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Rostock zooplankton studies off West Africa

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ABSTRACT: Since the beginning of the 'seventies, upwelling research has become increasingly popular in the path of the Canary and Benguela Current, because of economic consideration, particularly in relation to fisheries and marine geology. Many expeditions were carried out between 1970 and 1977, including 8 cruises of the German R.V. "A. v. Humboldt" operating from Rostock. Measurements covered scales ranging in time from minutes to several years and in space from hundreds of metres to several thousands of kilometres. Zooplankton studies focussed on quantitative, metabolic, taxonomic, and parasitological aspects. Plankton was collected with a WP-2-UNESCO standard net to a maximum depth of 200 m. The epipelagic mesozooplankton consists mainly of copepods, especially calanoids with developmental times of about 20 to 23 days. After an upwelling event, zooplankton is able to double its biomass. This typical biomass increase is independent of coastal distance and depth. The upwelling response lasts about 3 weeks in near-surface waters, and 6 to 8 weeks in depths below 75 m. A relationship was observed between the duration of seasonal upwelling (that means the numbers of single upwelling events) and the cumulative increase of biomass. This net growth rate of zooplankton biomass is most pronounced at the shelf break, the area with the highest fish biomass, and in the upper 25 m. Differences between the expected and the real rate values in conjunction with the known amount of nutritive demands of fishes allow the estimation of the fish biomass in a given area. The near coastal Ekman upwelling, which is an event in the time scale of about two weeks, also shows seasonality in some areas. Off Northwest Africa the largest expansion was recorded in the first half of the year, extending from 10° N to 24° N, more than 400 km offshore and at least down to 200 m. It contracts in the second half of the year to an area between 20° N and 22° N, 100 to 200 km off the coast and in an average depth of 25 m. These zooplankton biomass patterns are superimposed by mesoscale phenomena, originated by other than Ekman upwelling events. Those are, for example, long coastal parallel waves, producing cells of intensified upwelling and downwelling, and eddies, caused by instabilities in a frontal zone parallel to the coast. Different water masses can be distinguished by indicator species, species combinations or the significant absence of species. This was demonstrated for chaetognaths. The calanoid *Calanus helgolandicus* (Claus, 1863), a typical species of the North Atlantic, indicates North Atlantic Central Water, whereas *Calanoides carinatus* (Krøyer,1849) is an indicator of South Atlantic Central Water. Finally, comparisons of near coastal current regimes, transport velocities, and developmental rates of calanoids allow one to conclude that a suitable mechanism is present to maintain plankton in the coastal environment.

INTRODUCTION

Economic reasons, relating particularly to fisheries and marine geology, encouraged upwelling research in the Canary and Benguela Current from the beginning of the 'seventies. At least during the CINECA programme (Cooperative Investigation of the Northern Part of the Eastern Central Atlantic), which was carried out under the umbrella of ICES, 14 countries participated in about 100 expeditions between 1970 and 1977 (Smed, 1982). This included 8 cruises of the German R. V. "A. v. Humboldt" operating from Rostock. These studies of the Warnemünde Institute of Marine Research and Rostock University have been sporadically continued up to now and extended into Namibian waters and the central part of the Atlantic. Measurements covered time scales ranging from minutes to several years and horizontal space scales from hundreds of metres to several thousands of kilometres. This research included studies in physical, chemical, and biological oceanography. Zooplankton studies focussed on the following:

Quantitative aspects

– 2-D seasonal patterns	Arndt & Brenning, 1977
– continental shelf wave patterns	Postel, 1982
– patterns influenced by submarine cañons	Postel, 1987
– conditions of boundary (upwelling) area versus that of central gyre area	Kaiser & Postel, 1978
– extension of upwelling effects	Postel, 1985
– effect of an average upwelling event,	
– 3-D seasonal patterns and	
– net growth rates	Postel, 1990
– links to fishery	Weiß & Postel, 1991

Metabolic aspects

– feeding activity of *Branchiostoma senegalense*	Gosselck et al., 1978
– growth of *Branchiostoma senegalense*	Gosselck & Spittler, 1979
– metabolic activity in relation to ROSSBY wave patterns and cyanobacteria distribution	Hernández-León et al., 1992

Taxonomic and ecological aspects

– chaetognaths	Köller et al., 1976 Arndt & Köller, 1977
– thaliaceans	Arndt & Wranik, 1977 Wranik & Arndt, 1978
– calanoids	Brenning & Fadschild, 1979 Brenning, 1980, 1981a, b, 1982a, b, 1983, 1984, 1985a, b, 1986 Chagouri, 1989
– *Branchiostoma* larvae	Gosselck, 1975 Gosselck & Kühner, 1973 Gosselck & Hagen, 1973 Flood et al., 1978, 1982

Parasitological aspects

Reimer et al., 1975
Reimer, 1977

The two aims of this paper are to draw attention to these unique data sets and to arouse interest in such areas again, where ecosystem development can be observed from an early to an equilibrium stage with all the ecological consequences over relatively short distances.

MATERIAL AND METHODS

In the 'seventies, large scale observations were carried out in the upwelling area off the coast of Northwest Africa (NWA), between Bahía de Garnet (25° N) and Cabo Roxo (10° N), from the near coastal area to the 21° W meridian. Further studies were performed on a section along the 30° W meridian, from 2° S to 15° N, a reference area in comparison to the coastal zone without Ekman upwelling and with ecological equilibrium conditions (Fig. 1). In 1989 an area was investigated between 32° N and 10° N, from the Middle Atlantic Ridge to about 21° W, to study the transition between the boundary part of the North Atlantic Central Gyre, which is influenced by coastal upwelling, and its centre. Mesoscale upwelling processes were studied, mostly off Cape Blanc/Cape Barbas, off Nouakchott (NWA) and off Southwest Africa (SWA) at 21° S, in the Namibian region (Fig. 1). A limited number of small scale studies were carried out off Cape Blanc (NWA).

Samples were collected, mostly in four depth ranges, from 200 to 0 m, from 200 to

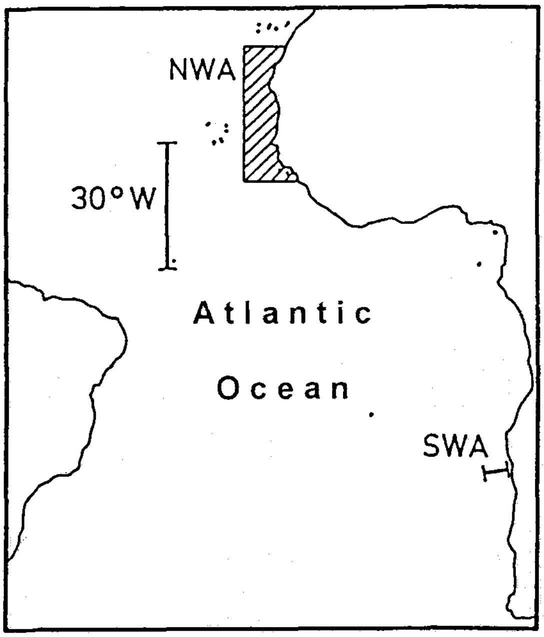


Fig. 1. Areas studied by R. V. "A. v. Humboldt" in the Atlantic Ocean: a large, seasonal study site off Northwest Africa (NWA), a reference area at 30° W without Ekman upwelling, and a mesocale transect off Namibia (SWA)

75 m; from 75 to 25 m; and from 25 to the sea surface, using the WP-2-net, which is recommended by UNESCO (Tranter, 1968). According to this author, this equipment quantitatively retains plankton between 0.2 to 10 mm size.

On the basis of various literature sources and data, it was estimated by Postel (1990) that plankton of this size range represents (in terms of dry mass) about one third of the total plankton in the euphotic zone of an upwelling area. This part consists of almost similar proportions of fine filter feeders (like meroplankton, appendicularians, doliolids, and small calanoids), of coarse filter feeders (e.g. medium-sized calanoids, and juvenile euphausids), and of predators (like cyclopoids, large calanoids, coelenterates, and polychaetes). Their developmental times range from 25 to 40 days. This plankton fraction is of nutritive relevance for fishes of commercial value, like *Scomber colias* (70 %), *Trachurus* sp. (60 %) and *Sardinella* sp. (50 %).

Dry mass was determined according to Lovegrove (1966). During different cruises, slight modifications in the field and in the laboratory procedures occurred, which sometimes caused remarkable influence on the data. The sum of methodical errors produced underestimations of 15 to 65 %, which were considered during a data validation procedure. The largest overestimation was represented by 21 % from using wire length instead of flow meters to calculate the filtrated water volume. Losses of about 48 % occurred when samples were frozen before oven drying (Postel, 1990).

For details of the taxonomic identification procedures, the reader is referred to the publications mentioned above under taxonomical and ecological aspects.

RESULTS AND DISCUSSION

Ecological consequences of an average coastal upwelling event

The results originate from a programme off Namibia which lasted three weeks during the upwelling season in October 1979. It consisted of a transect, perpendicular to the coast, from 30 km to 170 km. The distance between the stations was 10 km, the measurements were carried out every 1.5 days. Figure 2 presents the geographical situation (2a), and the successive progress of ecosystem development from the near shore upwelling centre to offshore conditions (2b to 2m) in terms of averages of 15 measurements. The diagrams should be studied from the right, the African coast line, to the left.

The sea level increases, indicating that winds favourable for upwelling shift the near shore surface water in an offshore direction (2b). Cold, low saline, oxygen poor, and nutrient rich water from deeper layers replaces it (2c to 2g). With increasing distance to the upwelling centre, temperature rises by solar radiation and the salinity increases by evaporation. Oxygen content starts to increase and successively to decrease due to changing importance of the balance between primary production and respiration losses. Nutrients are affected in the same manner. Chlorophyll-*a* content as indicator for phytoplankton biomass reaches a maximum at about 30 km down stream of the upwelling site (2h). With increasing distance to the shore the ecosystem is increasingly stabilized. The decreasing dominance index in conjunction with the increasing diversity index is an indication of this phenomenon (2l; 2m) in the same way as the number of zooplankton groups, which increases from 16 at 30 km to 25 at 170 km offshore. The development of the mean abundances in the dominant taxonomic groups underline this ecosystem zonation: the optimum of nauplia is followed by the small and by the medium sized calanoids farther offshore, and is finally followed by the thaliaceans, a group which is dominant far away from the upwelling centre (2k). The zooplankton dry mass pattern in two depth levels on transects perpendicular to the coast (2i; 2j) corresponds with the calanoid abundances in Figure 2k. The highest values of biomass and abundances were encountered between 130 and 160 km offshore.

Offshore transport velocity was estimated in three different ways in the upper 60 m (Ekman layer), based on wind drift, current measurements, and the calculated development rates of copepods, which are temperature related. The results showed that a distance of ten kilometres was covered within two days. All these data led to the conclusion, that the maximum of phytoplankton biomass occurred in about two days, and that of copepods between 20 and 23 days after an upwelling event.

The doubling of zooplankton biomass after a single mean upwelling event is remarkable. This can also be observed in the following example, where a measuring approach was used, which was designed very differently.

Seasonal patterns

Seven cruises were carried out during different seasons off NWA between 25° N and 10° N on 7 transects which were perpendicular to the coast up to about 21° W (Fig. 3);

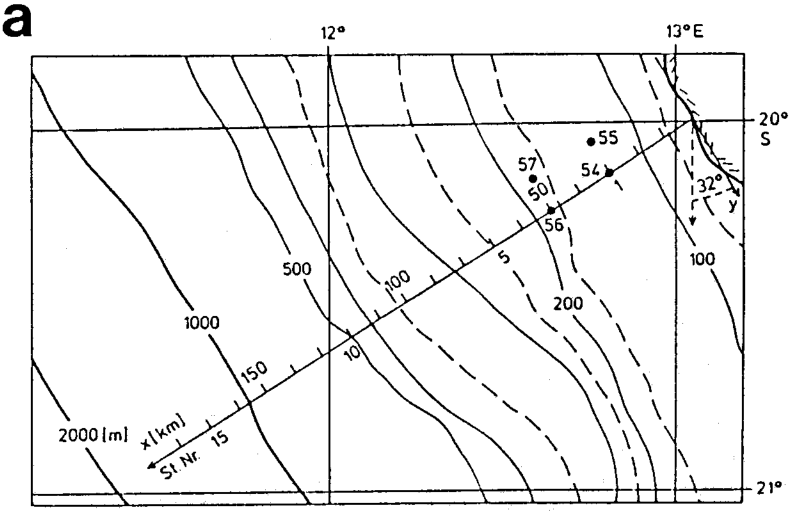
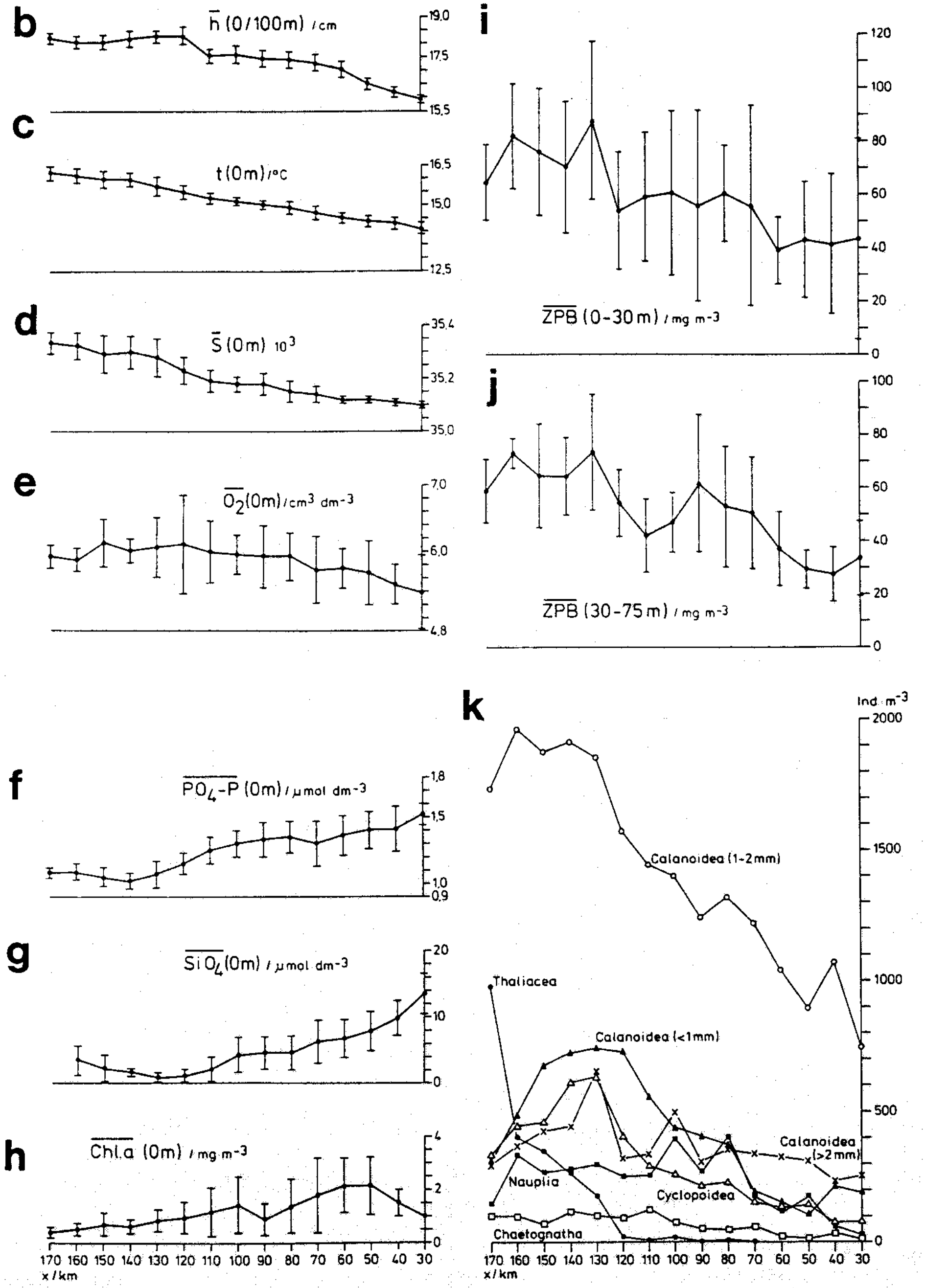


Fig. 2. Position of the cross-shelf measuring profile, which was repeated every 36 hours from October 16th to November 11th 1979 off Dune Point, Namibia (2a), and the temporal averaged cross-shore distribution (including confidence ranges, $p < 0.05$) of the sea level difference between the sea surface and the 100 m reference plane (2b), the temperature (2c) and salinity (2d), the oxygen- (2e), phosphate- (2f), silicate- (2g), and chlorophyll-a-concentration (2h) at the sea surface, the zooplankton dry mass in the upper 30 m (2i), the zooplankton dry mass between 30 and 75 m depth (2j), the zooplankton abundance (2k), the dominance index, according to Simpson (1949), cited by Odum (1980) (2l), and diversity index, according to Shannon & Weaver (1949), cited by Odum (1980), for meso-zooplankton in the upper 30 m, (2m); (Hagen et al., 1981; Postel, 1990)


b
$\bar{h}$ (0/100m) / cm
19,0
17,5
15,5
c
t (0m) / °C
16,5
15,0
12,5
d
$\bar{S}$ (0m) 10^3
35,4
35,2
35,0
e
$\overline{O_2}$(0m) / cm³ dm⁻³
7,0
6,0
4,8
f
$\overline{PO_4\text{-}P}$ (0m) / µmol dm⁻³
1,8
1,5
1,0
0,9
g
$\overline{SiO_4}$(0m) / µmol dm⁻³
20
10
0
h
$\overline{Chl.a}$ (0m) / mg m⁻³
4
2
0
170 160 150 140 130 120 110 100 90 80 70 60 50 40 30
x / km
i
$\overline{ZPB}$ (0-30 m) / mg m⁻³
120
100
80
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40
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0
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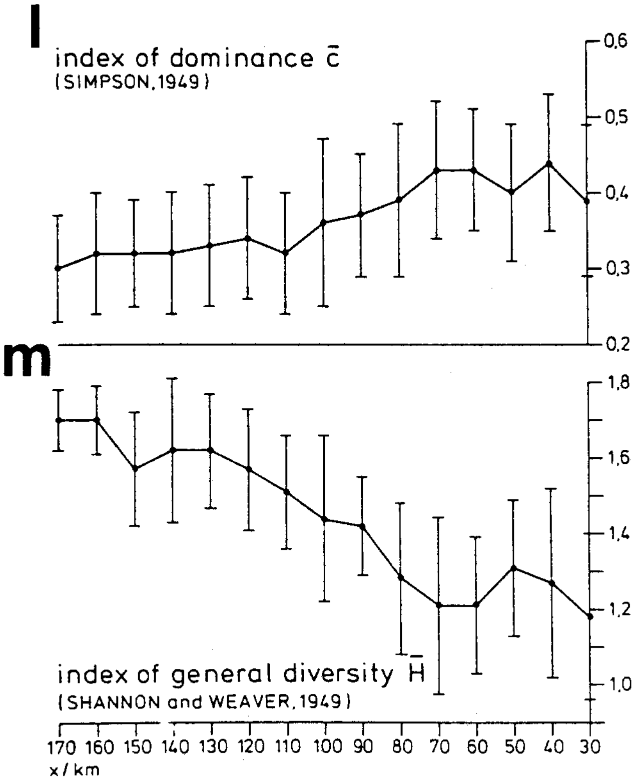
$\overline{ZPB}$ (30-75 m) / mg m⁻³
100
80
60
40
20
0
k
Ind m⁻³
2000
1500
1000
500
0
Calanoidea (1-2mm)
Thaliacea
Calanoidea (<1mm)
Calanoidea (>2 mm)
Nauplia
Cyclopoidea
Chaetognatha
170 160 150 140 130 120 110 100 90 80 70 60 50 40 30
x / km



observations were done in different years of similar upwelling intensities (Arfi, 1985). The amount of data was sufficient to carry out the seasonal analysis on the basis of mean values obtained over the shelf, the shelf break, and the offshore area, from the sea surface down to the bottom or to a maximum depth of 200 m. In the latter region, vertical subdivisions into the upper 25 m layer, the intermediate one down to 75 m, and a sublayer from 75 to 200 m, were possible (Postel, 1990).

To find the typical zooplankton biomass response to upwelling, the seasonal course of the sea surface temperature difference between near coastal stations and the offshore area, calculated by Speth et al. (1978), was compared with the zooplankton pattern. The situation off the shelf break in the upper 200 m is shown as an example in Figure 4. Coincidence of physical and zooplankton patterns was observed south of 23° N. Around 20° N, upwelling and a correspondent higher biomass is pronounced all the year round. South of it, a negative deviation of sea surface temperature and a higher zooplankton biomass are recorded during the first half of the year. A similar relationship, but with opposite sign, also holds for the second half of the year. In the offshore region, north of 23° N, upwelling was not reflected in the changes of zooplankton biomass, because nutrient poor North Atlantic Central Water (NACW) prevails in the upwelling source water, instead of the nutrient rich South Atlantic Central Water (SACW).

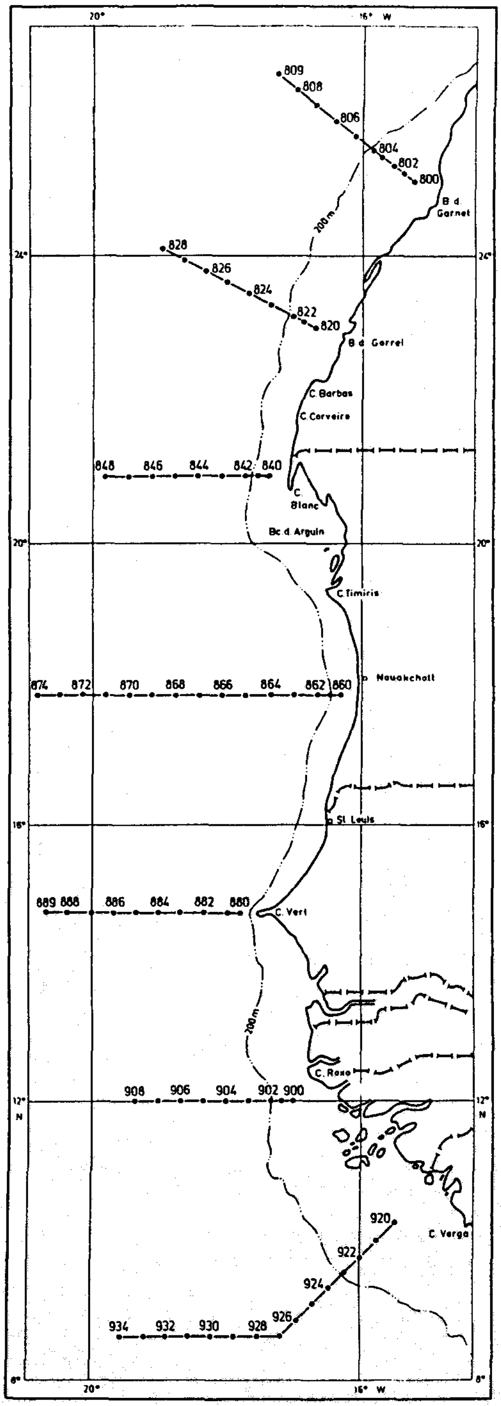
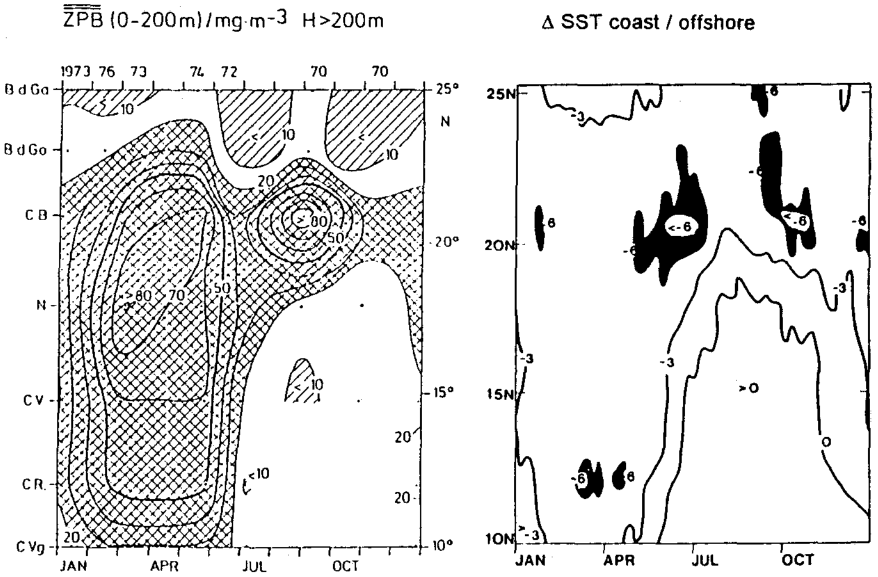


Fig. 3. Standard profiles off Northwest Africa, where zooplankton was sampled in August/September 1970, October/November 1970, June/July 1972, December 1972/January 1973, February/March 1973, May 1975, and partly in February 1976



$\overline{\overline{ZPB}}$ (0-200m)/mg·m^{-3} H>200m

Δ SST coast / offshore

Fig. 4. Mean zooplankton biomass density in the 200 m surface layer of the oceanic region off Northwest Africa (water depth > 200 m, longitude < 20° W) as a function of latitude and season, in comparison with the seasonal variation in the difference of sea surface temperature of the same latitude (Δ SST/K) between the central Atlantic and coastal regions, averaged between 1969 and 1976 (after Speth et al., 1978)

The zooplankton dry mass pattern in Figure 4, which corresponds with the upwelling indicated by the pattern of temperature differences at the surface, is bounded by the 20 mg · m^{-3} isoline. The mean dry mass in the upper 200 m of the reference area at 30° W (Fig. 1), which is free of upwelling, is 10 mg · m^{-3}. The comparison shows that the doubling of biomass is the typical response to a single upwelling event. This is in accordance with the observation off Namibia (see above). The same holds true for the different strata – above 25 m, between 25 and 75 m and from 75 to 200 m. The seasonal signal is strongest offshore.

In addition to the developmental time of the mesozooplankton, which lasts 20 to 23 days in the upper 75 m after an upwelling event off Namibia, an upwelling response of 6 to 8 weeks is observed in depths greater than 75 m off NWA (Postel, 1990).

A significant relationship was observed between the duration of seasonal upwelling (that means the numbers of single upwelling events with typical time scales of about two weeks) and the cumulative increase of biomass in the near coastal area, the shelf break and the offshore region (Fig. 5). This relationship reflects the net growth rate of zooplankton biomass, which is most pronounced at the shelf break (Fig. 5b), the area with the largest fish biomass, and in the upper 25 m (Fig. 5a), according to Postel (1990). Differences of the expected and the real rate values in conjunction with the known amount of nutritive demands of fishes allow the estimation of the fish biomass in a given area (Weiß & Postel, 1991).

When the typical "response" biomass of the upper 25 m is taken as the basis, the

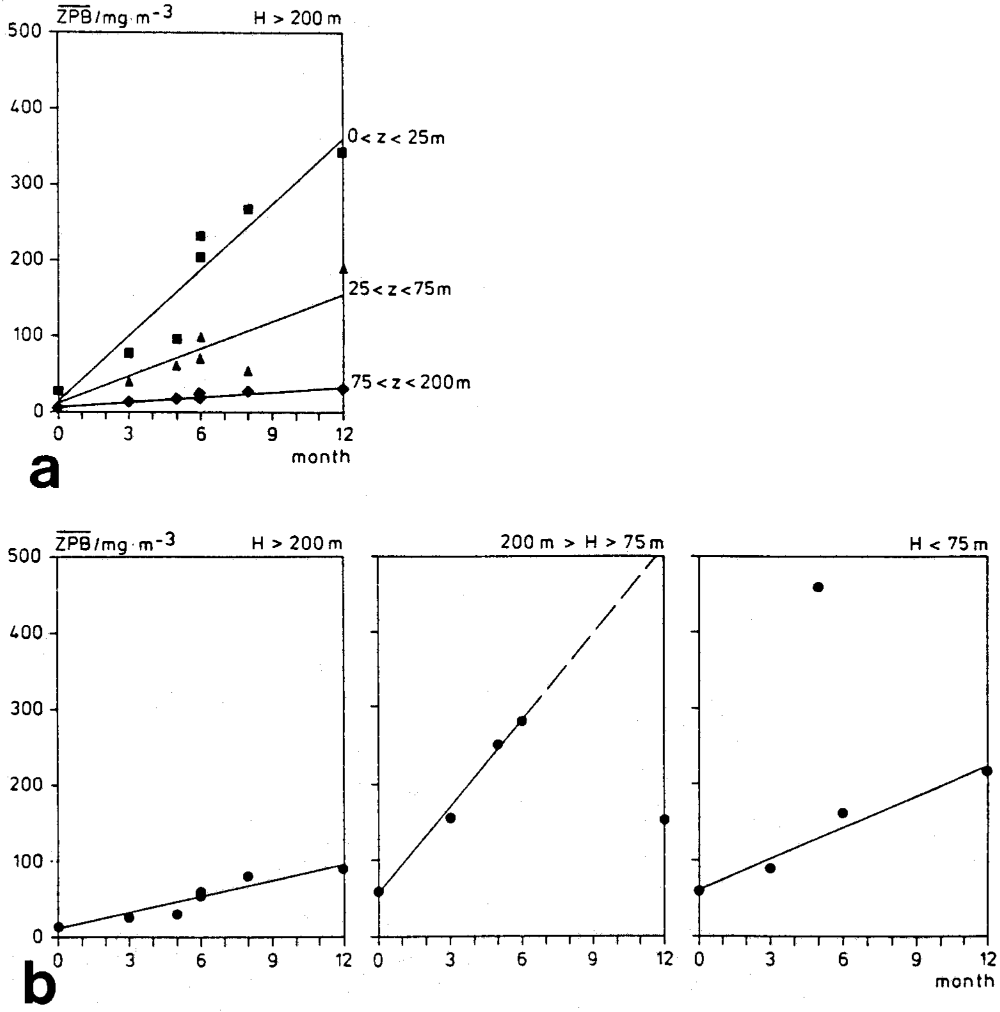


Fig. 5. Relationship between the duration of upwelling season (months) and the highest zooplankton dry mass during this time (mg · m^{-3}) due to a cumulative biomass increase from event to event, in the upper 200 m

5a: in the three defined sublayers of the 200 m surface layer in the oceanic region (water depth H > 200 m);

5b: separately for the whole layer down to a depth of 200 m in the oceanic (H > 200 m), shelf edge (200 > H > 75 m), and near shore regions (H < 75 m)

seasonal extension of the area, influenced by coastal upwelling, was largest in the first half of the year, from 10° N to 24° N, more than 400 km offshore and down to a depth of more than 200 m. It shrinks in the second half of the year to an area between 20° N and 22° N, with a coastal distance of 100 to 200 km and a mean depth of 25 m (Postel, 1990).

Mesoscale disturbances

Eddies

The area between 18° N and 22° N off NWA is a region with a high potential eddy energy (Dantzler, 1977). Here, the variability of large scale zooplankton patterns is remarkable throughout the year (Postel, 1990). Eddies with diameters of several tens of

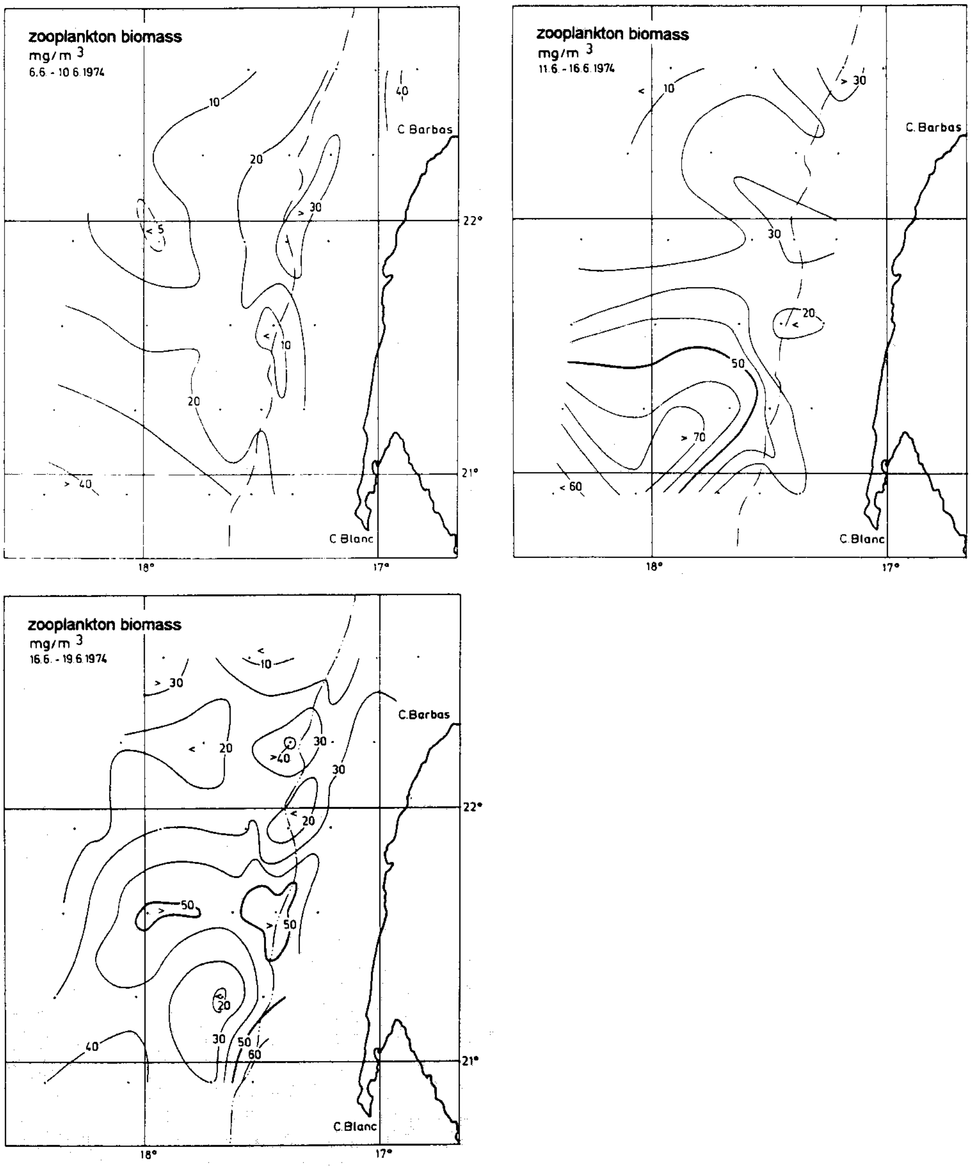


Fig. 6. Zooplankton biomass during three eddy resolving plankton surveys, conducted between Cap Barbas and Cap Blanc (Northwest Africa) every five days during June 1974

kilometres were observed during some weeks (Tomzcak, 1973; Hagen, 1977). To record this phenomenon, mesoscale studies were carried out in this area. A grid was used with distances between the stations from 18 km to 37 km (Fig. 6). The extensions of the grid were about 100 × 200 km. Samples were collected in the upper 25 m every third day at the same position. The mean biomass during the total sampling period was about 30 mg · m^{-3}. A zooplankton patch with a dry biomass larger than the average was shifted from southwest to northeast during the period under investigation. It correlates with a cyclonic eddy. In its centre, a lower biomass was observed, which can indicate new upwelled water. The physical structure is described by Schemainda & Schulz (1976).

Continental shelf waves

Figure 7 shows examples of temporal and spatial-temporal variability of oceanographical properties, especially zooplankton dry mass, with typical time scales of several days, caused by long coastal parallel waves, propagating poleward at the shelf edge. The hydrographical background is described by Mysak (1980), Hagen et al. (1981) and others.

Figure 7a presents a time series of 11 days duration with plankton catches every 3 hours in the upper 30 m layer, carried out on the shelf off Namibia in November 1976. The dotted line indicates a 5.5 days co-sinus oscillation to illustrate the most pronounced period.

Figure 7b demonstrates the entropy spectrum of the same time series. The spectral analysis method separates the total variability into single contributing amounts. Peaks of energy density are signs of significant patterns. In Figure 7b the highest amount is in the range of 5 or more days, which corresponds to the period scale of continental shelf waves, (cf. Postel, 1982). The reason for their influence on zooplankton biomass might be the vertical transport velocity, which is orientated to the surface in the crest of the wave (upwelling) and vice versa, in connection with vertical differences of plankton concentrations and always the same sampling depth.

Figure 7c shows the spatial–temporal pattern of zooplankton biomass residuums in the layer between 30 and 75 m. Residuums were calculated by subtraction of a trend from

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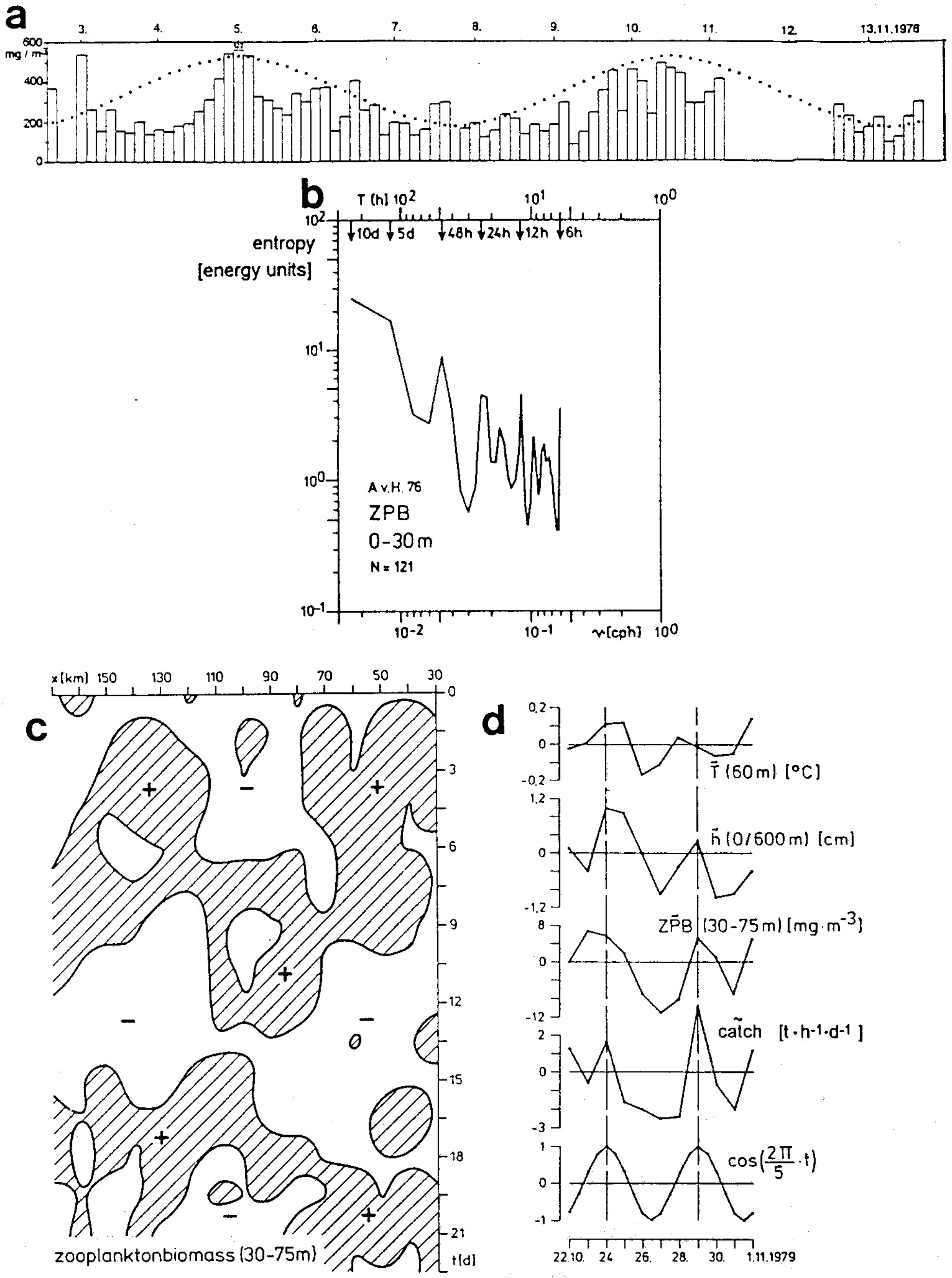
Fig. 7. Examples of significant zooplankton dry mass variability in the time range of several days detected off Namibia:

7a: during a time series of 11 days duration on the shelf off Namibia in November 1976 with plankton catches every 3 hours in the upper 30 m layer;

7b: in the spectral energy density, estimated according the Maximum Entropy method, of the same time series, in energy units; υ [cph] means frequence in cycles per hour , T means period , = $1/\upsilon$; (according to Postel, 1982);

7c: in the spatial-temporal pattern of zooplankton biomass residuums in the layer between 30 and 75 m. The measurements were carried out between 30 km and 170 km on a transect which was perpendicular to the Namibian coast every 1.5 day in October 1979 (Fig. 2a). Residuums were calculated by subtraction of a trend from the original data (see text). Hatched areas indicate the positive anomaly;

7d: in comparison to the course of the residuums of temperature at the bottom of the Ekman layer, the sea level difference between the sea surface and the 600 m reference level, the zooplankton dry mass between 30 and 75 m of the hourly catch effort of fishing vessels in the area , and the 5 days cosinus oscillation, which illustrates the most pronounced variability period; according to Hagen et al. (1981)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7.
8.
9.
10.
11.
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13.11.1976
600
mg / m³
400
200
0
b
T (h) 10²
10¹
10⁰
10d
5d
48h
24h
12h
6h
entropy
[energy units]
10²
10¹
10⁰
10⁻¹
A.v.H. 76
ZPB
0-30m
N = 121
10⁻²
10⁻¹
ν[cph]
10⁰
c
x(km) 150
130
110
90
70
50
30
0
3
6
9
12
15
18
21
t(d)
+
−
zooplanktonbiomass (30-75m)
d
0,2
0
-0,2
T̄ (60m) [°C]
1,2
0
-1,2
h̄ (0/600m) [cm]
8
0
-12
ZP̄B (30-75m) [mg·m⁻³]
2
0
-3
catch [t·h⁻¹·d⁻¹]
1
0
-1
cos(2π/5·t)
22.10.
24
26.
28.
30.
1.11.1979

the original data. Trend estimation was done by linear regression between the actual biomass data and the distance to the coast. The hatched area represents the positive anomaly. The measurements were carried out every 36 hours, between 30 km and 170 km on a transect which was perpendicular to the Namibian coast, from an upwelling centre to offshore conditions, in October 1979 (Fig. 2a). The trend of these data includes mainly the signal of ecosystem succession downstream of the upwelling centre. The residual biomass pattern is superimposed on it. This pattern is another example of the influence of long coastal parallel waves on zooplankton concentrations, resolved in time and space. The "chess-board like" structure in Figure 7c is the proof of such a relationship (cf. Hagen et al., 1981).

The influence of continental shelf waves on patterns of oceanographic properties is additionally underlined by Figure 7d. Here the de-trended course of the sea level difference between the sea surface and the 600 m reference level (h [0/600 m]), caused by continental shelf waves, correlates with temperature anomalies T (60 m). Cold water means more intense upwelling. Both patterns coincide with the zooplankton biomass deviation (from the long scale trend) and that of the hourly catch effort of fishermen. The co-sinus oscillations illustrate the dominant 5 day period. The results in Figure 7d are based on the same programme described above (Fig. 2a and 7c). The data are also residuals of a linear trend. Such a trend might be caused by hydrographic features, with scales, which are larger than that, produced by continental shelf waves. It was determined by linear regression against time, using the data, which were averaged over the first 30 km.

Water masses

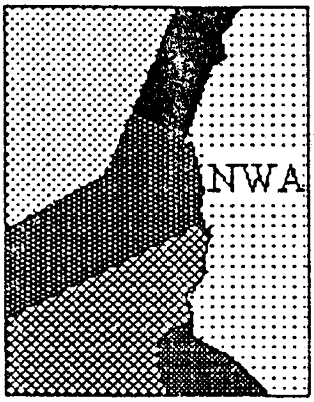
Water masses are distinguished by different characteristics. From the physical point of view, salinity and temperature are the most usual parameters (Sverdrup et al., 1942; Tomczak & Hughes, 1980; Wolf & Kaiser, 1978). In the case of upwelling research, the nutrient content is a further suitable tool for classification (e.g. Tomczak & Large, 1989; Klein, 1992). To search for indicator species is the methodological tool of biologists. Köller & Arndt (in prep.) tried to use chaetognaths for that purpose. They found that different species combinations, and sometimes the absence of one or more species, indicate different water masses (Table 1). So the lack of *Sagitta regularis* shows nutrient-poor NACW in general. Additional differences in species combinations subdivide surface and upwelled NACW. Further results with respect to upwelled SACW, tropical surface water, and tropical coastal water are given in Table 1, which also includes a rough distributional map of these dominant water masses, typical for the second half of the year.

Figure 8 shows the abundance of two calanoids in the temperature salinity diagram. *Calanus helgolandicus* (Claus, 1863), a typical species of the North Atlantic, is in the salinity range of NACW, whereas *Calanoides carinatus* (Krøyer, 1849) indicates SACW (Brenning, 1980).

Reproduction and maintenance of calanoids in near coastal areas

Chagouri (1989) compared temperature-dependent developmental times of *Calanus carinatus* and transport velocities of water masses according to Hagen (1981) in the coastal current regime down to 200 m to prove maintenance mechanisms for these

Table 1. Distribution of chaetognaths off Northwest Africa (ab. = abundance [ind. · m^{-3}], fre. = frequency [%]), according to Köller & Arndt (in prep.); bold letters mean indicator species, absent species are listed in lowest part of table



░	ab.	fre.
–		
S. minima	12.2	65.9
S. serratodentata	3.4	18.4
S. lyra	0.6	3.2
S. hexaptera	0.4	2.2
P. draco	0.4	1.9
S. regularis		

North Atlantic Central water (low nutrient level)

■	ab.	fre.
S. minima	**12.9**	**68.5**
S. minima	12.9	68.5
S. serratodentata	1.8	9.6
S. tasmanica	0.8	4.2
S. friderici	0.7	3.7
S. regularis		

upwelled North Atlantic Central water (low nutrient level)

▦	ab.	fre.
S. tasmanica	**5.6**	**22.5**
S. decipiens	**0.4**	**2.2**
S. friderici	8.8	35.4
S. tasmanica	5.6	22.5
S. minima	5.3	21.3
Eukrohna	2.1	8.5
S. enflata		
P. draco,		
K. mutabbii		

upwelled South Atlantic water (high nutrient level)

▩	ab.	fre.
S. enflata	**5.8**	**52.6**
K. mutabbii	**0.4**	**3.6**
S. enflata	5.8	52.6
S. serratodentata	1.8	16.3
S. subtilis	0.9	7.8
S. hispida	0.7	6.3
S. regularis		
S. tasmanica		

tropical surface water (low nutrient level)

▓	ab.	fre.
S. hispida	**120.1**	**47.6**
S. hispida	120.1	47.6
S. friderici	107.2	42.5
S. enflata	16.7	6.6
S. tasmanica		
S. hexaptera		
Eukrohnia,		
S. decipiens		

tropical coastal water (high nutrient level)

organisms in the near coastal ecosystem. Subsequently, she designed a diagram (Fig. 9). According to this, the development starts with nauplius stage I in the fresh upwelled water of the near coastal zone and continues up to the copepodite IV stage just before reaching a downwelling area, which is connected to a coastal parallel front. Subsequent transport probably occurs by recirculation in less than 100 m depth. Animals will be also trapped by the coastal parallel undercurrent, the origin of upwelling water. The net result is a combination of zonal and meridional transport components, which are directed offshore and equatorwards and vice versa. The transport would last about 21 days, which corresponds with the above-mentioned, calculated developmental times for copepods off Namibia. A complete life cycle takes place in such a current regime, which can, therefore,

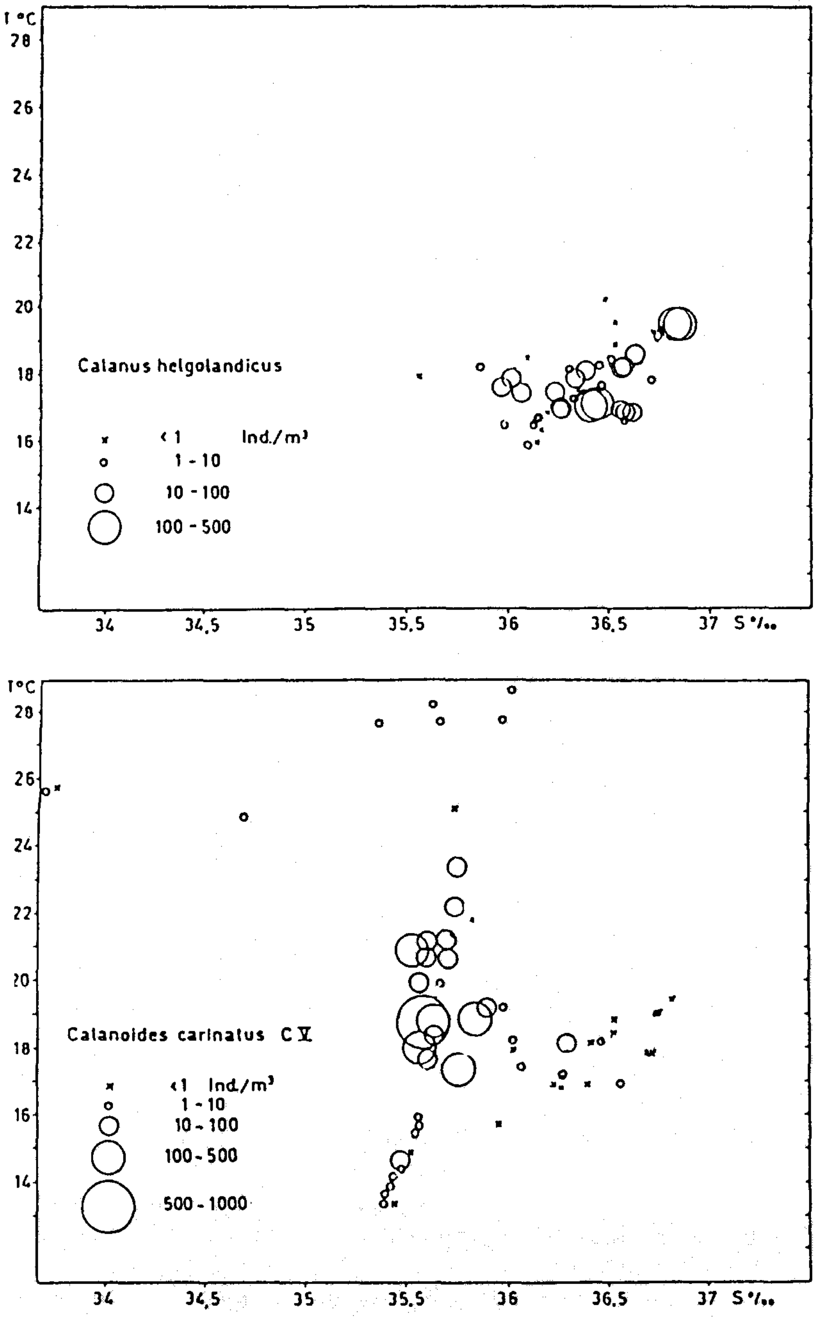


Fig. 8. Differences in the occurrence of *Calanus helgolandicus* (Claus, 1863) and *Calanus carinatus* (Krøyer, 1849) according to their temperature salinity demands (C V is copepodit stage V), according to Brenning (1980)

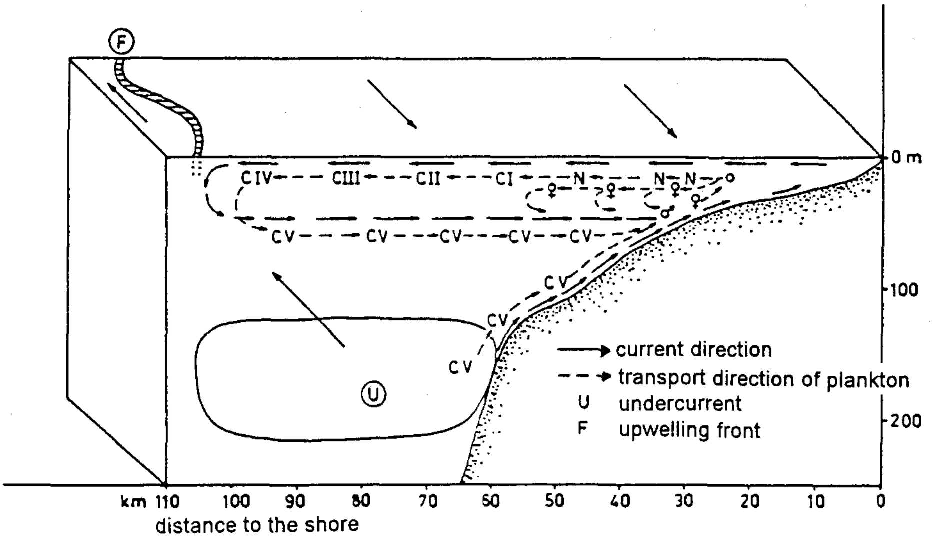


Fig. 9. Tentative diagram to demonstrate maintenance mechanisms of *Calanus carinatus* (Krøyer, 1849) in the near coastal area off Northwest Africa by a coupling mechanism of the development and current velocities in the system of main currents parallel and perpendicular to the coast according to Chagouri (1989)

be considered as a suitable maintenance mechanism for this taxonomical group in the near coastal area.

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