that the distribution patterns of the latter might integrate larger scales in space and time than could be resolved by either physical method alone. It had been suggested that the scales of passive transport of *C. carinatus* in a gyre off Somalia might be as large as 5000 km (Smith 1982) and during non-upwelling in the Gulf of Guinea up to 10 months long (Brenning 1981).

It had been shown that *C. carinatus* is not an open ocean species (Vives 1974, 1982; Chagouri 1989). It is distributed along the continental slopes and its reproduction is associated with coastal upwelling (Binet 1979; Arashkevitch et al. 1996, and literature therein). Contrasting with a variety of terms used to denote its type of distribution, we prefer the term "pseudoceanic" (as defined for ichthyogeography by Hulley, 1981). Chagouri (1989) suggested that in the Atlantic the centres of distribution are in the Brazil- and Benguela Current upwelling areas. The species spreads farther northwards along the Gulf of Guinea and in the Northeast Atlantic boundary current area, but

neither in the western tropical nor northwestern Atlantic. It can be very abundant in the Gulf of Guinea and off Mauritania, but was previously considered to be rare off Morocco and the Iberian Peninsula (Boucher 1982 and literature therein). Recent data prove the regular presence of summer populations southwest of the British Isles (Williams and Conway 1988). Except for this latter study, information on the quantitative distribution or reproductive biology of *C. carinatus* is scant north of the Canary Islands.

The biology of *C. carinatus* has been thoroughly studied from the upper layers in the Gulf of Guinea (Binet 1979), off Mauritania (Postel et al. 1993) and off South Africa (Verheye et al. 1992), to name only a few recent comprehensive reviews from the eastern Atlantic.

Verheye et al. (1992) suggested that "diapausing" *C. carinatus* found remote from the coastal upwelling systems might be an appropriate tracer for large-scale drift. Reviews and models of the life cycle of the species were presented by Binet (1979, 1991), Brenning (1981) or Postel et al. (1993). The whole life cycle of *C. carinatus* occupies a total depth range from near the surface to generally some 800 m and extremes of 2000 m. When resting, its copepodid stage C5 concentrates at some 500 - 800 m depth and can survive there up to 10 months (Brenning 1981), or up to 5 months in a more conservative estimate (Kosobokova et al. 1988). Resting periods were believed to be the non-upwelling seasons in the tropics, when the surface waters are hot, and the either low productive or cool period from autumn to spring in the NE-Atlantic Ocean.

The area north of Cape Blanc ( $21^{\circ}$  -  $25^{\circ}$ N) is an area of permanent upwelling, elsewhere along the NW-African coast upwelling occurs seasonally, namely during summer off Morocco and Portugal and during winter off Mauritania and Senegal (Wooster et al. 1976). In tropical latitudes the resting C5s drift northwards along the slope with the NW-African upwelling undercurrent (Postel et al. 1993) with its distinct admixtures of less saline South Atlantic Central Water "SACW" (e.g. Hamann et al. 1981). However, *C. carinatus* occurs also in other water masses and can not be considered to be an indicator of SACW (Brenning 1981). The temperature/salinity ("TS") -characteristic of the undercurrent changes farther north

due to increasing mixing of **SACW** with North Atlantic Central Water "**NACW**" and Mediterranean Outflow Water "**MOW**" (Mittelstaedt 1989). Antarctic Intermediate Water "**AAIW**" may contribute also to this admixture (Fiekas et al. 1992). Converging TS-characteristics of **AAIW**, **NACW** and **SACW** in the lower temperature range make it impossible to define for more northern areas the water-mass composition and thus the origin of the intermediate salinity minimum precisely (Fig. 1).

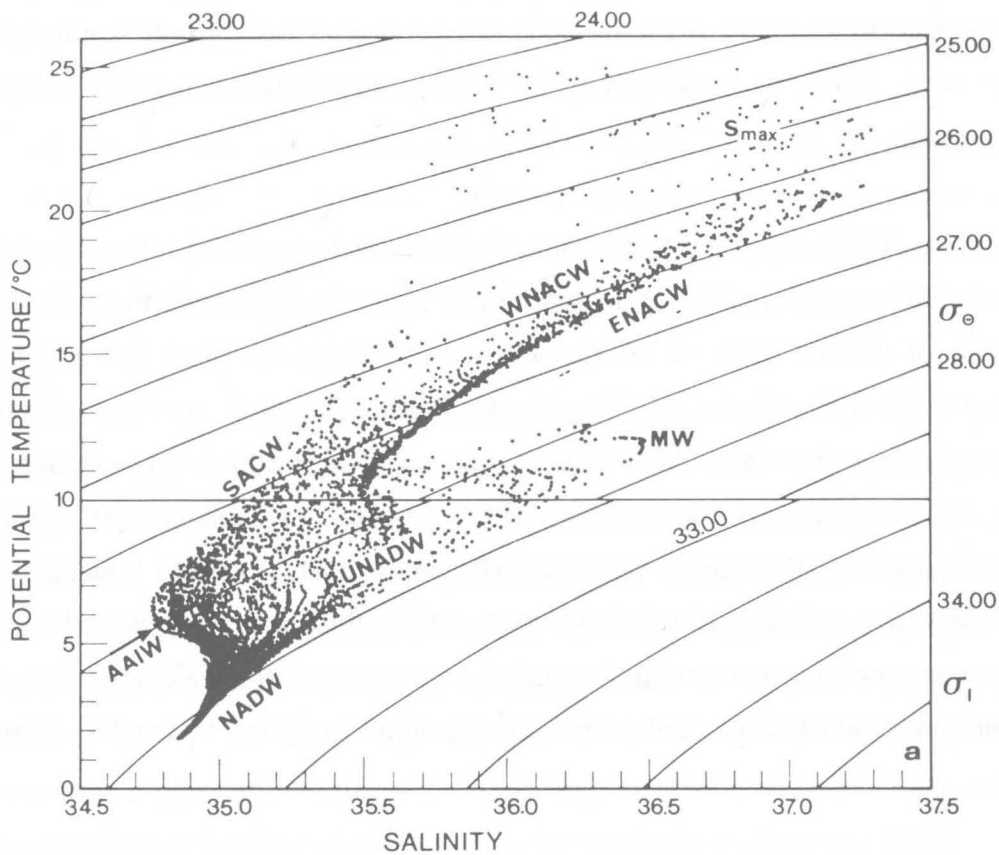


Fig. 1: The water masses in the tropical NE-Atlantic, exemplified by their temperature/salinity relations (from Fiekas et al. 1992). Abbreviations: **AAIW** = Antarctic Intermediate Water; **ENACW** = Eastern North Atlantic Central Water; **MW** = Mediterranean Water; **NADW** = North Atlantic Deep Water; **SACW** = South Atlantic Central Water; **UNADW** = Upper North Atlantic Deep Water; **WNACW** = Western North Atlantic Central Water.

The undercurrent is believed to be less than 100 km wide (Barton 1989). The horizontal and vertical exchange of water masses with latitude as well as cross-slope plus the anticipated variability of the undercurrent in time and space rendered it impossible to test the hypothesis of its consistency by physical methods alone (Barton 1989). Off Mauritania, fish larval distributions in combination with simultaneous current-meter measurements and water mass analysis allowed to trace the undercurrent, which flows there just beneath the surface (Hamann et al. 1981). Barton recommended to use this combination of biological and physical parameters also off Morocco, where the undercurrent is believed to descend to depths below 200 m (Mittelstaedt 1982). However, for off Morocco or even farther northwards no fish species so far is known to have an appropriate vertical distribution and time scale during its planktonic phase.

As demonstrated by Weikert (1984) for the area off Mauritania and Cape Blanc, quantitative plankton distributions can indicate the transport of *C. carinatus* by the undercurrent irrespective of any TS-analysis. Consequently, the resting stage of this species was believed by us to be an adequate tracer to study plankton dispersal also by the deeper poleward intermediate undercurrent off Morocco and Portugal. We presumed that the resting period of *C. carinatus* would last from October to March and thus planned our surveys accordingly. Furthermore, originally we did not have the intention to contribute in any detail to the life-cycle of this copepod species. Therefore no biological survey was made during the reproductive season when the bulk of the population is believed to dwell in the surface layers.

## **2. Material and methods**

### **2.1. Individual surveys and their multidisciplinary framework**

In the framework of WOCE a German project "Eastern Boundary Currents (EBC)" was carried out (Hagen et al. 1992). Hydrographically this project comprised 5 cruises, of which the CTD and oxygen data were published (Hagen and John 1995, data available from the WOCE-databank). The present paper puts emphasis on the three seasonal, multidisciplinary surveys conducted by RV "Heincke" along the continental slopes off the Iberian Peninsula and Morocco (Tables 1 & 2). The stations

are shown by figure 2. Furthermore, comparable multidisciplinary data obtained during two earlier cruises by RV "Meteor" from some stations above the Moroccan continental slope (Tables 3 & 4, see also Fig. 2) as well as from the adjacent open ocean are used (Table 5).

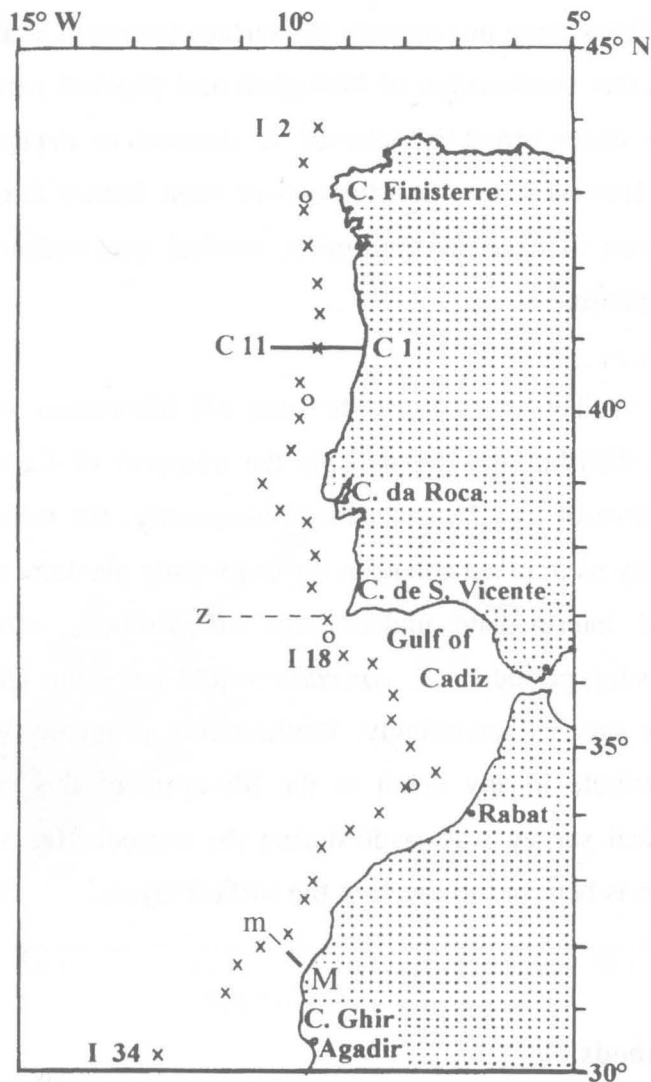


Fig. 2: Approximate locations of the standard isobath-parallel stations I 2 to I 34 (crosses), and of the 3 cross-slope transects C, z and m - M (lines). Capital letters refer to CTD plus plankton stations, lower case letters to hydrographical transects. I-stations west of the Iberian Peninsula were surveyed in spring and autumn 1991 and winter 1992. I-stations off Morocco were surveyed only in the same autumn and winter. The C-transect was run in spring and the z-transect in autumn 1991. The m - M survey was made in winter as well as in spring 1983. Circles denote some recent current meter deployments discussed in the text.

Additional information was obtained from the arrays of current-meters moored during and beyond the time of the plankton/CTD surveys described here (Hagen et al. 1994) and from earlier data to be summarized below. Regrettably several additional current-meter moorings along the Moroccan and Portuguese continental slope were lost.

The results will be presented below in their actual sequence of cruises. For the respective discussion a seasonal order facilitates the understanding of the maturity cycle of *C. carinatus* and its effect on the presumed "passive tracer", which, however, displayed an active behaviour already during the winter survey.

## 2.2. The EBC-surveys

Three surveys followed largely the 2000 m isobath at a station distance of about 30 nautical miles, and a sequence of fixed "isobath, I" stations I 2 - I 34 was selected (Table 1) for CTD-O<sub>2</sub> casts and plankton tows. Not all stations could be visited during each cruise. EBC 1, RV "Heincke" cruise 09 in March 1991, covered the stations I 2 - I 16. EBC 3, "Heincke" 17, sampled in October 1991 the stations I 12 - I 34. EBC 4, "Heincke" 20 was run in January 1992 along the stations I 2 - I 32.

Only one cross-slope transect could be surveyed by both disciplines off northern Portugal due to reduction of ship time (Fig. 2 & Table 2, also EBC 1 in March 1991). This transect is below referred to as the "C"-transect. The location of these closely spaced stations C 1 - C 11 in respect to the bottom topography is shown below in the figures, or Table 2, respectively.

All individual numbers for multidisciplinary EBC-stations or casts have been standardised in this paper to the mentioned I or C station numbers. An identical orientation of the transects and denominations concordant with earlier publications facilitates comparisons with the detailed and much broader original hydrographic information (Hagen et al. 1994; Hagen and John 1995).

Table 1: The standard isobath-parallel stations shown in Fig. 2. Reference table of nominal standard positions to the actual station or haul numbers of individual cruises.

| Iso. Sta. | Position<br>Lat. Long. |             | Project: EBC 1 |       |       | EBC 3      | EBC 4 |       |       |
|-----------|------------------------|-------------|----------------|-------|-------|------------|-------|-------|-------|
|           |                        |             | CTD #          | MUV # | NEU # | all same # | CTD # | MUV # | NEU # |
| I 1       | 46° 18' N              | 07° 40' W   | 01             | 01    | 01    |            | 01    | 01    | 01    |
| I 2       | 43° 53' N              | 09° 33' W   | 02             | 03    | 02    |            | 02    | 02    | 02    |
| I 3       | 43° 27' N              | 09° 52.5' W | 03             | 04    | 03    |            | 03    | 03    | 03    |
| I 4       | 42° 50' N              | 09° 51' W   | 04             | 05    | 04    |            | 04    | 04    | 04    |
| I 5       | 42° 17.5' N            | 09° 44' W   | 06             | 06    | 05    |            | 05    | 05    | 05    |
| I 6       | 41° 50' N              | 09° 38' W   | 07             | 07    | 06    |            | 06    | 06    | 06    |
| I 7       | 41° 22' N              | 09° 34' W   | 08             | 08    | 07    |            | 08    | 07    | 07    |
| I 8       | 40° 53' N              | 09° 36.5' W | 09             | 09    | 08    |            | 09    | 08    | 08    |
| I 9       | 40° 23.5' N            | 09° 52' W   | 10             | 10    | 09    |            | 10    | 09    | 09    |
| I10       | 39° 53' N              | 09° 54.5' W | 11             | 11    | 10    |            | 11    | 10    | 10    |
| I11       | 39° 26' N              | 10° 07' W   | 12             | 12    | 11    |            | 12    | 11    | 11    |
| I12       | 39° 00' N              | 10° 38' W   | 19             | 20    | 17    | 25         | 13    | 12    | 12    |
| I13       | 38° 42' N              | 10° 17' W   | 14             | 15    | 13    | 24         | 14    | 13    | 13    |
| I14       | 38° 27' N              | 09° 47' W   | 15             | 16    | 14    | 23         | 15    | 14    | 14    |
| I15       | 37° 57' N              | 09° 39' W   | 18             | 18    | 16    | 22         | 16    | 15    | 15    |
| I16       | 37° 25' N              | 09° 42' W   | 17             | 17    | 15    | 21         | 17    | 16    | 16    |
| I17       | 36° 59' N              | 09° 22' W   |                |       |       | 20         | 18    | 17    | 17    |
| I18       | 36° 30' N              | 09° 04.5' W |                |       |       | 19         | 19    | 18    | 18    |
| I19       | 36° 19' N              | 08° 35.5' W |                |       |       | 18         | 21    | 19    | 19    |
| I20       | 35° 55.5' N            | 08° 13' W   |                |       |       | 16         | 22    | 20    | 20    |
| I21       | 35° 25.5' N            | 08° 13' W   |                |       |       | 15         | 23    | 21    | 21    |
| I22       | 35° 00' N              | 07° 55' W   |                |       |       | 14         | 24    | 22    | 22    |
| I23       | 34° 39' N              | 07° 29.5' W |                |       |       | 13         | 25    | 23    | 23    |
| I24       | 34° 21' N              | 07° 58.5' W |                |       |       | 11         | 26    | 24    | 24    |
| I25       | 34° 03' N              | 08° 27' W   |                |       |       | 10         | 27    | 25    | 25    |
| I26       | 33° 49' N              | 08° 58' W   |                |       |       | 09         | 28    | 26    | 26    |
| I27       | 33° 34' N              | 09° 29' W   |                |       |       | 08         | 29    | 27    | 27    |
| I28       | 33° 06' N              | 09° 34' W   |                |       |       | 07         | 30    | 28    | 28    |
| I29       | 32° 43' N              | 09° 48.5' W |                |       |       | 06         | 31    | 29    | 29    |
| I30       | 32° 16' N              | 10° 05' W   |                |       |       | 05         | 34    | 31    | 30    |
| I31       | 32° 00' N              | 10° 35.5' W |                |       |       | 04         | 35    | 32    | 31    |
| I32       | 31° 42.5' N            | 11° 00' W   |                |       |       | 03         | 36    | 33    | 32    |
| I33       | 31° 15' N              | 11° 18' W   |                |       |       | 02         |       |       |       |
| I34       | 30° 17' N              | 12° 33' W   |                |       |       | 01         |       |       |       |



This paper exceptionally will refer also to one cross-slope transect from which only CTD-data are available. This transect "z" will demonstrate the upwarping of **MOW** at Cape Sao Vicente and was surveyed during EBC 2 (September 1991, see Fig. 2). Station data as well as the figures for density and oxygen have been published by Hagen and John (1995).

Table 2: The cross-slope stations of the spring survey shown in Fig. 2.  
(Project EBC 1; RV "Heincke" cruise 09, 18. - 20. 03. 1991)

| Cross Sta. | Position  |             | Bottom depth (m) | CTD # | MUV # | NEU # |
|------------|-----------|-------------|------------------|-------|-------|-------|
|            | Lat.      | Long.       |                  |       |       |       |
| C 1        | 40° 50' N | 08° 45' W   | 24               | 34    | 32    | 28    |
| C 2        | "         | 08° 51' W   | 41               | 33    | 31    | 27    |
| C 3        | "         | 08° 57.5' W | 60               | 32    | 30    | 26    |
| C 4        | "         | 09° 05.5' W | 103              | 31    | 29    | 25    |
| C 5        | "         | 09° 12.3' W | 136              | 30    | 28    | 24    |
| C 6        | "         | 09° 19' W   | 209              | 24    | 24    | 20    |
| C 7        | "         | 09° 26' W   | 1448             | 23    | 23    | 19    |
| C 8        | "         | 09° 32.5' W | 2652             | 22    | 22    | 18    |
| C 9        | "         | 09° 42.5' W | 3038             | 27    | 25    | 21    |
| C10        | "         | 09° 52.5' W | 3302             | 28    | 26    | 22    |
| C11        | "         | 10° 12' W   | 3620             | 29    | 27    | 23    |

### 2.3. The EBC-methods

CTD-O2 data were obtained from the sea surface generally down to 1600 m by means of the OM-87 system and calibrated by reversing thermometers and salinity/oxygen samples (see Hagen et al. 1994). An earlier model of this CTD-system has been described by Möckel (1980).

Along the continental slope (and at the deeper cross-slope stations) plankton was sampled vertically between 1000 - 0 m and at the surface, with nets of 300  $\mu$ m mesh size.



The vertical hauls were made with a multiple-opening-closing vertical net "MUV" (with depth gauge) as described by Weikert and John (1981). Opening/closing depths were during the EBC-cruises consistently 1000, 800, 600, 400 and 200 m.

Surface samples were collected by horizontal tows with a neuston net "NEU" with integrated flowmeter (after Hempel and Weikert 1972; 0 - 25 cm depth).

Samples were preserved immediately after capture and completely sorted for *C. carinatus*, separating both sexes of adults and the copepodid stages C5, C4 and  $C \leq 3$ . For the purpose of this study it would not matter if none of these stages would have been caught quantitatively, since our surveys are comparable at least at a relative scale. Nevertheless, stages from C4 onwards should have been retained quantitatively. SE-Atlantic C3 might be retained quantitatively by 300  $\mu\text{m}$  (Verheye 1991, extrusion not taken into account), but underestimations can not be completely excluded on the basis of the regional size variation of stages (e.g. Petit and Courties 1976).

To distinguish copepodids of C5 as members of the old, overwintering generation from younger ones in good nutritional condition, two combinations of three characters each were defined.

- Young generation: body opaque and pigmented, with a single extended, yellow lipid drop or several yellow lipid globules; most setae of the antennae present.
- Old generation: body by and large translucent and colourless; of the previously large lipid drop at maximum small remnants visible; the majority of setae of the first antennae broken off.

#### 2.4. Earlier surveys

During RV "Meteor" cruise 64, a cross-coast transect was surveyed twice (in January and April 1983) off Morocco at about 32°N. This transect is below referred to as the "M-transect" for the multidisciplinary data (or "m" for the CTD-only part, see Fig. 2, Tables 3 & 4). Both surveys included a couple of MUV-stations above the shelf edge and continental slope. Details on the stations and methods were published (Siedler et al. 1983). Mittelstaedt (1989) dealt with the hydrographical results.

The January-survey was carried out by the authors of the present study and applied the very same sampling procedure as described for EBC. However, a finer vertical resolution with steps 30 to 100 m wide was obtained by repeated sampling, and fishing was done down down to 1150 m (Table 3). The results have below been grouped to broadly comparable strata as sampled during EBC.

Table 3: The cross-slope stations of the M-winter survey off Morocco (Fig. 2).  
(RV "Meteor" cruise 64, 15. 01. 1983)

| M/m<br>Sta. | Position<br>Lat. | Long.      | Bottom<br>depth (m) | CTD<br># | MUV<br># | Muv<br>depth (m) |
|-------------|------------------|------------|---------------------|----------|----------|------------------|
| m09         | 32° 20.0'N       | 10° 43.2'W | 3250                | 9        | -        |                  |
| m10         | 32° 13.2'N       | 10° 28.2'W | 2660                | 10       | -        |                  |
| m11         | 32° 06.9'N       | 10° 12.6'W | 1880                | 11       | -        |                  |
| M12         | 32° 01.8'N       | 09° 56.4'W | 720                 | 12       | 23       | 150- 0           |
| M12         | "                | "          | 770                 |          | 24       | 350-150          |
| M13         | 31° 58.6'N       | 09° 48.6'W | 50                  | 13       | failed   |                  |
| M14         | 32° 00.2'N       | 09° 53.5'W | 115                 | 14       | -        |                  |
| M15         | 32° 01.1'N       | 09° 56.2'W | 375                 | 15       | 26       | 150- 0           |
| M15         | "                | "          | 600                 |          | 27       | 350-150          |
| M16         | 32° 02.0'N       | 09° 59.4'W | 1400                | 16       | 28       | 150- 0           |
| M16         | "                | "          | 1420                |          | 29       | 350-150          |
| M16         | "                | "          | 1400                |          | 30       | 750-350          |
| M16         | "                | "          | 1320                |          | 31       | 1150-750         |

From April 1983, MUV-samples were provided by D. Schnack. These MUV-tows included a micro-net of 55  $\mu$ m mesh-size and 45 mm diameter, mounted centrally in the MUV-mouth. It is unknown how far this combination affected the filtration efficiency of the sampler and avoidance reactions of the target species. Again, a high number of smaller strata was sampled and combined by us to broadly comparable steps. Repeated tows (up to three for individual steps and stations, see Table 4) have below been averaged.

Table 4: The cross-slope stations of the M-spring survey off Morocco (Fig. 2).  
(RV "Meteor" cruise 64, 04. - 07. 04. 1983)

| M/m<br>Sta.<br>(m) | Position<br>Lat. | Long.     | Bottom<br>depth (m) | CTD<br># | MUV<br># | Muv<br>depth |
|--------------------|------------------|-----------|---------------------|----------|----------|--------------|
| M290               | 32°02.6'N        | 10°03.0'W | 1650                | 290      | 650      | 1150-750     |
| M290               | 32°02.1'N        | 10°02.1'W | 1510                |          | 651      | 750-350      |
| M290               | 32°02.4'N        | 10°00.8'W | 1520                |          | 652      | 150- 0       |
| M290               | "                | "         | 1540                |          | 653      | 350-150      |
| M293               | 31°55.9'N        | 09°46.2'W | 38                  | 293      | 654      | 30- 0        |
| M294               | 31°58.5'N        | 09°51.2'W | 98                  | 294      | 655      | 90- 0        |
| M296               | 31°59.9'N        | 09°51.4'W | 118                 | 296      | 656      | 90- 0        |
| M296               | "                | "         | 118                 |          | 657      | 90- 0        |
| M297               | 32°01.6'N        | 09°58.8'W | 1130                | 297      | 659      | 350-150      |
| M297               | 32°01.8'N        | "         | 1182                |          | 660      | 750-350      |
| M297               | "                | "         | 1198                |          | 661      | 150- 0       |
| M298               | 32°01.7'N        | 10°01.6'W | 1470                | 298      | 662      | 1150- 0      |
| M299               | 32°06.6'N        | 10°08.8'W | 1500                | 299      | 663      | 1150-150     |
| m300               | 32°09.0'N        | 10°18.0'W | 2305                | 300      | -        |              |
| m301               | 32°13.5'N        | 10°29.2'W | 2575                | 301      | -        |              |
| m302               | 32°16.5'N        | 10°39.2'W | 3219                | 302      | -        |              |
| M303               | 31°55.9'N        | 10°12.2'W | 810                 | 303      | failed   |              |
| M303               | "                | "         | 820                 |          | failed   |              |
| M303               | 31°55.6'N        | 10°13.2'W | 650                 |          | 666      | 450- 0       |

During autumn 1984, "Meteor" cruise 69 yielded eleven MUV-tows from the adjacent open ocean. The hauls were made by one of the present authors between broadly 28°N and 35°N and 20°W to 27°W (Table 5). Five steps of 100 m each were sampled from the surface to 500 m depth, otherwise as for the EBC-surveys. Details for that cruise and hydrographical information were given by Meincke et al. (1985).

Table 5: The reference stations from the adjacent open ocean.  
 "Meteor" cruise 69, 25.10.-05.11.1984, sampled depth 0 - 500 m.

| Sta. | Position  |           | MUV # |
|------|-----------|-----------|-------|
|      | Lat.      | Long.     |       |
| 226  | 33° 10' N | 21° 56' W | 04    |
| 235  | 35° 01' N | 26° 25' W | 07    |
| 239  | 35° 02' N | 26° 35' W | 10    |
| 247  | 28° 00' N | 26° 30' W | 13    |
| 247  | 28° 00' N | 26° 25' W | 15    |
| 247  | 28° 01' N | 26° 21' W | 17    |
| 247  | 28° 01' N | 26° 21' W | 19    |
| 247  | 28° 01' N | 26° 24' W | 21    |
| 252  | 28° 00' N | 24° 28' W | 23    |
| 254  | 27° 59' N | 22° 23' W | 25    |
| 257  | 28° 10' N | 20° 25' W | 28    |

## 2.5. Presentation of data

Meridional transects are figured with north at the right and zonal transects with east to the right. In the figures of the hydrographical sections the boundaries of **MOW** were depicted by enhancing the  $S = 35.8$  isohaline. This value was chosen because it was consistently shown also in the literature compared. We decided not to depict the relative salinity minimum by any fixed value. In the literature compared, respective values varied from  $S = 35.6$  to  $35.8$  for the area off Morocco (for literature and an explanation see the introduction). A value of  $35.6$  or  $35.7$  would depict an intermediate salinity minimum nicely through all our own data. However, it would include an obvious change in water mass off northern Portugal (with coinciding change of the population structure) and it would be hydrographically ambiguous for some salinity lenses off central Portugal.

The numbers of individuals of each sex or stage per stratum were quantified to abundance values  $n/1\text{m}^2$  (MUV) or  $n/1000\text{m}^2$  (NEU). The actually sampled areas during EBC were on average  $0.26\text{ m}^2$  vertically and  $574.5\text{ m}^2$  horizontally. The corresponding standard deviations were 0.02 and 43.7, with a total of 384 MUV strata (plus 55 from the open ocean) and 83 NEU tows, respectively. The MUV-tows during the "Meteor" cruises were slightly larger. To reduce some of the noise inherent to plankton data, abundance values in the larger scale isobath transects were subsequently averaged longshore by smoothing over 3 values.

No averaging was done for any of the high-resolution cross-slope transects, because hydrographical conditions, bottom depth and population structure varied between closely adjacent stations and affected directly the distribution patterns.

## 2.6. Seasonality of the Mediterranean Outflow Water

During our surveys we encountered differences in the vertical extension and cross-slope transport of **MOW** and suspected variability in time. The formation of **MOW** depends on air-sea interaction over the whole Mediterranean Sea, which is subject to seasonal and interannual variations (Garrett et al. 1990). Therefore the variability found in the **MOW** is probably seasonal.

The variability within the **MOW** was investigated on the basis of salinity and temperature data from a box in the region of the Azores Current between the Azores and Madeira. The box covered most of the "Control Volume AR 11" suggested by WOCE.

This investigation is based on the CTD- and XBT-data set from 1974-1992, which was available at the Institut für Meereskunde, Kiel. Additionally oceanographic station data, high resolution CTD/STD data and the XBT data set from the National Oceanographic Data Center (NODC 1992, data from 1906-1991) were used.

The amount of profiles in this area down to 2000 m (5424 profiles) was sufficient to calculate seasonal means with a good spatial coverage, but not monthly means. The seasons were defined as follows:

Winter: 15 Jan. - 14 Apr., spring: 15 Apr. - 14 June, summer: 15 June - 14 Oct., autumn: 15 Oct. - 14 Jan.

The data set was split for seasons, checked for duplicate profiles and a quality test was run. The data set was gridded using a horizontal resolution of  $1/3^\circ$  in meridional and  $2/5^\circ$  in zonal direction, and 16 layers down to 2000 m in the vertical direction. The layer thickness increased from 35 m at the surface to 250 m underneath 1000 m. To interpolate the values, a Lagrangian interpolation (described in NODC 1974) was used in the vertical and the objective analysis from Hiller and Käse (1983) in the horizontal direction. The calculated correlation scales (necessary for the objective analysis) were anisotropic with zonal and meridional values of 230 km and 100 km, respectively. From the gridded data set those data points were rejected which were either within one correlation scale from the box edge, or when their error variance from the objective analysis exceeded 10% of the total variance.

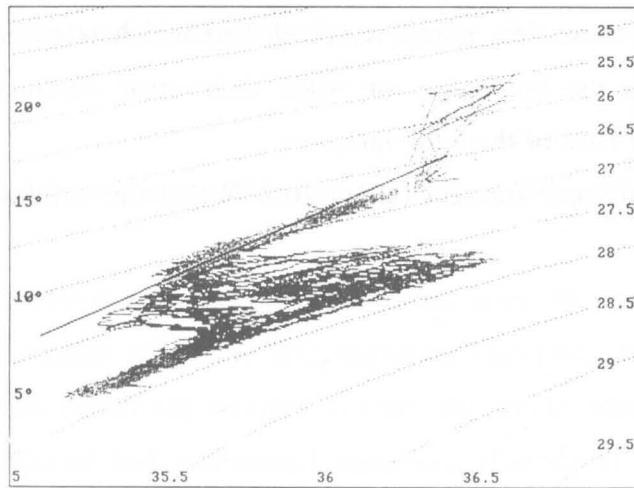
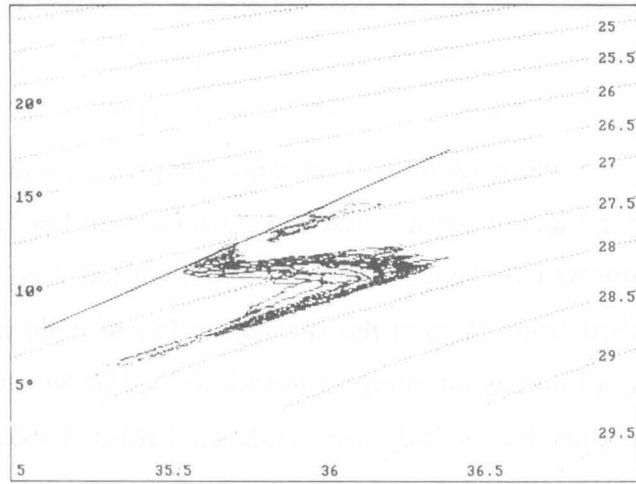
Only the eastern most meridional transect (along  $16.8^\circ$  W) of the valid salinity data will be shown below.

### 3. Results

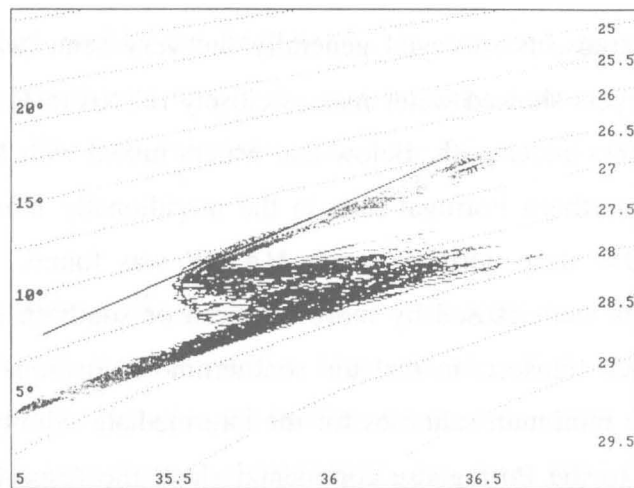
#### 3.1. Water masses along the NE-Atlantic continental margin

The three isobath-parallel transects surveyed generally the very same water masses each (Fig. 3). The upper layers showed water masses closely related to **NACW**, with a mixture of less saline waters underneath. Below that waters mixed with **MOW** were found, somewhat less off northern Portugal than in the meridionally more extended transects. Beneath the **MOW** deep northern water **NADW** was found. Differences between individual transects were caused by more northern or southern locations of the terminal stations of each transect, in that the southernmost positions during the autumn transect yielded the minimum salinities for the intermediate salinity minimum and the transect restricted to the Portuguese continental slope the respective highest values. This spring transect showed a surface anomaly from a low saline river plume, whilst the autumn survey yielded warm surface waters. Respective details, when relevant for our study, will be presented further below.

Spring 1991  
 EBC 1  
 Stations  
 I 2 - I 16  
 Iberia  
 only



Autumn 1991  
 EBC 3  
 Stations  
 I 12 - I 34  
 Morocco  
 and  
 Iberia



Winter 1992  
 EBC 4  
 Stations  
 I 1 - I 32  
 Morocco  
 and  
 Iberia

Fig. 3: Temperature/salinity relationships along the three isobath-parallel transects. The straight line depicts the characteristics of North Atlantic Central Water NACW.

### 3.2. Winter and spring 1983, cross-slope transect

The hydrographical situations shown by Figs. 4 & 5 were discussed in detail by Mittelstaedt (1989). Noteworthy are the upwelling situations indicated by the upwarping of isotherms and isohalines above the shelf edge during both surveys. The undercurrent is marked by the vertical spread of the isolines between approximately 150 and 600 m depth off the continental slope. The intrusion of **MOW** can be identified by peak values in salinity below 1100 m. There exists an intermediate salinity minimum layer above the **MOW** between approximately 400 and 1100 m. Compared with monthly means of surface data (DHI 1967) or of upwelling intensity (Wooster et al. 1976), both surveys represent average conditions for the season of sampling.

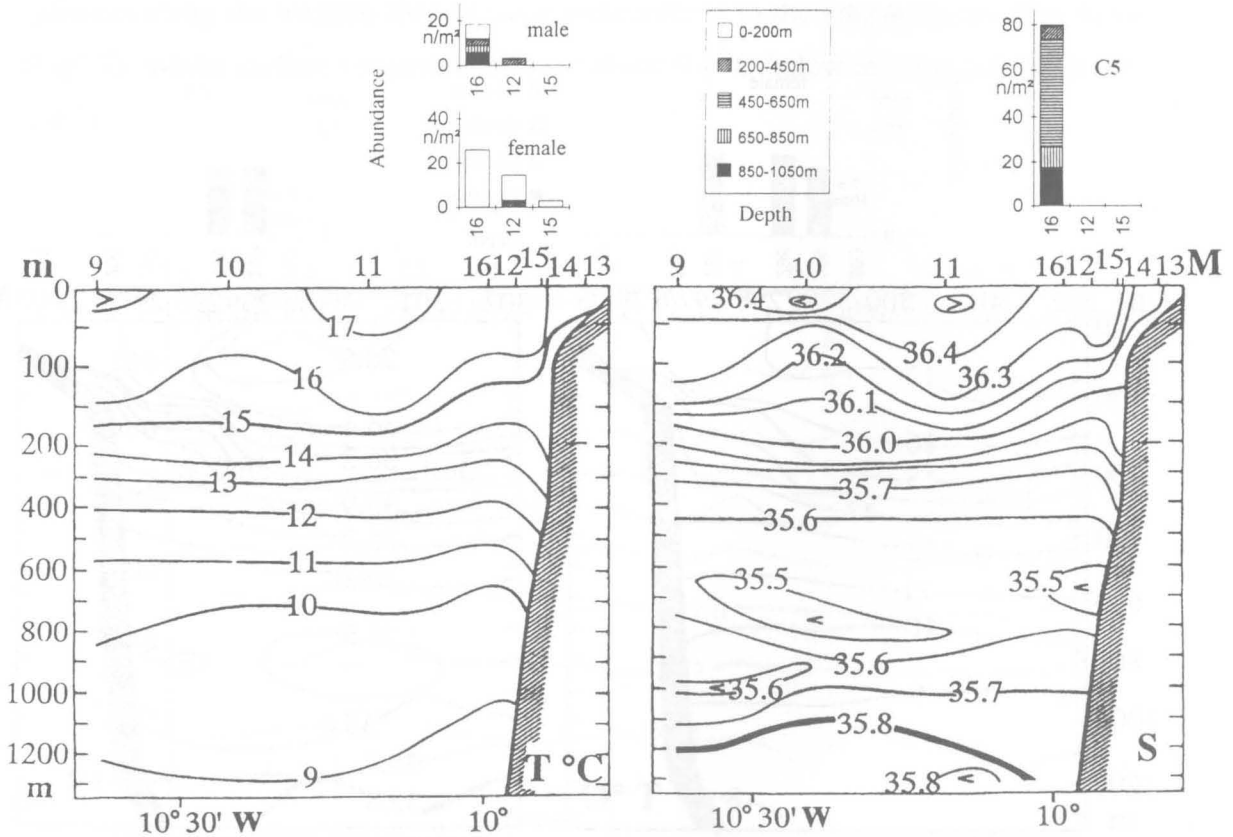


Fig. 4: The cross-slope distribution of *Calanoides carinatus* (top) and the corresponding hydrographical structure of temperature (left, lower panel) and salinity (lower panel, right) during winter 1983 along transect m - M. For details see text.



During January, resting, old generation C5s were found exclusively at the most offshore station sampled, above a bottom depth of 1400 m. Stage C5 was caught between 200 and 1150 m, but was concentrated below 450 m (the stratum 1050 - 1150 m, not shown in Fig. 4, contributed a further 23.2 C5/1m<sup>2</sup>). There occurred some males and females (Fig. 4) plus a single individual of stage 4 (station M 12, 0 - 30 m depth). Females had a shallow and males a broad vertical distribution.

During April (Fig. 5) the species had either a low abundance, or it was undersampled. Due to a gear failure no data are available for depths below 550 m at station M 303. A few C5s occurred above the slope and the shelf edge at depths 350 - 1150 m (note deviating depth strata). With exception of one dubious specimen, the C5s belonged to the new generation. Females were more abundant than C5s, and only one single male was caught at the shelf edge. Females were shallow distributed at the shelf edge, but at medium depth above the slope.

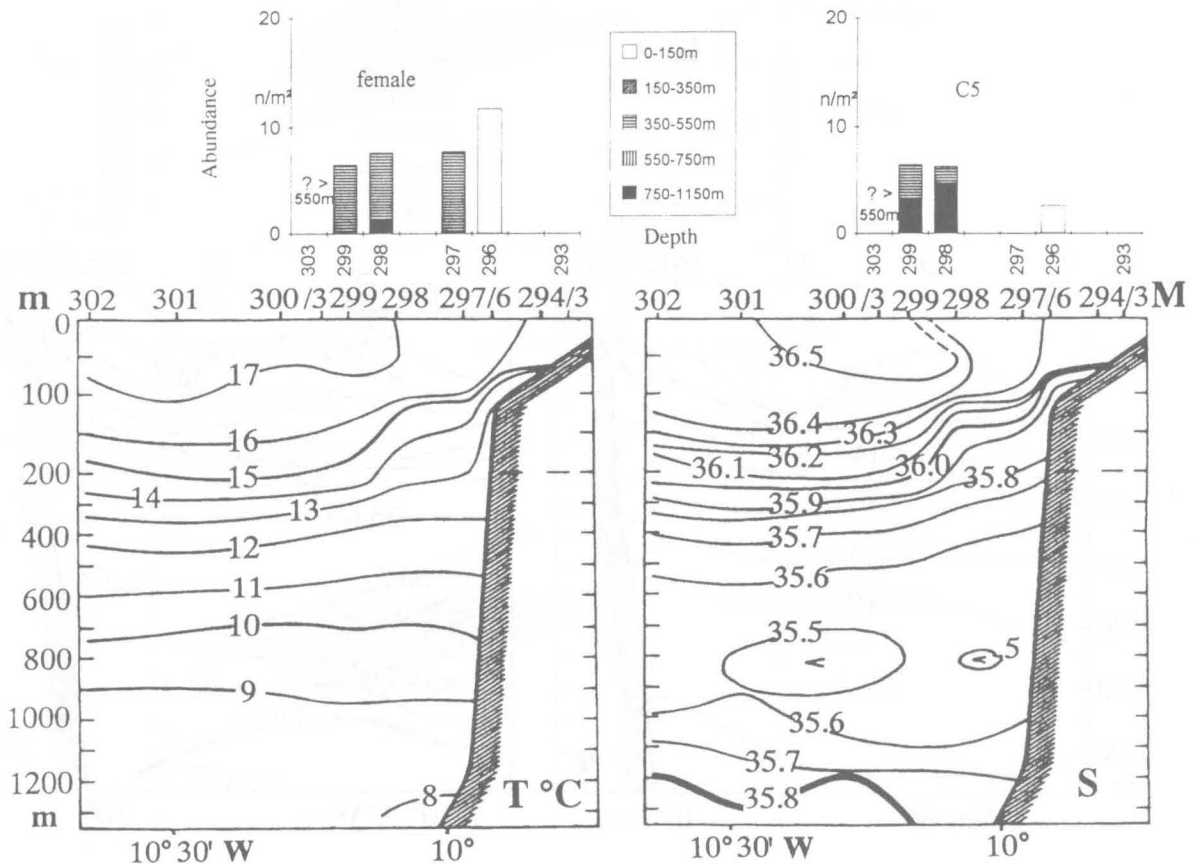


Fig. 5: The cross-slope distribution of *Calanoides carinatus* (top) and the corresponding hydrographical structure of temperature (left, lower panel) and salinity (lower panel, right) during spring 1983 along transect m - M.

### 3.3. Autumn 1984, open ocean data

During autumn 1984, in the open ocean only one single carcass of copepodid stage C5 was caught. It was found in tow # 21 in the lowermost depth stratum sampled (400 - 500 m). Other stages were absent from at least the upper 500 m. The surface waters at these stations were warm, saline and well stratified (Meinke et al. 1985: Fig. 1.3). These results are here included in order to show that the maturing winter population at the Portuguese continental slope discussed below did not have its source in oceanic waters.

### 3.4. Early spring 1991, isobath-parallel transect

The spring survey had been made in March after and during gale force winds and the stratification of the surface waters had not yet developed (Fig. 6). The surface salinities along the western Iberian slope were similar to the long-term monthly means (Fig. 7), whilst surface temperatures were about  $0.5^{\circ}\text{C}$  below average (compare DHI 1967).

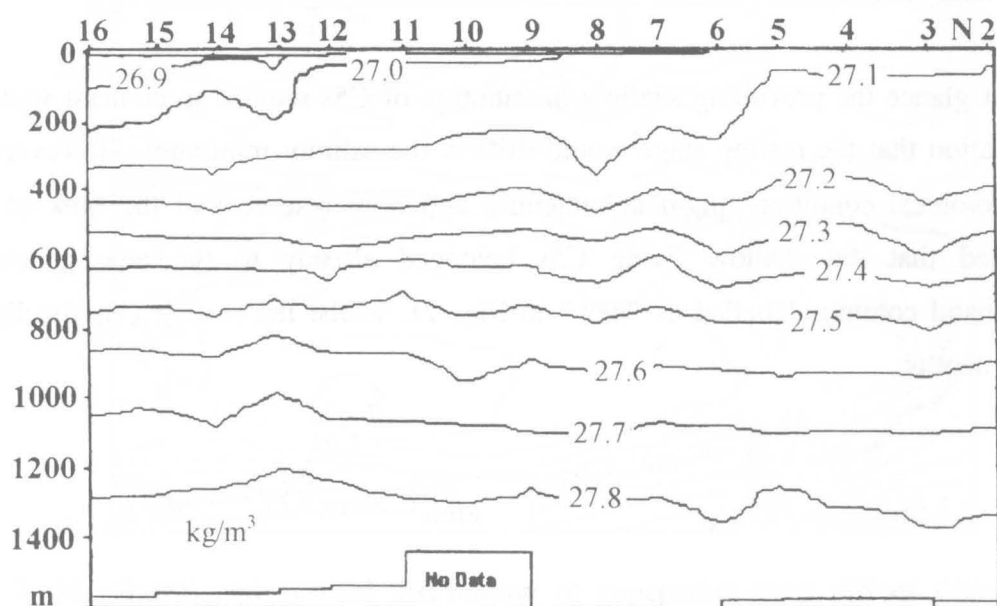


Fig. 6: The density structure along the isobath-parallel transect during spring 1991.

There was a horizontally continuous layer of salinity  $\leq 35.7$ , with a narrow vertical extension at stations I 11 - 12. There were two small lenses and a northern wedge of salinity  $\leq 35.6$  (Fig. 7). At least the southern lens and the northern wedge belonged to different thermohaline regimes, as suggested by the spread of isopycns in the north (Fig. 6).

Unfortunately, the survey did not cover the pronounced **MOW** front off Cape Sao Vicente, hence its minimum depth remains unknown. However, at the southern stations I 15 - 16 the upper boundary of **MOW** was shallow at about 500 m, descending from station I 10 to  $\geq 600$  m in the north.

Some copepodids C5 of *C. carinatus* occurred at all MUV-stations, but they were more confined to southern Portugal (station I 13 - 15). The NEU contributed higher numbers at these same stations, too (Fig. 8). Furthermore, both samplers yielded adult *C. carinatus*. Females were more abundant than males. Young copepodids C3 and C4 occurred in high numbers in the south (Figs 8 & 9). Among the total of advanced stages in the MUV (C4, C5, adults), C4 contributed 27.6 %, C5 30.9 %, females 32.9 % and males 8.7 %. While meridionally C5s, males and younger stages had similar distributions with relative maxima in the south, females spread along the entire transect (Fig. 9).

At first glance the prevailing shallow distribution of C5s seemed to contrast with our expectation that the resting stage would drift in the salinity minimum. However, the morphological condition (pigment, antennae and lipid reserves) of the bulk of C5s indicated that the shallow living C5s belonged already to the new generation (right-hand columns labelled as "new" in Fig. 7), whilst the resting C5s dwelled at larger depths.

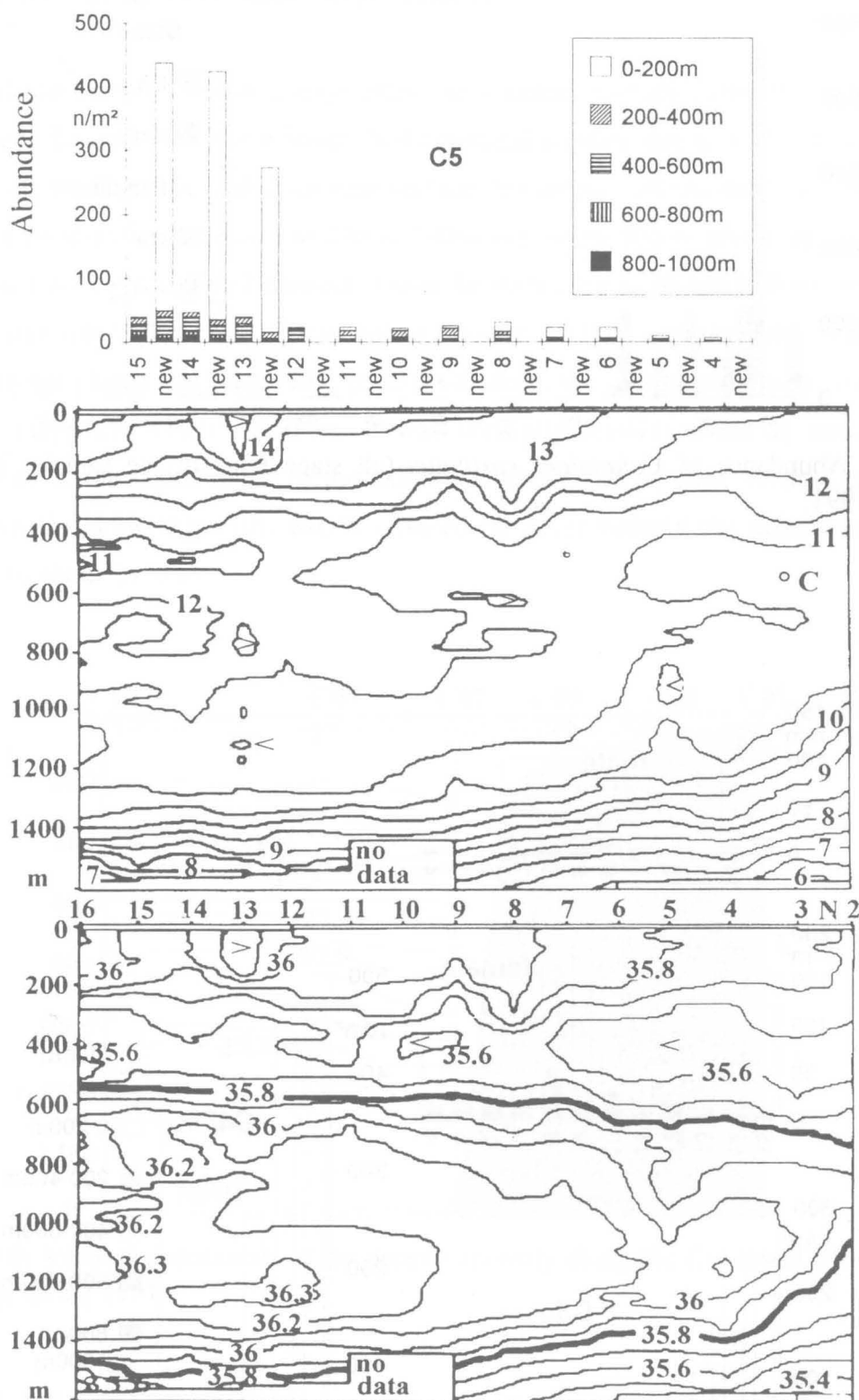


Fig. 7: Meridional and vertical distribution of copepodite stage C5 of *Calanoides carinatus* during spring 1991 in 5 MUV-plankton strata (top), and the hydrographical parameters temperature (middle) and salinity (bottom). The envelope of Mediterranean Outflow Water  $S = 35.8$  is enhanced. Columns per station distinguish the old (left) and the new generations (right).

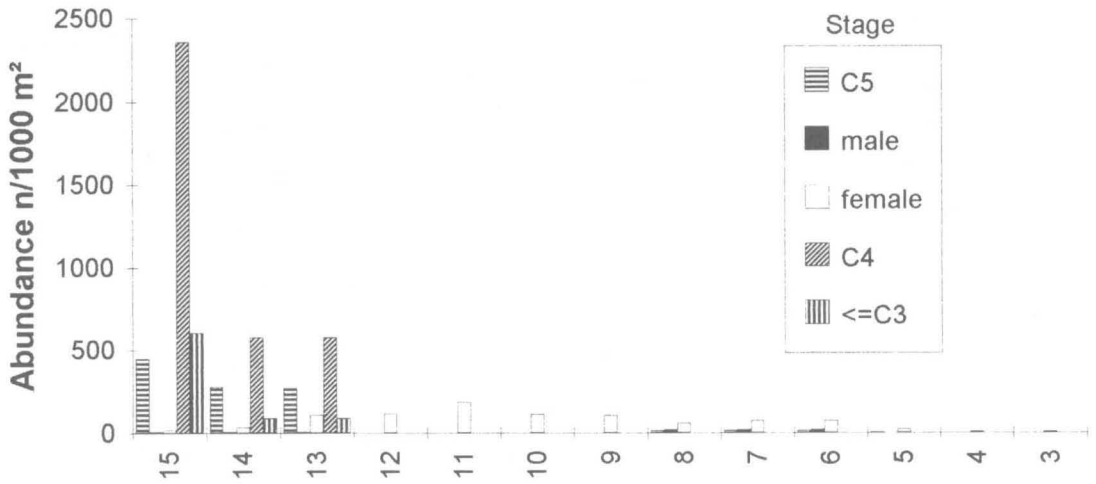


Fig. 8: Abundance of *Calanoides carinatus* (all stages) in surface samples during spring 1991.

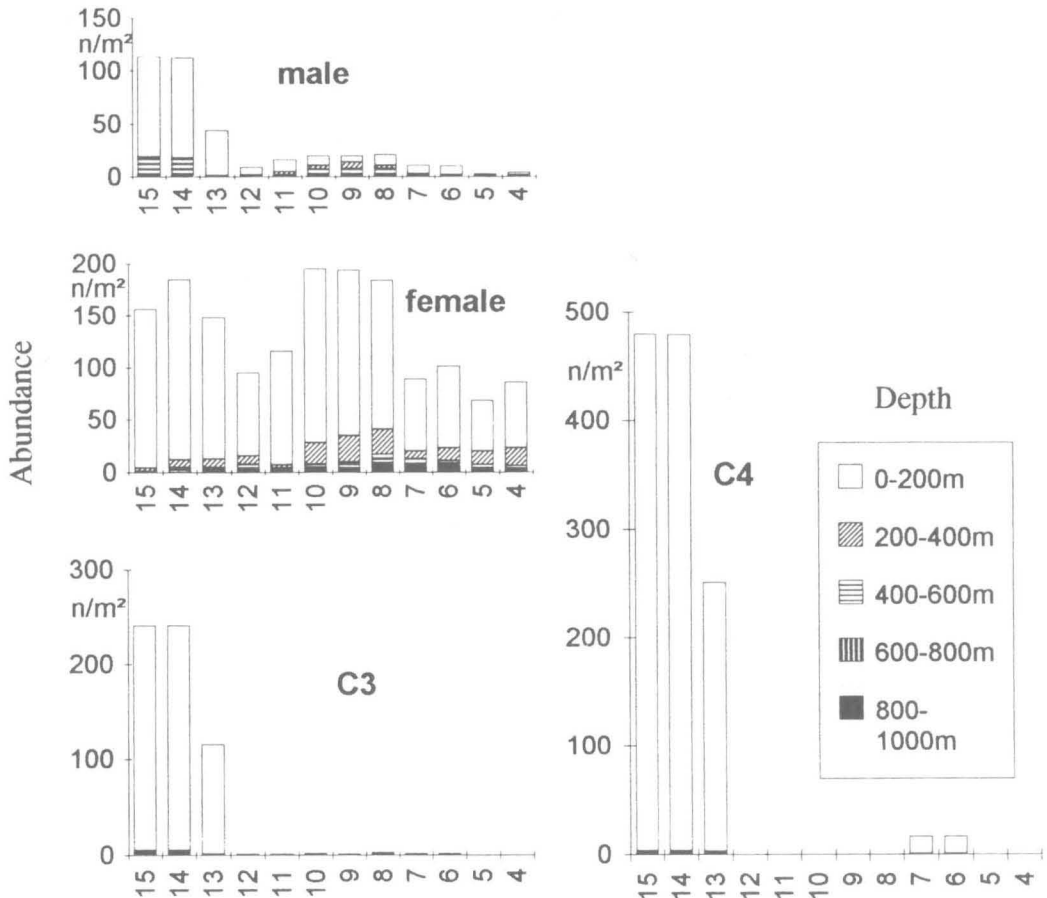


Fig. 9: Meridional and vertical distribution of adult *Calanoides carinatus* and of the new generation copepodite stages C3 and C4 during spring 1991.

### 3.5. Early spring 1991, cross-slope transect

The C-transect was begun 2 days after the southern isobath station I 16 had been finished. The coastal surface waters had a vertical stability due to a river plume (Figs 10 & 11, inadequately scaled for near-surface structures). Off the shelf edge there was almost no stratification down to 230 m (offshore), or to 300 m above the deep slope as found in the preceding I-transect. From the shelf edge to midshelf there were some upwelling-like structures of less saline, cooler and oxygen-depleted waters (for oxygen see Hagen and John 1995: p. 15). Offshore, the salinity minimum covered the depth range 270 (330) - 550 m. It was vertically least extended at station C 8. Isopycnals in the depth range of the salinity minimum show some vertical spreading towards the slope (Fig. 10). **MOW** covered the layer beneath the salinity minimum down to about 1450 m.

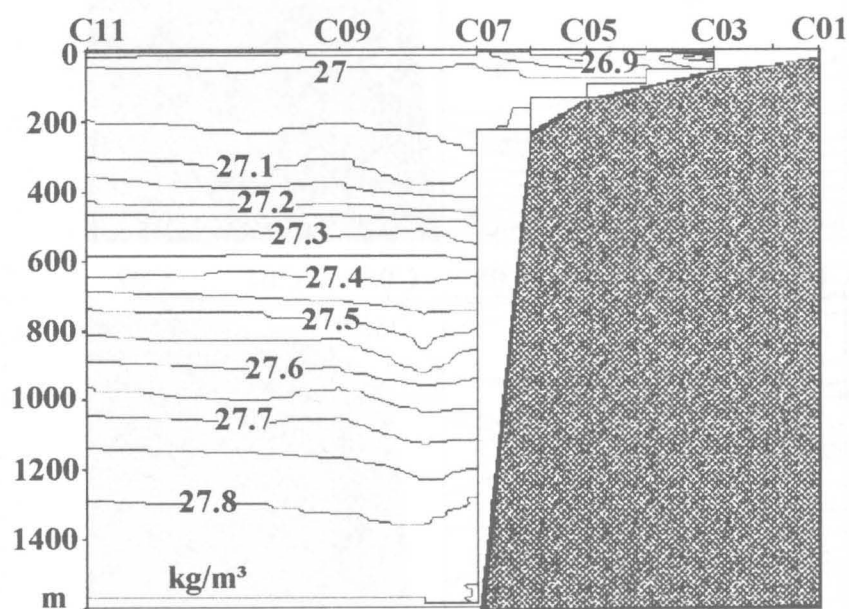


Fig. 10: Vertical distribution of the density anomaly along the C-transect off Portugal during spring 1991.

This cross-slope survey confirmed the results described above for the comparable stations (I 8 and C 8 were closely adjacent geographically and C 8 was surveyed 3 days later). The comparatively rare stage C5 belonged exclusively to the old generation. C5s had deep vertical distributions in the salinity minimum and also in the

**MOW** at the slope stations C 8 and 10, but were caught in the upper 200 m closer inshore (Fig. 11).

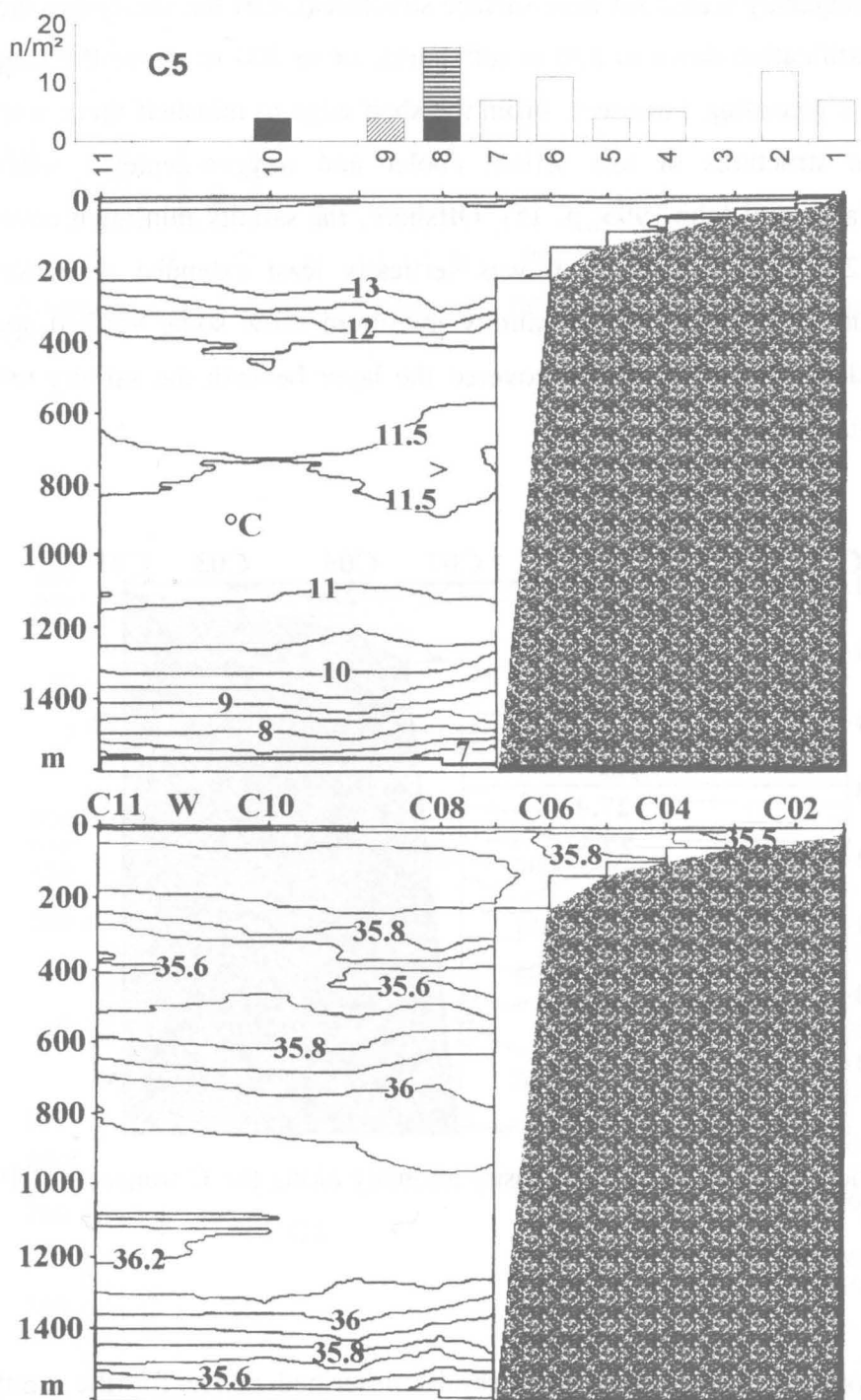


Fig. 11: Vertical distribution of copepodite stage C5 of *Calanoides carinatus* and the corresponding hydrographical structures along the spring C-transect off Portugal (otherwise as for Fig. 7). No young copepodids C5 were caught.

Females were by far more abundant and occurred from midshelf to at least station C 11. Males and the rare C4 copepodids had, although in lower abundance, distributions similar to those of females. Information on the cross-slope distribution of females derived from MUV and NEU-data was fairly consistent (Fig. 12).

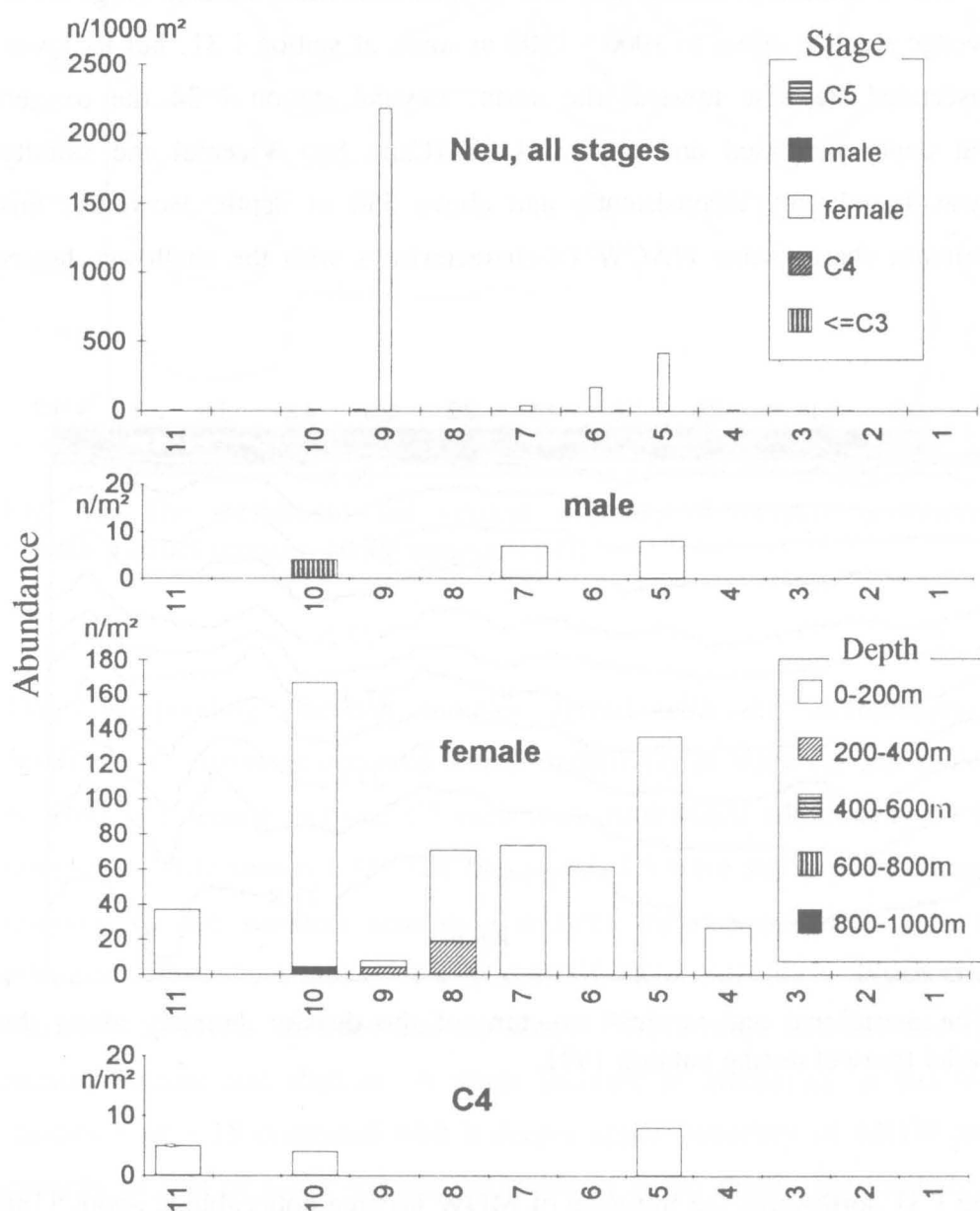


Fig. 12: Cross-slope distribution of *Calanoides carinatus* off Portugal during spring. Top: From surface samples (stages C $\leq$ 3 to adults were present). Lower panels: Adults and early copepodids from MUV samples.



### 3.6. Autumn 1991, isobath-parallel transect

During autumn the surface waters were vertically stratified (Figs 13 & 15). The meridional gradients of temperature and salinity were well in agreement with the long-term monthly means (compare DHI 1967). From the seasonal thermocline downwards, temperature and salinity decreased almost gradually down to 400 m in the south, or to about 260 m off central Portugal. Below these depths, from the south a wedge or lens of minimum salinity and low oxygen saturation intruded (Figs 14 & 15). This wedge reached down to 1000 - 1300 m south of station I 31, but its lower boundary ascended stepwise towards the north. Beyond station I 24 the oxygen saturation at depth increased and beyond I 18 (Cape Sao Vicente) the salinity minimum was found only inconsistently and above 550 m depth. However, this salinity minimum shares some **NACW-TS**-characteristics with the shallower layers (Fig. 3).

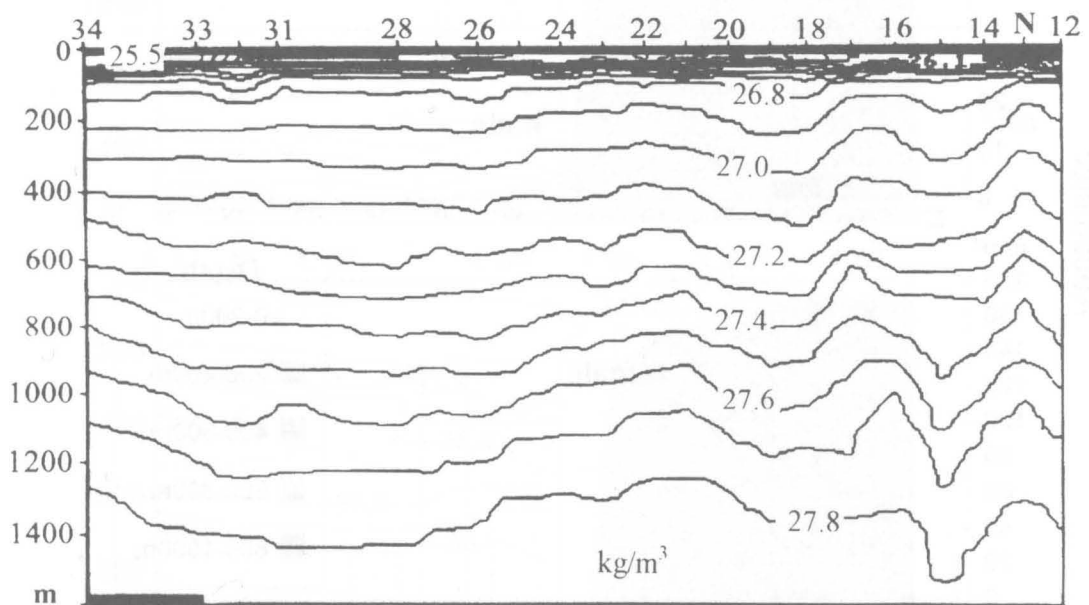


Fig. 13: The meridional and vertical structure of the density anomaly along the isobath-parallel transect during autumn 1991.

From station I 31 northwards the intrusion of **MOW** became noticeable at about 1180 m depth, increasing its vertical range from station I 27 onwards and extending distinctly over the depth range 500 - 1600 m north of the pronounced, meddy-like salinity front and temperature disturbances at station I 18 (Fig. 13). The upper

boundary of **MOW** occurred as shallow as 460 m, but varied considerably in depth between adjacent stations. Below about 1500 m temperature and salinity decreased again more gradually with depth, but with steeper gradients in the north (this CTD-transect was surveyed down to 2000 m).



Fig. 14: The meridional and vertical structure of oxygen saturation along the isobath-parallel transect during autumn 1991.

The corresponding plankton samples agreed with the thermohaline structures described. *C. carinatus* occurred almost exclusively as stage C5 and at depths >400 m. Only one female and one C5 each were contributed additionally by the neuston samples at NEU station I 33. The copepodids C5 were still pigmented and had lipid reserves. At the southern stations abundance maxima coincided with the salinity minimum. The abundance of copepodids C5 decreased drastically off the Gulf of Cadiz, when **MOW** intruded into the sampled depth range and the salinity minimum became narrow and shallow. A slight increase in abundance at the northernmost stations I 14 - 15 coincided with a deeper upper boundary of **MOW** and, perhaps casually, a lens of lower oxygen saturation at larger depth. Surprisingly, those few specimens caught north of the **MOW** front south of Cape Sao Vicente were contributed by the deeper samples, and not, as anticipated, from the salinity minimum stratum above the **MOW**.

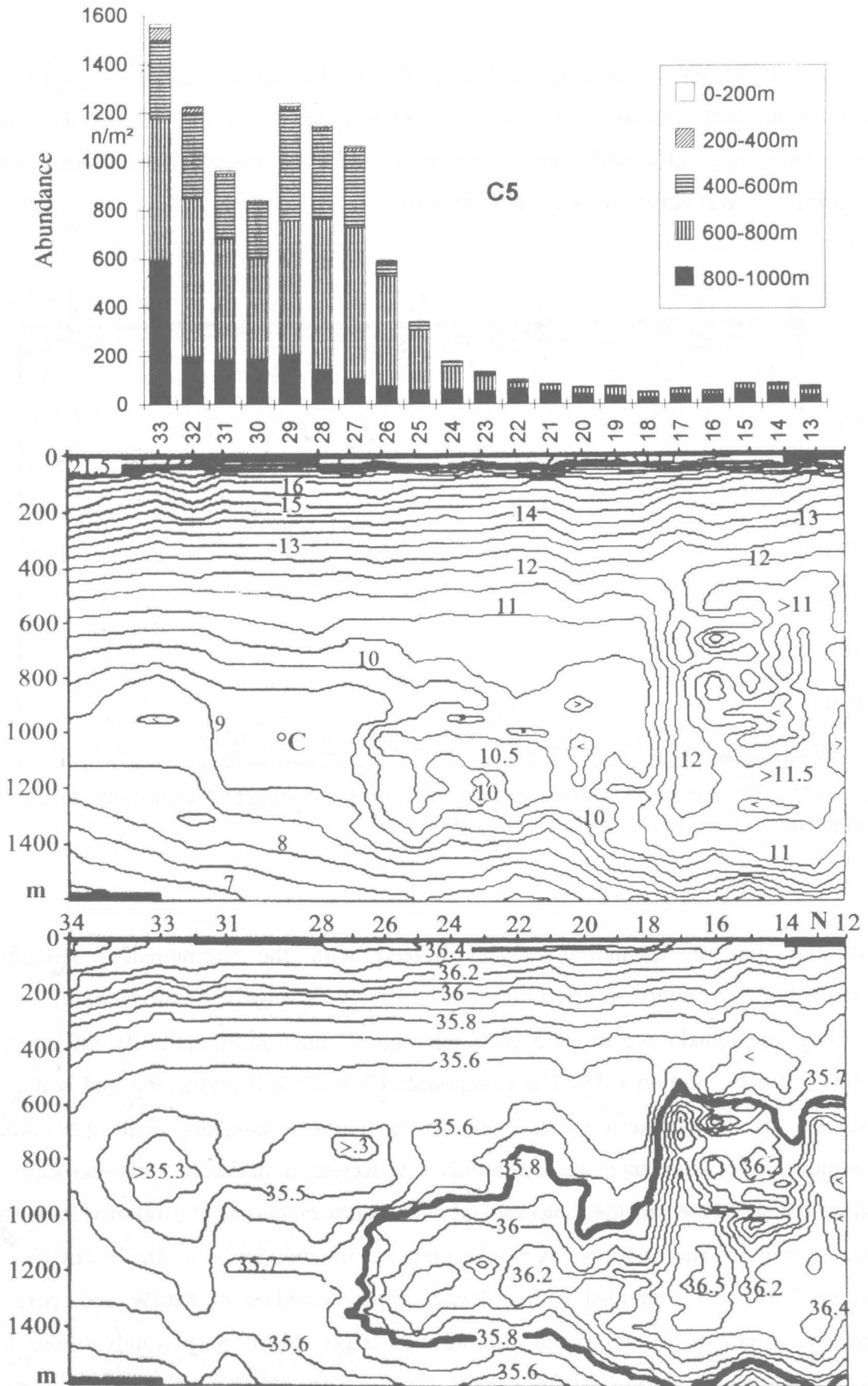


Fig. 15: Meridional and vertical distribution of copepodite stage C5 of *Calanoides carinatus* during autumn 1991 and the corresponding hydrographical structures (as for Fig. 7).

### 3.7. Winter 1992, isobath-parallel transect

During the survey in winter 1992, surface waters were generally well mixed as a result of strong winds (Fig. 16). The thickness of the homogeneous surface layer increased towards the north, where the upper 400 m were oxygen saturated (Fig. 17).

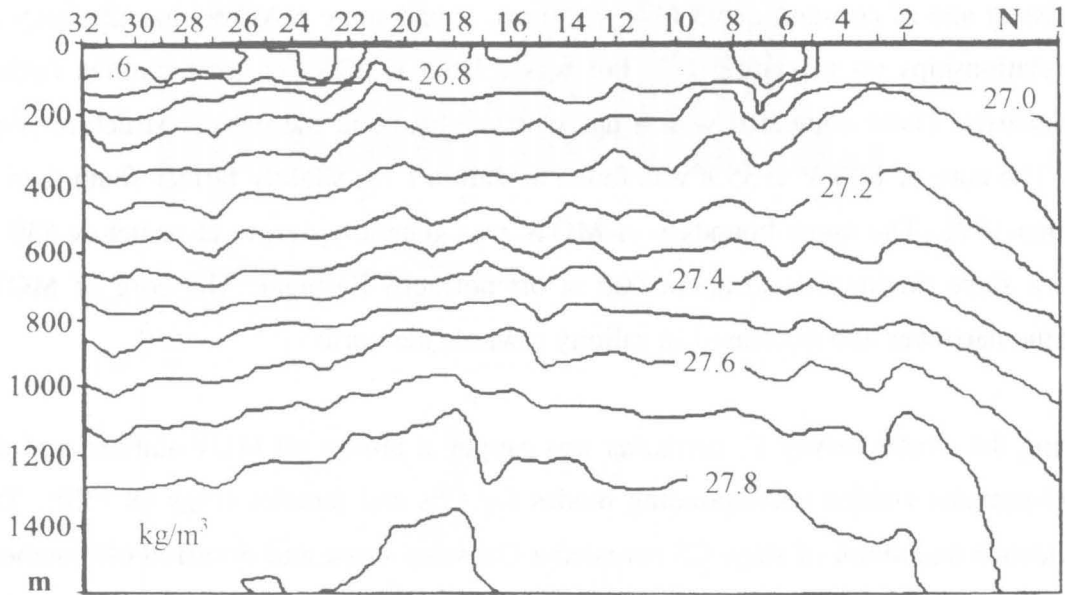


Fig. 16: The meridional and vertical structure of the density anomaly along the isobath-parallel transect during winter 1992.

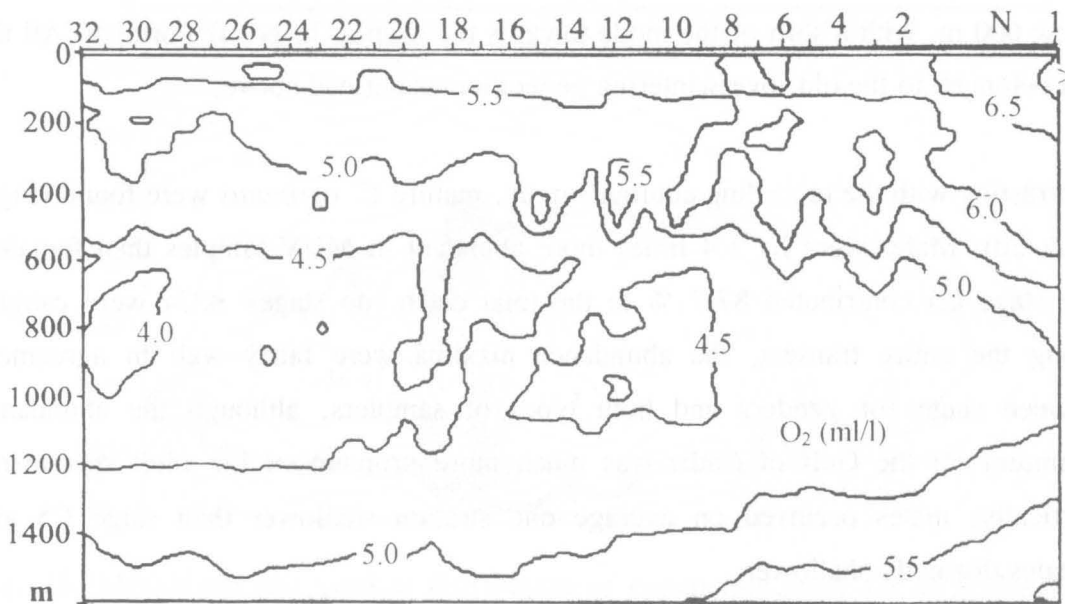


Fig. 17: The related structure of oxygen saturation during winter 1992.

However, surface temperatures and salinities were about  $1.5^{\circ}\text{C}$  and  $S=0.3$  units above the climatic average (compare DHI 1967), and higher than in spring 1991 (Fig. 18). Otherwise generally similar vertical and meridional trends as described for the autumn cruise were observed, but off Morocco south of station I 26 the salinity minimum was of some 35.6 instead of ca 35.4 during autumn. Nevertheless, the layer of low salinity ranging between 35.6 and 35.7 was a feature meridionally almost consistent and of constant depth (370 - 550 m). It had some **NACW**-characteristics in TS-relationships up to station I 5, but was related with lower temperatures farther northwards. These coincided with a noteworthy change in the density structure (Fig. 16). The core of **MOW**  $\geq 35.8$  was found at station I 18, slightly farther south than in autumn 1991. The upper boundary of **MOW** was generally deeper at or below 530 m with a slope downwards to about 600 m off northern Portugal. The core of **MOW** became narrower and decreased in salinity towards the north.

During the winter survey *C. carinatus* was caught at almost all MUV-stations and the NEU-samples yielded corresponding modes for C5s and females (Figs 18 - 20). The abundance maximum of stage C5 revealed a Gaussian shape and occurred off southern Portugal (centre at stations I 9 - I 15). It had about half the magnitude as during autumn off Morocco. The population decreased in abundance at the three northernmost stations. Copepodids C5 occurred regularly in the layer 400 - 600 m corresponding with the salinity minimum layer, but the bulk was consistently found below 600 m, with a shift of the mode towards the deepest layer off Portugal. All the C5s belonged to the old, overwintering generation as defined above.

Contrasting with the preceding autumn survey, mature *C. carinatus* were found (Figs. 19 & 20). Males were by 3.4 times more abundant in MUV-samples than females. The stage C5 contributed 87.7 % to the total catch, no stages  $\leq C4$  were caught. Along the entire transect, the abundance maxima were fairly well in agreement between stages or genders and both types of samplers, although the abundance minimum off the Gulf of Cadiz was much more pronounced for adult specimens. Vertically, males occurred on average one stratum shallower than stage C5 and females distinctly shallower.

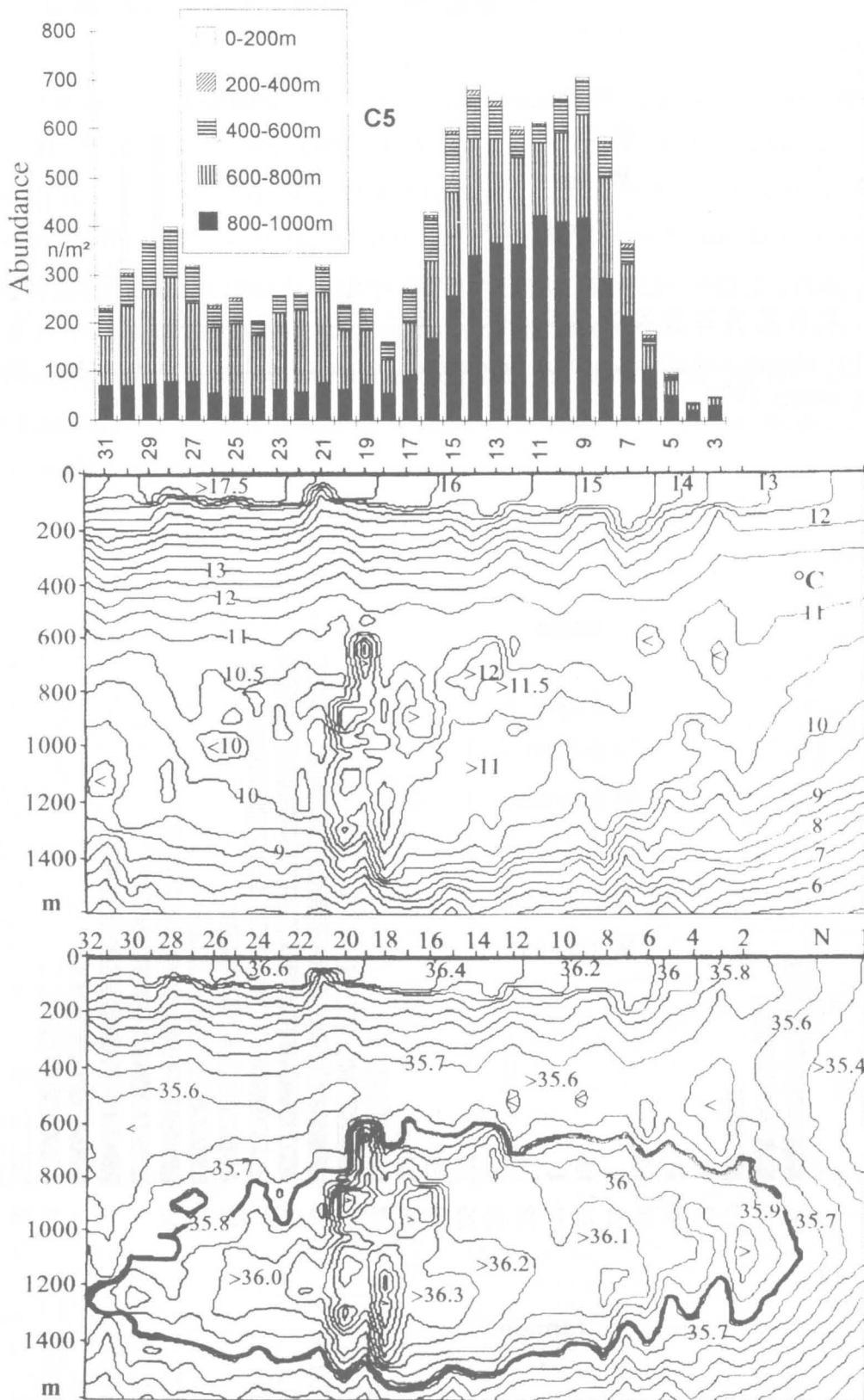


Fig. 18: Meridional and vertical distribution of copepodite stage C5 of *Calanoides carinatus* during winter 1992 and the corresponding hydrographical structures (as for Fig. 7).

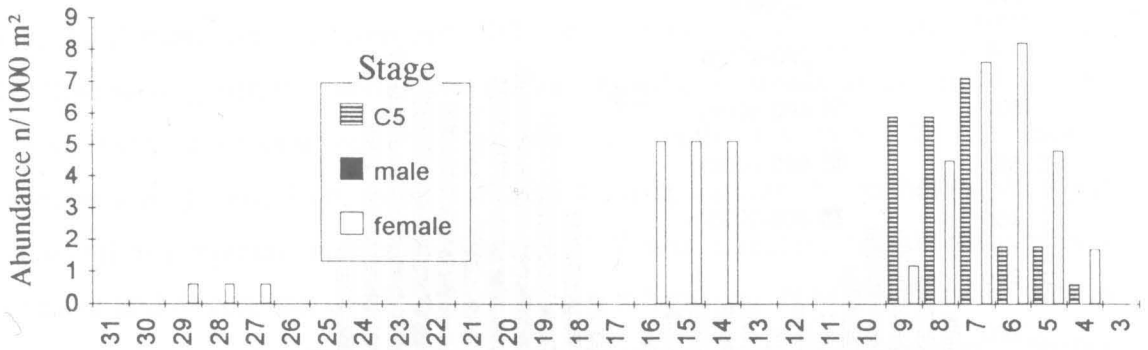


Fig. 19: Meridional abundance of *Calanoides carinatus* (all stages) in surface samples during winter 1992.

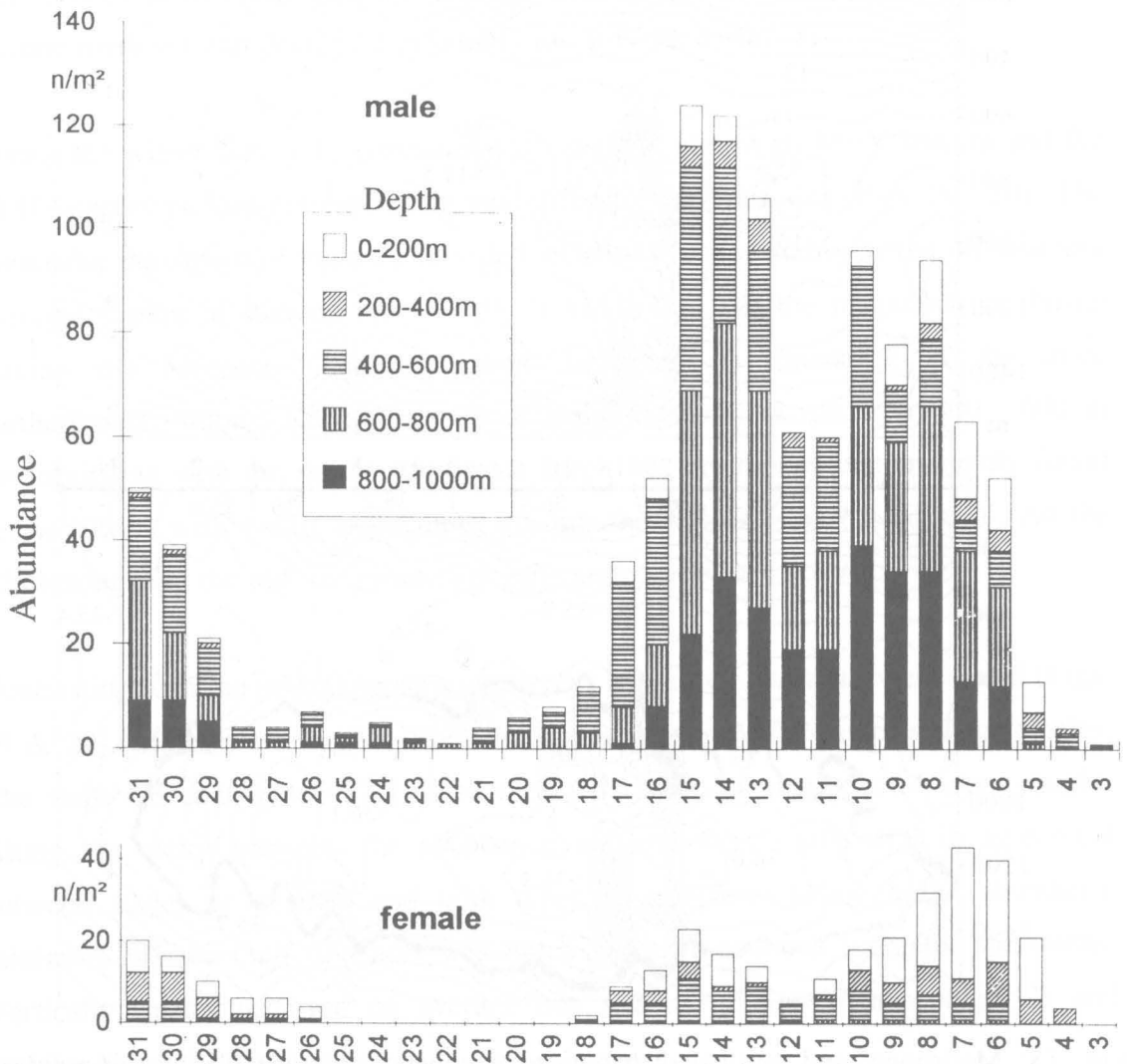


Fig. 20: Meridional and vertical distribution of adult *Calanoides carinatus* during winter 1992.



### 3.8. Seasonality of Mediterranean Outflow Water

We assume that the data base is not biased by interannual variability. Along  $16.8^{\circ}\text{W}$  during all four seasons the core of **MOW** was found at the same depth of approximately 1150 m (Fig. 21). The southward extension was less during winter compared to the other seasons. At this geographical longitude the largest vertical extension of **MOW** including highest salinities was observed during spring. The vertical extension was smallest during summer. Temperature (not illustrated) behaved conformingly with salinity for the lower boundary of **MOW**, but did not depict its upper boundary. It remains unknown if there is a seasonality in the Mediterranean outflow in the Gulf of Cadiz.

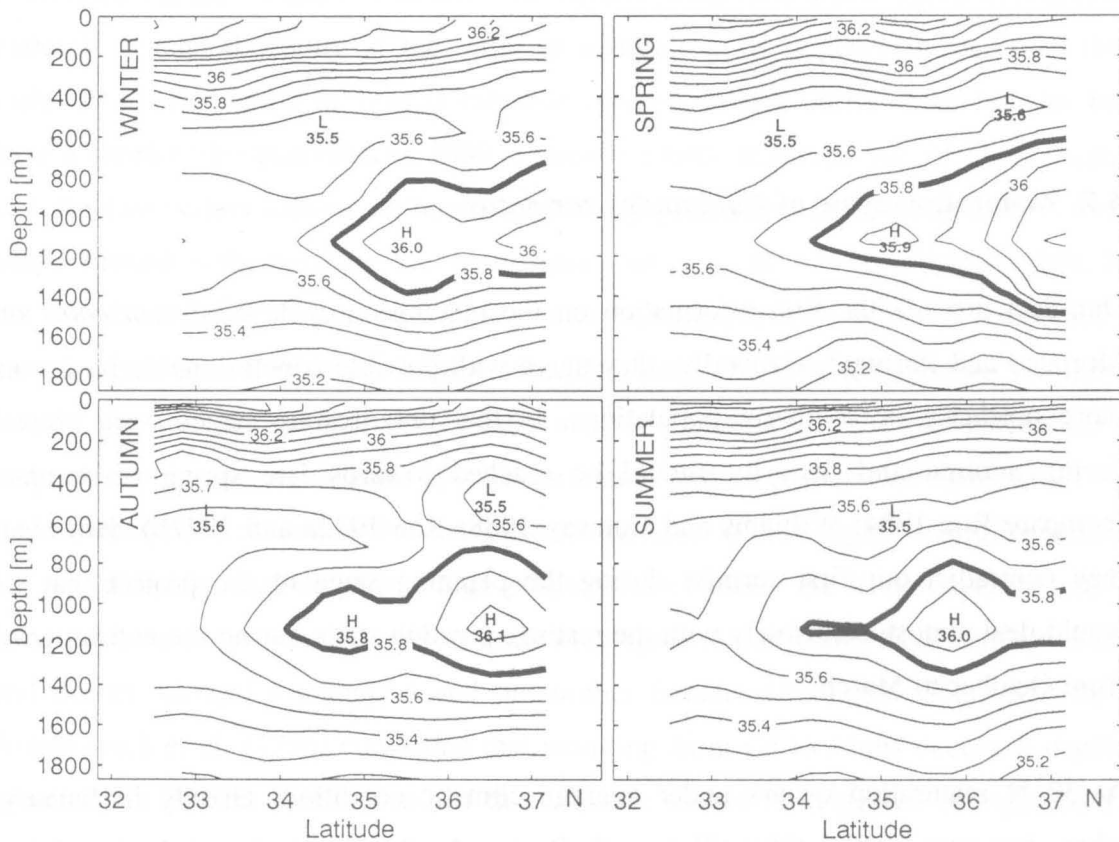


Fig. 21: The seasonal variations of the vertical and meridional extension of Mediterranean Outflow Water along  $16.8^{\circ}\text{W}$ , exemplified by the depths of the isohaline  $S = 35.8$  (enhanced). The scaling of isohalines is  $S = 0.1$ . H (high) and L (low) stand for extreme values.



## 4. Discussion

### 4.1. The intermediate salinity minimum

An intermediate salinity minimum above the **MOW** is a generally consistent feature along the Moroccan and Iberian continental slope. As laid out above (Figs 1 & 3), its water-mass composition can not be defined precisely. It has some **NACW**-affinities with admixtures of less saline water masses. Lowest salinity values and oxygen saturations for the intermediate salinity minimum were found at the southernmost stations. The isobath-parallel transects suggest a consistency of this layer northwards to at least Cape Sao Vicente during autumn and also off Portugal during spring and winter. An exception make the northernmost stations at Cape Finisterre, where the density structure as well as high oxygen saturations suggest that these stations belonged to a different hydrographical regime. We presume that the intermediate salinity layer has a southern origin and that its salinity increases towards the north by admixtures of **NACW** and **MOW**.

### 4.2. Maturation cycle of *Calanoides carinatus*

Our data provide the first information on the maturation cycle of *C. carinatus* off Morocco and Portugal. Generally, they agree with possible conclusions derived from more northerly or southerly populations, in that only resting stages were present during autumn and maturity should be reached towards late spring or summer (compare Roe 1984; Williams and Conway 1988; Roe 1972a and 1972b). However, they contradict our first surmise during the planning stage of the project that we would deal almost exclusively with the resting, preadult stage during the entire period from October to March.

At 32°N maturation occurs under average climatic conditions already in January, when, however, resting C5s still prevail. During April the majority of the population is mature. Our results further suggest that maturation off northern Morocco and Portugal started as early as January, when temperature and salinity at the surface were about 1.5°C and S=0.3 units higher than the long-term monthly mean. In contrast

with previous literature (e.g. Roe 1972b; Binet and Suisse De Sainte Claire 1975; Chagouri 1989; some but not all profiles by Petit and Courties 1976), males were in the north by far more abundant than females at the onset of maturation. At 32° N the sex ratio was about even in January, but in favour of females in spring.

It becomes evident from the literature cited above (or data for *Calanus helgolandicus* in Roe 1984) that sex ratios can only be reasonably comparable if they were determined from the entire distribution range of the population. Only Roe (1972b) and partly Petit and Courties (1976) presented data from a comparably wide depth range. Arashkevich et al. (1996) did not describe sex ratios and the other contributions focussed on surface waters only.

Considering a possible bias in our data due to not sampling the entire depth range, such bias should result in an overestimation of the proportion of the shallower distributed females (Figures 9 & 20). We therefore conclude that a high proportion of males is a general feature at the onset of maturation. It is generally accepted that males of *C. carinatus*, or related calanoid species, mature earlier than females but have a shorter life-span (Hirche 1980, Conover 1988). Reproduction of *C. carinatus* in temperate waters follows outbursts of primary production (Armstrong et al. 1991) and is limited in the north by low temperatures of some 10 - 15 °C (Hirche 1980). In our study area nutrients may be limiting during autumn, too, as light and temperature are during winter. Our winter survey coincided with a positive temperature anomaly, but the normal seasonal increase of light intensity. Particularly the thermal anomaly may have triggered ontogenetic upward migration and an outburst of maturation. As males mature earlier, and at the very onset of maturation their higher mortality should not yet have a noticeable effect, high proportions of males are to be expected. Data from the onset of maturation off Congo in May agree in that males have a much wider and deeper vertical distribution and outnumber females (Petit and Courties 1976). Arashkevich et al. (1996) concluded that moulting from C5 to adults occurs at depths greater than 300 m, that the end of the diapause should be triggered endogenously, and that the ascent to surface layers occurs by active migration instead of upwelling water.

At least along the Portuguese slope spawning had occurred as early as in March (even

under slightly cooler conditions than average), since then the juvenile stages C3 and C4 were already abundant off southern Portugal (stations I 13 - I 15). In March females were more abundant than males, as is usually the case in reproductively active calanoid copepod populations (Green et al. 1993).

#### 4.3. Vertical distribution of *C. carinatus*

Perhaps due to the rather coarse vertical resolution of the samples at hand, no diurnal variation of the depth distributions of any developmental stage became apparent.

As concluded by Roe (1972b), Petit and Courties (1976), Brenning (1981) and Arashkevich et al. (1996), the developmental stages and genders of *C. carinatus* have different depth preferences, which may also change seasonally. Most of the data presented here conform with previous results in that the resting copepodid stage C5 occurred primarily at mesopelagic depth, whilst mature *C. carinatus*, feeding C5s and the stages C3 & C4 lived in upper layers.

However, attention must be paid to some peculiarities in the vertical distributions described above. The resting stage off Morocco occurred during autumn and winter mainly at 400 - 800 m, which conforms with the literature cited above. A change occurred when in the Gulf of Cadiz and off Portugal **MOW** intruded into that depth range. Then the bulk of stage C5 shifted to below 800 m depth. The occurrences below 1050 m at 32° N also coincide with the depth range of **MOW**.

The change in the relative vertical distribution of C5 with intrusion of **MOW** was independent of its absolute abundance at the respective stations and could not be explained by any individual physical parameter alone. This contrasts with our first surmise that C5 would concentrate in the salinity minimum layer just above the **MOW**. Off Portugal resting C5s dwell in a vertical range from 400 to at least 1000 m. Their vertical range includes the upper **MOW**. The deeper occurrence within the **MOW** may be explained by the turbulent mixing revealed by the hydrographic structure at Cape Sao Vicente. The cylindrical structure in the two isobath-parallel transects is not a meddy, since a meddy is less stratified than its surroundings (Bower

et al. 1995). This structure proved to be a rise of **MOW** at the slope during transect z (Fig. 22). A very similar structure of upsloping **MOW** off Cape Sao Vicente was reported previously from different surveys (Zenk and Armi 1990, transect "S"; Daniault et al. 1994, transects "A 109" & "C"). It was also present one year after our survey in September 1992 (Käse and Zenk 1996: Fig. 12.5). This stability in time and space also suggests that this structure is a permanent front. According to Daniault et al. (1994) mixing and thus salinity variance is at maximum near Cape Sao Vicente.

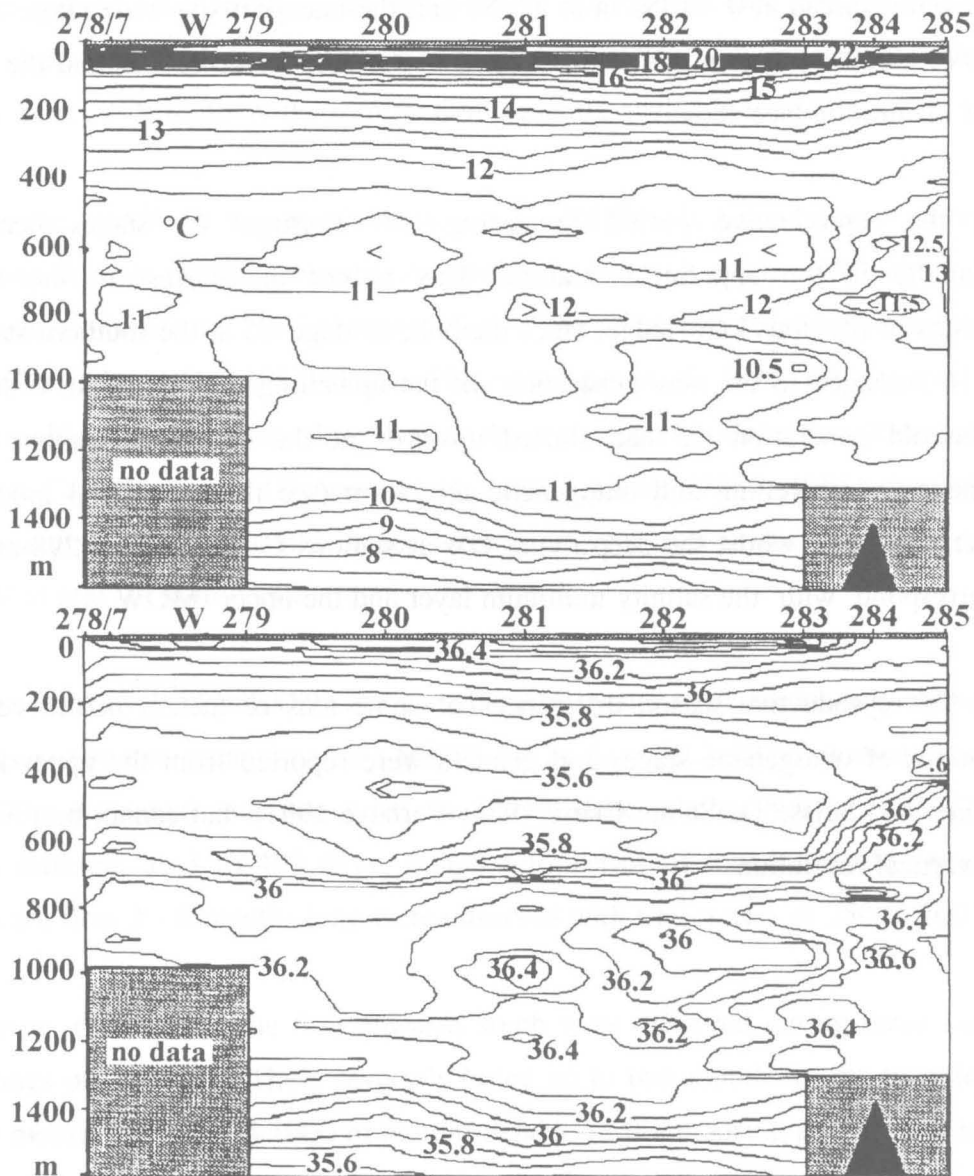


Fig. 22: The vertical distribution of temperature (top) and salinity (bottom) along the z-transect in September 1991. Otherwise as for Fig. 7.

It has been pointed out by Roe (1972b) that the few quantitative studies at hand are unable to show what happens below 1000 m depth. It cannot be ruled out that the actual centre of distribution of resting C5 during autumn and winter was below the depth range sampled, as might be suggested by the C5-mode below 1800 m depth in the Bay of Biscay reported by Farran (1926). Baars et al. (1994) reported that in the Indian Ocean C5s were abundant also in the deepest stratum sampled (1000 - 1500 m).

The deep to medium depth distribution of males (bulk generally at 400 - 800 m, or almost evenly spread at 0 - 1050 m at 32°N) and the unexpectedly wide range of the females (0 - 600 m) during winter are related to the deep mode of C5s and the early onset of maturation (see above).

During the reproductive period in spring, off Portugal all stages occurred preferentially in the uppermost stratum. This is not in contrast to the above conclusions or previous knowledge, since the bulk of stage C5 at the southern stations I 12 - 16 belonged to the new generation. In the upwelling regime of the C-survey even the old generation C5 had shifted upwards at the shallower stations as a consequence of upwelling and ontogenetic migration (see the conceptual model in Postel et al. 1993), whilst the deep living C5s at stations C 8, C 10, M 298 and M 299 correspond with the salinity minimum layer and the upper **MOW**.

During the reproductive season differences of some tens of meters in the vertical distributions of ontogenetic stages and genders were reported from the upper layers (e.g. Binet and Suisse De Sainte Claire 1975; Verheye 1991), but cannot be revealed by our vertical resolution.

#### 4.4. Northward transport

##### 4.4.1. The present knowledge of poleward along-slope currents

Barton (1989) summarised the existing information from a large number of individual current meter deployments along the NW-African and Iberian continental slope, reaching from the Gulf of Guinea to NW Spain. Meanwhile some additional data became available from the west coast of the Iberian Peninsula (Ambar 1984, 1985; Ambar and Fiuza 1994; Daniault et al. 1994; Hagen et al. 1993; Haynes and Barton 1990) and northern Morocco (Hagen et al. 1994). Float experiments have been carried out for the **MOW**-layer off western Iberia, but not yet for the salinity minimum layer (Zenk et al. 1992; Käse and Zenk 1996). Nevertheless, for the slope realm from 27° N to 36° N the information presently available is still scant.

Within the **MOW** off western Portugal a poleward flow is a prevailing feature, but it does not show a constant velocity. According to Daniault et al. (1994) the velocities are highest in a narrow band along the slope. The respective mean velocities were 3 - 11 cm/s (Ambar 1984, 1985; Barton 1989; Daniault et al. 1994; Hagen et al. 1994). Geostrophic core velocities decreased from >10 cm/s at Cape Sao Vicente to >5 cm/s at Cape Finisterre (Daniault et al. 1994). Ambar (1984, 1985) showed that a southward surface flow could induce a temporary reversal in the uppermost layer of **MOW** at 600 - 770 m depth.

As reviewed by Barton (1989) and corroborated by the more recent data above cited, a poleward undercurrent above the **MOW** can be found at least temporarily in all data sets. The individual time series for the intermediate depths, however, have durations as different as 3 to 405 days. In the time series of longer duration periods of poleward flow 2 - 8 months long were observed with trajectories of 250 to 700 km.

However, reversals of the flow towards south were observed during three long-term moorings off Portugal. These reversals lasted up to two months in the two shallower slope moorings (910 and 1000 m bottom depth). In the mooring above 2000 m depth reversals lasted at maximum one month. Directional shifts occurred at the end of the year and mid spring. Southward trajectories decreased with depth (Fig. 23). It remains unknown, whether these reversals comprised the entire current regime, or if

they were a local effect caused by an offshore detachment of an actually persisting poleward undercurrent.

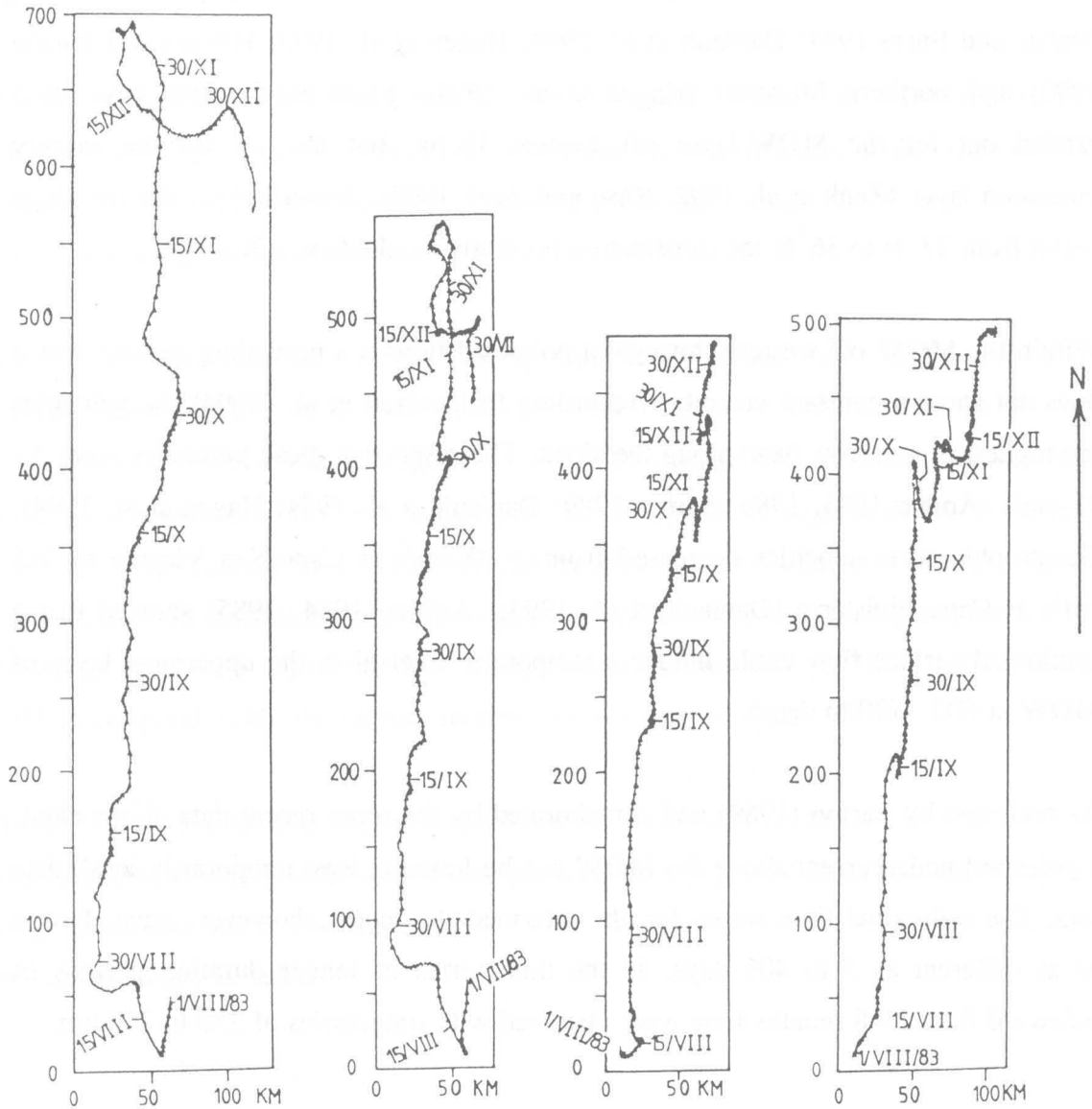


Fig. 23: Progressive vector diagrams showing the poleward flow off central Portugal above bottom depth of 910 m from 30 July 1983 to 14 January 1984. Diagrams from left to right stand for the mooring depths 220, 370, 610 and 770 m. Combined from Ambar (1985: Figs 24 - 27).



Where any generalisation to "mean currents" has been attempted in the literature (see the references in Barton 1989), undercurrent core velocities have been cited to be 8 - 25 cm/s off Mauritania and  $>10$  cm/s at about  $22^{\circ}$  N. Off Portugal, at  $40^{\circ}$  N and at the depth range 200 - 750 m, a "mean northward flow in excess of 3 cm/s" was cited.

More recent longer time series off Morocco and Portugal yielded mean along-slope velocities of 3 - 4 cm/s at  $34^{\circ}$  N and  $40^{\circ}$  N and 2 cm/s off Cape Finisterre within the intermediate salinity minimum (Hagen et al. 1994). However, the corresponding modes of velocities were in the class 6 - 12 cm/s in these data (with 46 - 80 % of the observations). The actual short-term current events off northern Portugal may exceed velocities of 20 cm/s (Ambar and Fiuza 1994; Haynes and Barton 1990).

Shorter time series yielded a mean of 6 cm/s in the undercurrent off Cape Sao Vicente (Hagen et al. 1994, 52 days), and 4 cm/s at transect M in April (Mittelstaedt 1989, 3 days).

Besides the variability of current-velocity the depth range of the undercurrent varies with latitude and with season. The seasonal variation follows changes in the meridional baroclinic pressure gradient, which is forced by wind-stress (Isemer and Hasse 1987). Wind-stress is generally southwards during spring and summer, and polewards during autumn and winter (Frouin et al. 1990). For the area in question, heat-flux probably contributes less to the intermediate undercurrent than to the flow of **MOW**.

The cross-slope extension of the undercurrent is believed to be less than 100 km (Barton 1989). Theoretical considerations (Emery et al. 1984) suggest that it is likely not much larger than 50 km, corresponding to the Rossby radius. This is corroborated by reversed flow at mooring positions slightly farther offshore and inshore (Hagen et al. 1994) as well as by the geostrophic sections figured by Daniault et al. (1994). The intrusion of **MOW** in the north probably causes further cross-slope and vertical variability. Thus it is difficult to compose individual mean values to any "average current velocity".



#### 4.4.2. The drift of resting copepodids C5

Off Morocco, our data do not allow any estimate where these resting copepodids actually had originated and how fast they had travelled. Their nutritional condition and pigmentation during autumn suggest that they had stopped feeding recently, whilst during winter their condition was worse. Resting C5s are also produced during upwelling and not only at the end of the upwelling season (Arashkevich et al. 1996). Off Morocco upwelling generally occurs south of 33° N and decreases in October, but may occur also in winter sporadically (Wooster et al. 1976). Copepodids C5, when occurring in large numbers, might have originated from anywhere farther south until 20° N, where upwelling is prolonged or perennial. Less abundant C5s might have come even from the very same area they had been caught, as they might have been recirculated by the opposing flows of the surface and undercurrent layers (Binet 1991), or they might have originated from one of the sporadic upwelling events closer by.

Although we cannot resolve the biological time scales off Morocco, the plankton data prove that the resting stage drifts northwards within the intermediate salinity minimum layer, at least during autumn and winter. The plankton data are corroborated by the synoptic current meter data (Hagen et al. 1994) as well as by the thermohaline properties during earlier CTD-surveys and a short-term mooring from spring 1983 at the M-survey (Mittelstaedt 1989, and literature therein). In combination, they allow the conclusion that the poleward transport of southern, intermediate water mixed between remainders of **SACW** and/or **AAIW** with **NACW** occurs in the 400 - 800 m layer off northern Morocco over most of the year and that it extends beyond the upwelling regime.

As summarized above, the along-slope currents in the off Portugal increasingly deep depth range of resting C5s flow polewards. Frouin et al. (1990) and Haynes and Barton (1990) concluded that during autumn and winter poleward flow above the slope is not only a general feature, but that it may include surface waters. This assumption is supported by the positive anomalies of surface temperature and salinity in our winter data. It is therefore likely that the winter population of *C. carinatus* was advected from the south.

The population structure and numerical abundance of *C. carinatus* during winter off Portugal suggest that this population might be the very same as encountered off Morocco 3 months before. The seven autumn-stations I 33 - 27 yielded a mode of abundance, composed of exclusively C5s with a total of 8047. The corresponding seven modal stations during winter (I 9 - 15) yielded 4555 C5s plus 647 males and 109 females, a total of 5311 individuals. In the meantime the autumn population has partly matured and diminished by 33 % by mortality and dilution. Males and particularly females ascended to shallower layers.

If we take for granted that the mode off Morocco during autumn and the mode off Portugal during spring represent the same population, the average net poleward velocity would have been at most 10.7 cm/s. This is a maximum estimate, because the actual northern slope of the mode during autumn was located with some likelihood northwestwards of the transect and therefore somewhat closer to the location of the mode during winter (see discussion below). Nevertheless, this current-speed estimate is of the same order of magnitude as the results of the direct current measurements summarized above.

#### 4.4.3. Time-variability of Mediterranean Outflow Water and cross-slope structures

From the autumn data alone, it might falsely be presumed that the poleward transport ceases off the Gulf of Cadiz with the intrusion of the **MOW**. However, we believe that our autumn survey did not actually cover the undercurrent regime and, consequently, not the core of the population either. Across the Gulf of Cadiz strong westward geostrophic transports of 5 respectively 8 Sverdrup (SV, 1 SV =  $10^6 \text{m}^3/\text{s}$ ) were calculated for the depth range of resting C5s before and during our autumn survey. In autumn 1992 also 5 Sv were estimated (Hagen et al. 1994: Figs. 4.6 and 4.9a). The **MOW** had an upper boundary as shallow as 500 m (station I 17), or 440 m in September 1991. During the winter survey, a reduced geostrophic transport of only 2 Sv (Hagen et al. 1994: Fig. 4.9b), a deeper lying upper boundary of **MOW**, and a continuous meridional belt of copepodids C5 of *C. carinatus* contrasted with the

autumn situation. Figure 21 presents evidence for seasonal variation of the upper boundary of the **MOW** along 17 °W. Whilst the core of **MOW** remained at constant depth, the upper boundary had its shallowest position at 600 m during spring at this geographical longitude. Comparable data for the area of our I-transect are lacking. Since an even shallower upper boundary of **MOW** off Cape Sao Vicente was found during at least three autumn surveys, we presume that the flow across the isobath-parallel transect was strongest during autumn. It had shifted the undercurrent in the Gulf of Cadiz westwards to an unknown extent at the time of our autumn survey.

In spite of the lack of synoptic cross-slope transect data in the Gulf of Cadiz we can present some indirect evidence to support our above conclusion. The lack of mature *C. carinatus* almost everywhere during autumn renders unlikely that the abundant winter population in the Gulf of Cadiz and off Portugal results from recent reproduction off Portugal. No early stages <C5 were encountered during the winter survey either. The pseudo-oceanic distribution pattern of the species mentioned in the introduction is confirmed by its absence in the adjacent open ocean during autumn 1984 as well as by its paucity only some 120 miles farther west of our transect (Roe 1984, data from April 1974). This makes it unlikely that the winter population originated from the deeper open ocean.

Further support is provided by the above mentioned five non-synoptic hydrographical cross-slope transects off Cape Sao Vicente. They all show an upsloping structure of Mediterranean Water across the positions of our transect, which is similar to the cylindrical structure observed during our biological autumn survey. That structure has shifted at least in all cross-slope data sets the poleward flow of less saline water some 25 km westward of our I-stations. Some offshore detachment of the intermediate salinity minimum is also found in the two northern sections illustrated by Danialt et al. (1994). It is apparently a seasonally and interannually consistent feature.

#### 4.4.4. A conforming distributional pattern of a tropical deep-sea fish

Williams and Conway (1988) have shown that *C. carinatus* is distributed consistently also across the Bay of Biscay and reproduces during summer southwest of the British Isles. For the area in question, the rare adult stray individuals of the deep-mesopelagic to bathypelagic fish species *Cyclothone livida* reveal a horizontal distribution very similar to that shown for *C. carinatus* (Badcock 1984). *Cyclothone livida* is a species endemic to the tropical East Atlantic and it is sluggish (as are all cyclothones). We therefore conclude that this species was expatriated by the slope undercurrent from the tropical NE Atlantic towards the British Isles, too.

## 5. Conclusions

The information obtained from the combined biological, temperature/salinity and mooring data confirms the hypothesis that the transport of resting *C. carinatus* along the western Iberian continental slope is generally polewards. The meridional consistencies of the hydrographical structure with the population structure as well as the temporal consistency of the current-meter data make it unlikely that the transport was mainly due to an eddy translation.

Contrary to the flow along the Moroccan continental slope, this poleward transport off Portugal is not restricted to the salinity minimum layer (off Portugal narrow at 400 - 600 m depth), but includes also the upper Mediterranean Outflow Water down to at least 1000 m. The spreading of **MOW** westwards caused losses of *C. carinatus* towards the open ocean (Fig. 24). However, the cross-slope data from northern Portugal suggest that the salinity minimum layer provides the main source water for the transport of the overwintering population of *C. carinatus*. This same water also feeds the Portuguese upwelling (John and Ré 1995) and transports the species into the productive layer, unless the ascent is an active migration.

The resting stage of *C. carinatus* occurred all along the Moroccan and European continental slope. The occurrences comprised both areas of permanent non-upwelling

as well as non-upwelling conditions in upwelling areas. We therefore consider it likely that the undercurrent regime at least seasonally interconnects the NE-Atlantic upwelling areas. It carries subsequent resting generations of *C. carinatus* from tropical/subtropical latitudes polewards along the Moroccan-Iberian slope from southern upwelling regimes to the adjacent northern ones (Fig. 24). The current system probably extends beyond Cape Finisterre towards the northernmost reproductive range of *C. carinatus* at the British continental slope, as does the **MOW**. The location of this flow across the Bay of Biscay, however, needs further study. Such studies should make use of floats additional to the methods described.

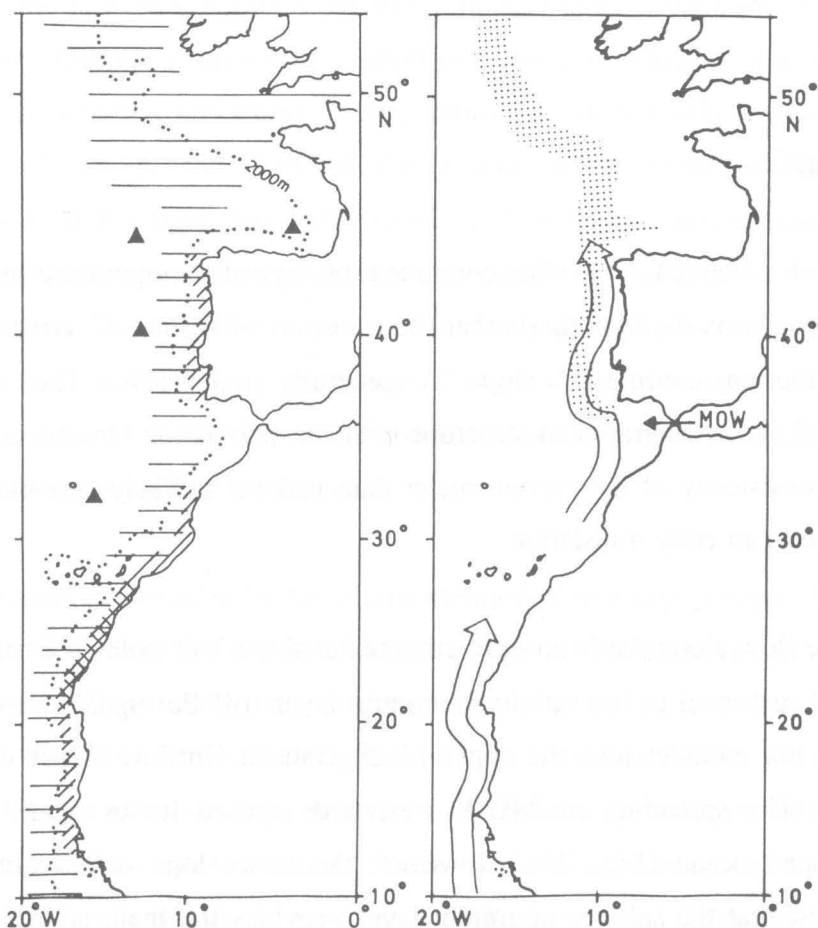


Fig. 24: The distribution and northward transport of *Calanoides carinatus* along the NW African and European continental slope. Left: The distribution of reproductive populations (horizontal hatching) and single records (solid triangles) of *C. carinatus* (after Williams and Conway 1988; Chagouri 1989; and own data). Diagonal hatching indicates seasonal coastal upwelling, diagonal cross-hatching permanent upwelling. Right: The drift of resting stage C5 of *C. carinatus* within the intermediate undercurrent (light arrows) and its entrainment within a part of the northward flow of underlying Mediterranean Outflow Water (**MOW**, shading).

## 6. Abstract

The poleward undercurrents of Eastern Boundary Current upwelling systems in the NE-Atlantic are presumed here to be interconnected, to coincide with the intermediate salinity minimum layer and to provide a faunistic link between and beyond the NE-Atlantic upwelling areas. This hypothesis was tested by multidisciplinary surveys (3 seasons, 6 cruises) along the Iberian and Moroccan slope by long-term current meter moorings, CTD casts and biological sampling.

The biological tracer chosen was the preadult resting stage (copepodid C5) of *Calanoides carinatus*, a copepod species abundant in the tropical African coastal upwelling areas. This stage, resting generally at subsurface depth, drifts northwards along the Moroccan slope. It concentrates off Morocco within the intermediate salinity minimum located above the Mediterranean Water and between 400 and 800 m depth. Off the Iberian peninsula the salinity minimum layer is narrower at approximately 400 - 600 m depth. Resting C5s occur in this salinity minimum layer as well as below it.

It is concluded that summer stocks of *C. carinatus* reported from southwest of the British Isles are maintained by resting C5s originating from upwelling regimes in the south. They are transported by the poleward undercurrent, which can be traced from tropical latitudes all along the continental slope to at least NW-Spain and perhaps the British Isles. The undercurrent crosses the Mediterranean Outflow off the Gulf of Cadiz. Off Portugal the poleward flow of Mediterranean Water contributes to the poleward transport of *C. carinatus*, too.

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