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ROSTOCK ZOOPLANKTON STUDIES OFF WEST AFRICA

by

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Abstract

Many cruises of the German r/v "A.v.Humboldt" operating from Rostock were carried out in the upwelling regions off West Africa since 1970. Zooplankton studies focussed on quantitative, metabolic, taxonomic, and parasitological aspects. Biomass studies covered scales ranging in time from minutes to several years and in space from hundreds of meters to several thousands of kilometres. The epipelagic mesozooplankton of these upwelling areas mainly consists of calanoids with developmental times of about 20 to 23 days. In that time zooplankton dry mass pikes after an upwelling event, with a double dry mass. The upwelling phenomenon shows seasonality in most of the investigated areas. Typical time and space scales were described. There is a relationship between the duration of seasonal upwelling, that means the numbers of single upwelling events, and the cumulative growth 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. The large scale zooplankton biomass patterns are superimposed by mesoscale phenomenons, originated by e.g. long coastal parallel waves and eddies. Water masses, including upwelling source water, are to identify by indicator species, e.g. chaetognaths and calanoids. Comparisons of transport velocities and developmental rates of calanoids allows to explain the current regime as a suitable maintenance mechanism for this taxonomic group in the near coastal area.

Introduction

Economical reasons, relating particularly to fisheries and marine geology, enhanced upwelling research in the Canary and Benguela Current since 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 at 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 were 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 space scales from hundreds of meters to several thousands of kilometres. This research included studies on 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
- boundary (upwelling) area versus 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
- ROSSBY wave patterns, cyanobacteria in relation to metabolic activity	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, 1981,a, b, 1982 a, b, 1983, 1984, 1985 a, 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 rouse interest in such areas again, where ecosystem development can be observed from an early to an equilibrium stage with all the ecological consequences over relative short distances. This contribution will review and sum up the results of some of the above mentioned papers.

Material and Methods

In the seventies large scale observations were carried out in the upwelling area off the coast of Northwest Africa (NWA), between Bahia 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. It was 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 at four depth levels, from 200 to 0 m, from 200 to 75m, 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 1/3 of the total plankton in the euphotic zone of an upwelling area. This third consists of about 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 time ranges from 25 to 40 days. This plankton fraction is of nutritive relevance for fishes of commercial value, like *Scomber colias* (70 %), *Trachurus spec.* (60 %) and *Sardinella spec.* (50 %).

Dry mass was determined according to Lovegrove (1966). During different cruises sligth modifications in the field and in the laboratory procedures occured, which sometimes caused remarkable influence on the data. Regular errors produced total underestimates of 15 to 65 % , which were considered during a data validation procedure. The largest overestimates arose with 21 % by using wire length instead of flow meters to calculate the filtrated water volume. In contrast losses of about 48 % occured after defreezing of stored samples to dry them in an oven (Postel, 1990).

For details of the taxonomic identification procedures, the reader is referred to the publications mentioned above.

Results and Discussion

Figure 1 presents the main study areas: (i) the one off Northwest Africa (NWA), with large scale and mesoscale studies, (ii) the reference area on the 30° W meridian, and (iii) the mesoscale research site off Namibia (SWA).

Ecological Consequences of an Average Coastal Upwelling Event

The results stem from a programme which lasted three weeks during the upwelling season in October 1979. It consisted of a transect off Namibia, which was 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 day. Fig. 2 presents the geographical situation (2.1), and the successive progress of ecosystem development from the near shore upwelling centre to offshore conditions (2.2. to 2.13) in terms of averages of 15 measurements. The diagrams should be studied from the right, the African coast line, to the left.

So, the sea level increases, indicating that upwelling favourable winds shift the near shore surface water in offshore direction (2.2). Cold, low saline, oxygen poor, and nutrient rich water from deeper layers replaces it (2.3 - 2.7). 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 shows an optimum surplus at about 30 km down stream of the upwelling site (2.8). With increasing distance to the shore the ecosystem is increasingly stabilised. The decreasing dominance index in conjunction with the increasing diversity index, calculated for different zooplankton groups is a qualitative indicator of this phenomenon (2.12; 2.13). Even the numbers of these zooplankton groups increase from 16 at 30 km to 25 at 170 km offshore. The development of the mean abundances of the most dominant taxonomic groups underline this ecosystem zonation: first the optimum of nauplia, followed by the small, and by the medium sized calanoids farther offshore, and finally followed by the thaliaceans, a group which is dominant far away from the upwelling centre (2.11). The zooplankton dry mass pattern in two depth levels on transsects perpendicular to the coast (2.9; 2.10) corresponds very well with the calanoid abundances in Fig. 2.11. 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 (i) wind drift, (ii) current measurements, and (iii) 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 maximum phytoplankton biomass occured about two day, 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 at 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). The observations are from different years of similar upwelling intensities. 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 200m. In the latter region, a vertical subdivision 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, as shown 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. Down to 20° N, upwelling and a correspondent higher biomass is pronounced all 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. The same relationship 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 of the properties of the upwelling source water. In this area, nutrient poor North Atlantic Central Water (NACW) prevails, instead of the nutrient rich South Atlantic Central Water (SACW) south of 21° N.

When the two patterns in Figure 4 are compared, it becomes obvious, that the zooplankton pattern is characterized by the isoline at 20 mg $*$ m^{-3} of dry mass. The mean dry mass in the upper 200m of the reference area at 30° W (Fig.1), which is free of upwelling, is 10 mg $*$ m^{-3}. That means, 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 of 25m, 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 , a shift of the upwelling response of 6 to 8 weeks is observed in depths larger 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. 5.2), the area with the largest fish biomass, and in the upper 25 m (Fig. 5.1) , 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 and Postel, 1991).

When the typical "response" biomass of the upper 25 m is taken as the basis, the seasonal extension 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 contracts 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 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 x 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 biomass pattern with dry mass larger than the average was shifted from south-west to north-east during the period under investigation. It correlates with a cyclonic eddy. In its centre, a lower biomass was observed, which indicates new upwelled water. The physical structure is described by Schemainda and Schulz (1976).

Continental Shelf Waves

Figure 7 shows examples of temporal and spatial - temporal patterns of oceanographical properties, especially zooplankton dry mass, with time scales of several days, caused by long coastal parallel waves.

Figure 7.1 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 7.2 demonstrates the entropy spectrum of the same time series, with energy accumulations in the range of daily variability (T = 24 h) and others. The highest amount is in the range of 5 and more days, which corresponds to the scale of continental shelf waves, propagating poleward at the shelf edge (c.f. Postel 1982).

Figure 7.3 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 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 (Figure 2.1). 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. The residual pattern is caused by hydrographic features, mainly by long coastal parallel waves, which were propagated poleward. The "chess board like" structure in Figure 7.3 is the proof of such a relationship (c.f. Hagen et al., 1981). The reason for the zooplankton biomass variability depending on these features may be the vertical shift of water masses due to these wave phenomena, which produce up- and down-wellings, and / or the vertical oscillation of water masses of different plankton concentrations.

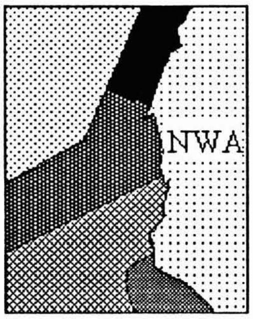
The influence of continental shelf waves on patterns of oceanographic properties is underlined by Figure 7.4. Here the detrended course of sea level variations (h [0 / 600 m]), caused by continental shelf waves, correlates with temperature anomalies T (60 m). Cold water means more intense upwelling. 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 days period. The results in Fig. 7.4 are based on the same programme described above (Fig. 2.1.; 7.3). The trend elimination was done in time, using the data measured and averaged over the first 30 km. The trend is caused by hydrographic features larger than continental shelf waves.

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 and Hughes, 1980; Wolf and Kaiser, 1978). In the case of upwelling research, the nutrient content is a further suitable tool for classification (e.g. Tomczak and Large, 1989; Klein 1992). To search for indicator species is the methodological task of biologists. Köller and Arndt (in prep.) e.g. 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 e.g. 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* (Kroyer,1849) indicates SACW (Brenning, 1980).

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 the table.



	ab.	fre.
no		
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)

Reproduction and Maintenance of Calanoids in Near Coastal Areas

Chagouri (1989) compared temperatur dependent developmental times of Calanoids and transport velocities of water masses according to Hagen (1981) in the coastal current regime down to 200m to prove maintenance mechanisms for these organisms in the near coastal ecosystem. Subsequently, she designed a diagram (Figure 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 occurs probably 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 equatorward, and *vice versa.* The transport would last about 21 days, which is in coincidence with the above mentioned, calcultated developmental times for copepods off Namibia. A complete life cycle takes place in such a current regime, which can therefore be considered as a suitable maintenance mechanism for this taxonomical group in the near coastal area.

Summary

Since the beginning of the seventies upwelling research became increasingly popular in the path of the Canary and Benguela Current, because of economical consideration, particularly in relation to fisheries and marine geology. Many expeditions were carried out between 1970 and 1977, including the 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 meters 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 mainly consists of copepods, especially calanoids with developmental times of about 20 to 23 days. During this three weeks zooplankton dry mass peaks after an upwelling event, doubling its biomass. This typical biomass increase is independent of coastal distance and depth. In depths below 75 m, the upwelling response lasts 6 to 8 weeks.

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 estimationof 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 NWA the largest extension was recorded in the first half of the year, from 10° N to 24° N, more than 400 km offshore and at least below 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 e.g. 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 also be found 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* (Kroyer,1849) is an indicator of South Atlantic Central Water.
Comparisons of near coastal current regimes, transport velocities, and developmental rates of calanoids finally allow to conclude that a suitable mechanism is present to maintain plankton in the coastal environment.

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We are gratefull to Dr. J. Alheit for linguistic corrections.

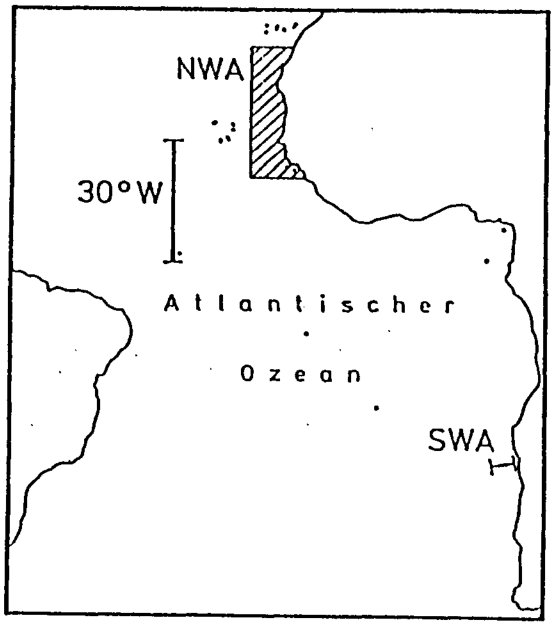


Fig. 1: Areas studied by r./v. "A.v.Humboldt" in the Atlantic Ocean: a large, seasonal study site off Northwest Africa (NWA), a reference area at 30° W without EKMAN upwelling, and a mesocale transect off Namibia (SWA).

2.1

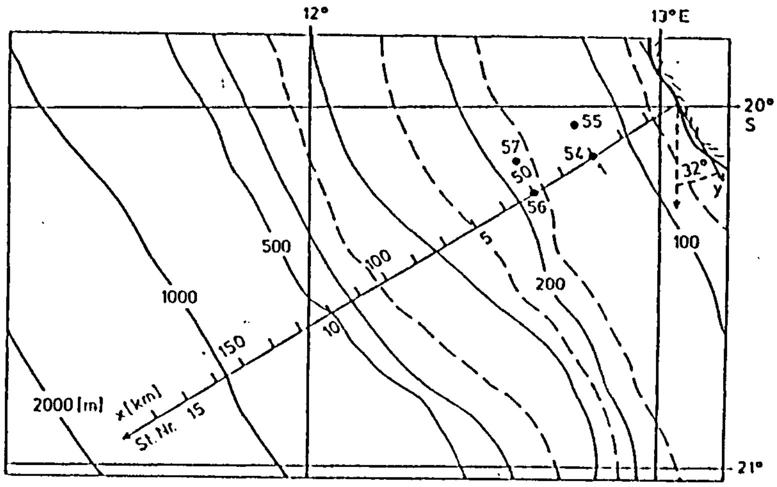
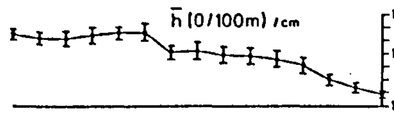


Fig. 2: Position of the cross - shelf measuring profile, which was repeated every 36 hours from October 16th to November 11th in 1979 off Dune Point, Namibia (2. 1), and the temporal averaged cross - shore distribution (including confidence ranges, $p < 0.05$) of the sea level difference h (0/100 m) (2. 2) , the temperature (2. 3) and salinity (2. 4) at the sea surface, the oxygen - (2.5), phosphate - (2. 6), silicate - (2. 7) , and chlorophyll-a - concentration (2. 8) at the sea surface, the zooplankton dry mass in the upper 30 m (2. 9), the zooplankton dry mass between 30 and 75 m depth (2. 10), the zooplankton abundance (2.11), the dominance index (2.12), and diversity index for mesozooplankton in the upper 30 m (2.13); (according to Hagen et al., 1981, and Postel, 1990).



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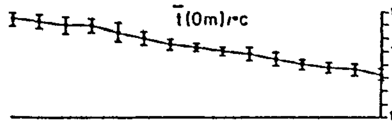

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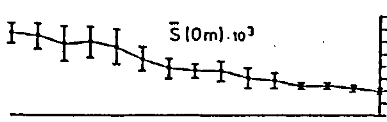

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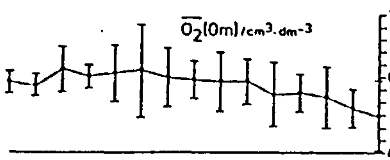

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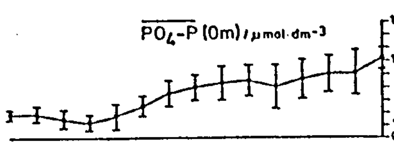

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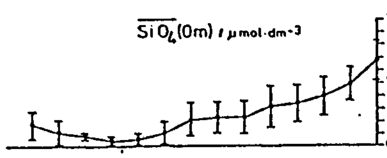

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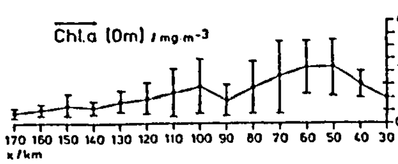

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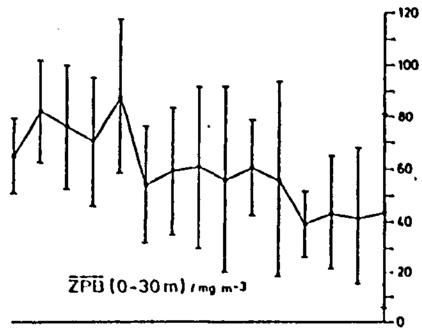

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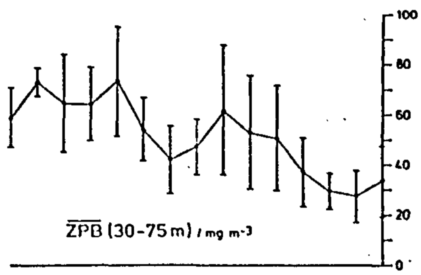

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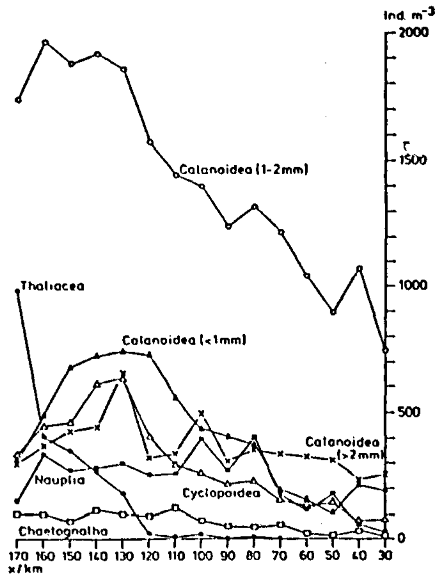

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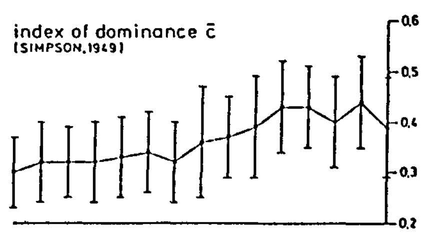

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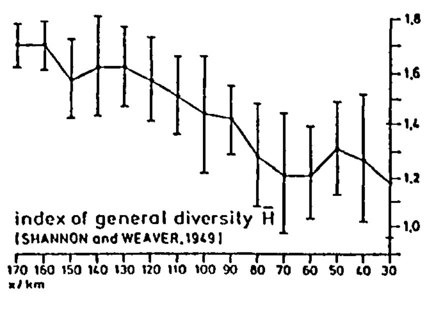

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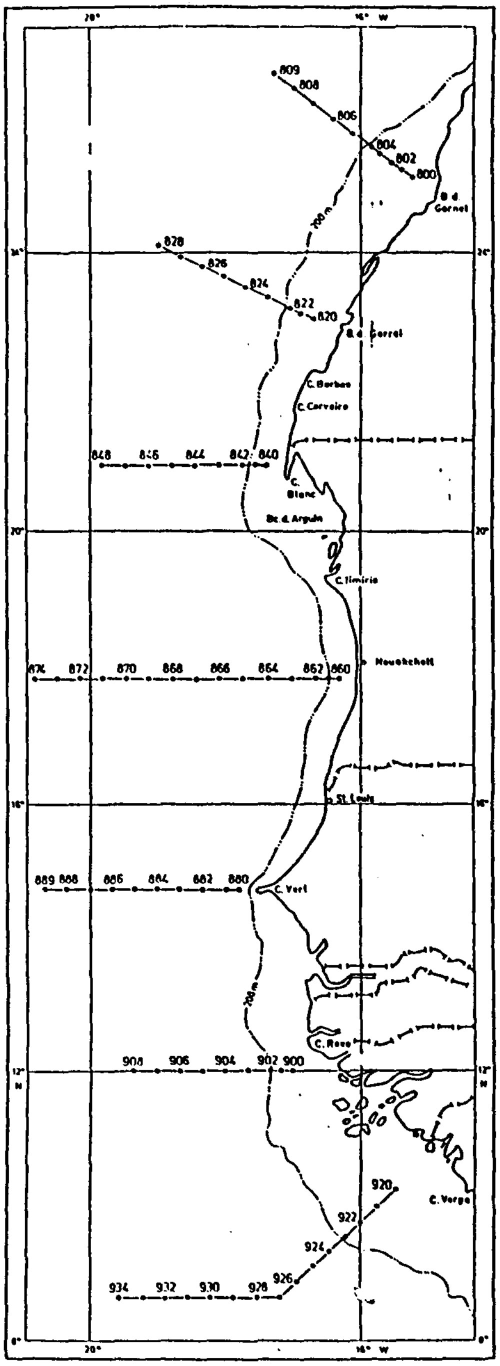


Fig. 3: Standard profiles off Northwest Africa, where zooplankton was sampled in August / September 1970, October / November 1970, June / July 1972, December 1972 / January 1973, February / March 1973, May 1975, and partly in February 1976.

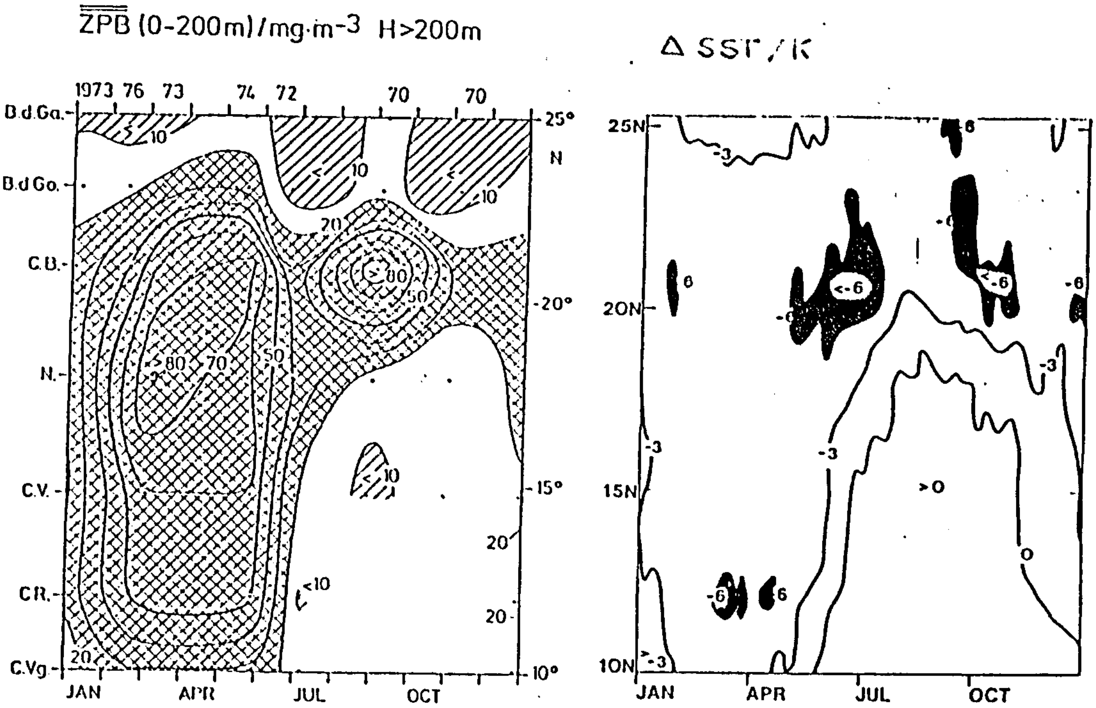
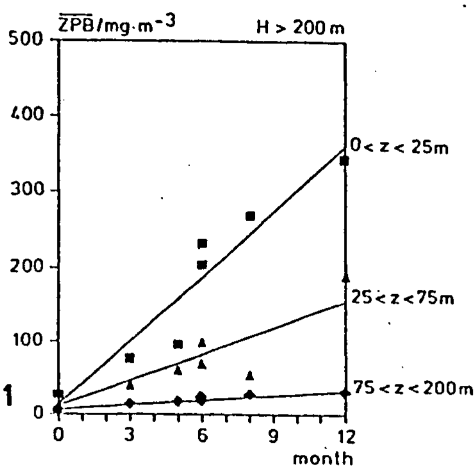


Fig. 4: Mean cross - shore zooplankton biomass density in the 200m surface layer of the oceanic region off Northwest Africa (Water depth > 200m, longitude < 20°W) as a function of latitude and season in comparison with the seasonal variation in the difference of sea surface temperature of the same latitude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

5.1



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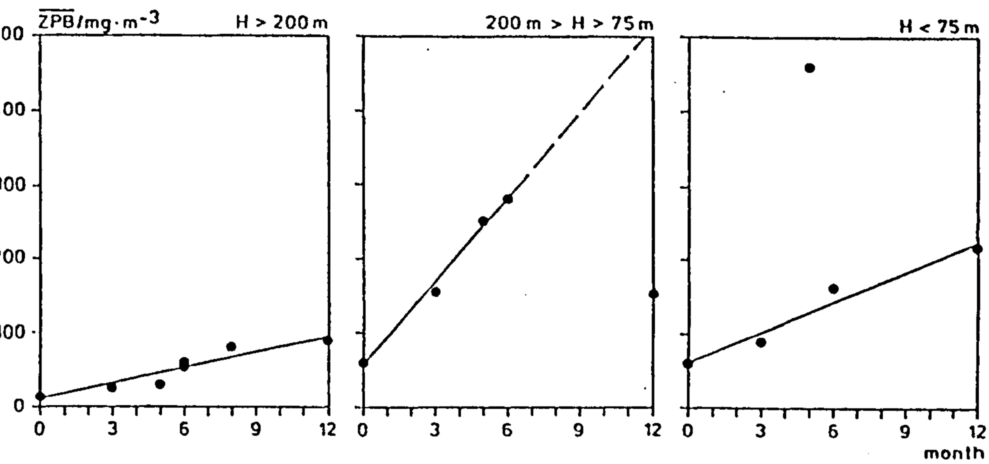

Fig. 5: Relationship between the duration of upwelling season (months), which is equal to the number of upwelling events, and the highest zooplankton dry mass during this time ($mg*m^{-3}$) due to a cumulative biomass increase from event to event, in the upper 200 m
5.1: in the three defined sublayers of the 200 m surface layer in the oceanic region (water depth H > 200 m) and
5.2: 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).

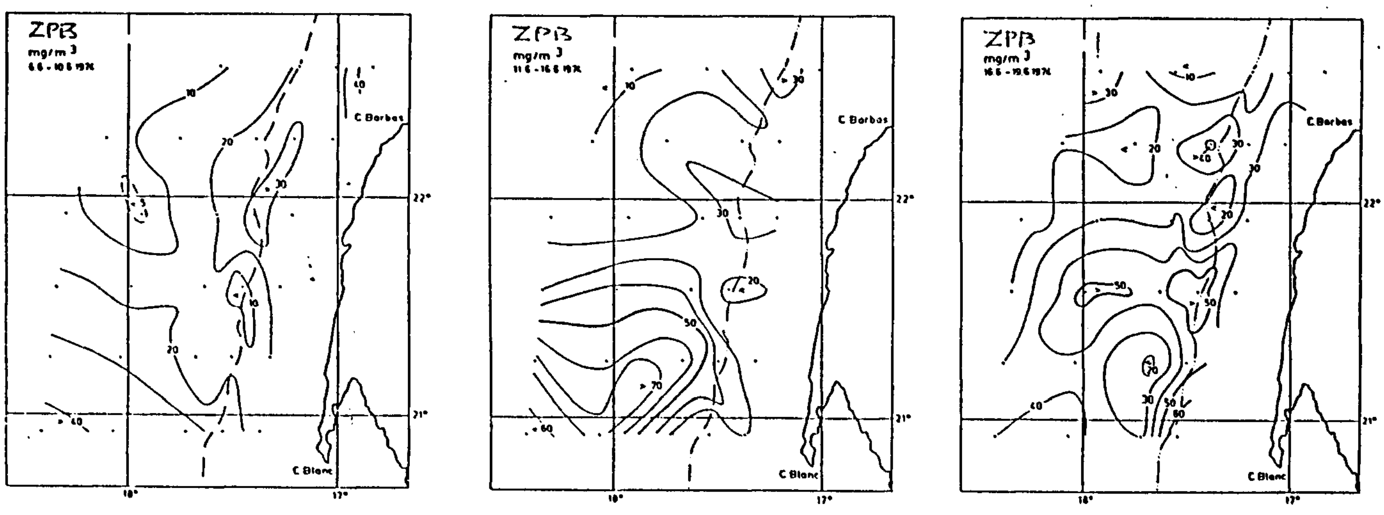

Fig. 6: Zooplankton biomass during three eddy resolving plankton surveys, conducted between Cap Barbas and Cap Blanc (Northwest Africa) every five days during June 1974.

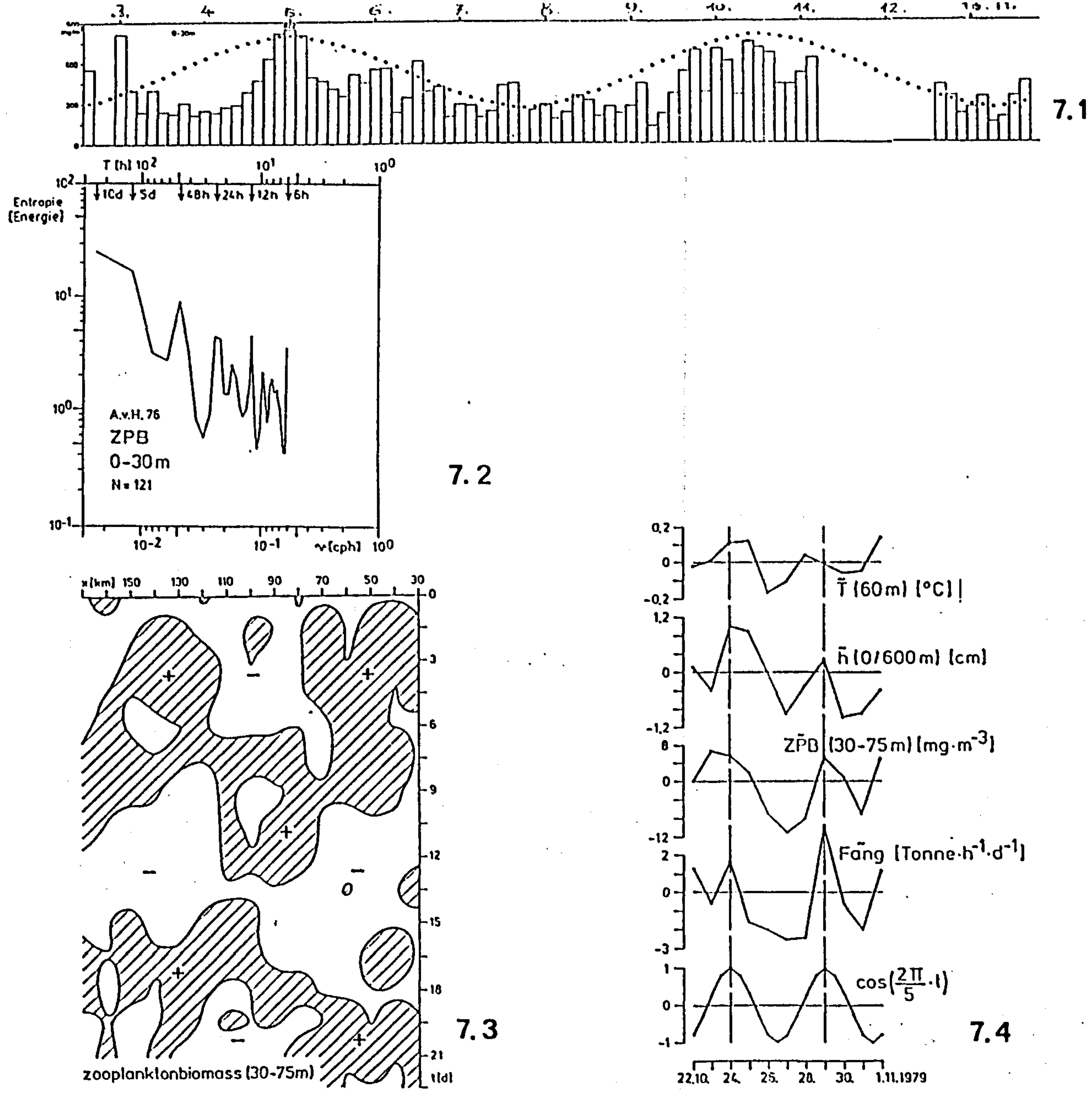

Fig. 7: Examples of significant zooplankton dry mass variability in the time range of several days, originated by long coastal parallel waves (e.g. continental shelf waves) detected off Namibia:

7. 1: 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 .

7. 2: in the spectral energy density, estimated according the Maximum Entropy method, of the same time series, in energy ("Energie") units / cycles per hour [cph] (according to Postel, 1982),

7. 3: 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 (Figure 2.1). Residuums were calculated by subtraction of a trend from the original data (see text). Hatched area indicates the positive anomaly.

7. 4: in the comparison of the course of the residuums of temperature at the bottom of the EKMAN layer, of 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 ("Fang"), and of a 5 days co-sinus oscillation, which illustrates the most pronounced variability period ; according to Hagen et al. (1981).

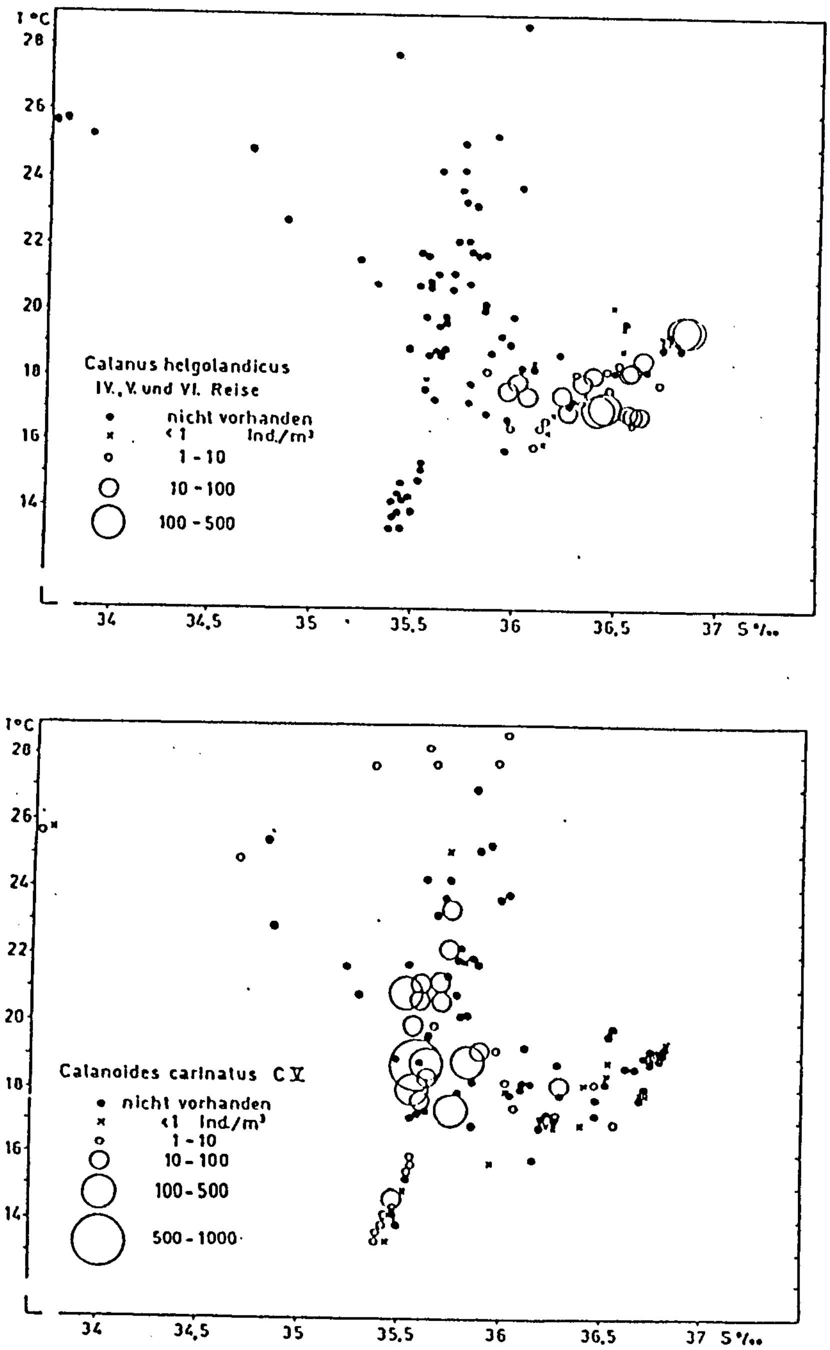

Fig. 8: Differences in the occurence of *Calanus helgolandicus* (Claus, 1863) and *Calanus carinatus* (Kroyer, 1849) according to their temperature salinity demands ("nicht vorhanden" means "no evidence", C V is copepodit stage V), according to Brenning (1980).

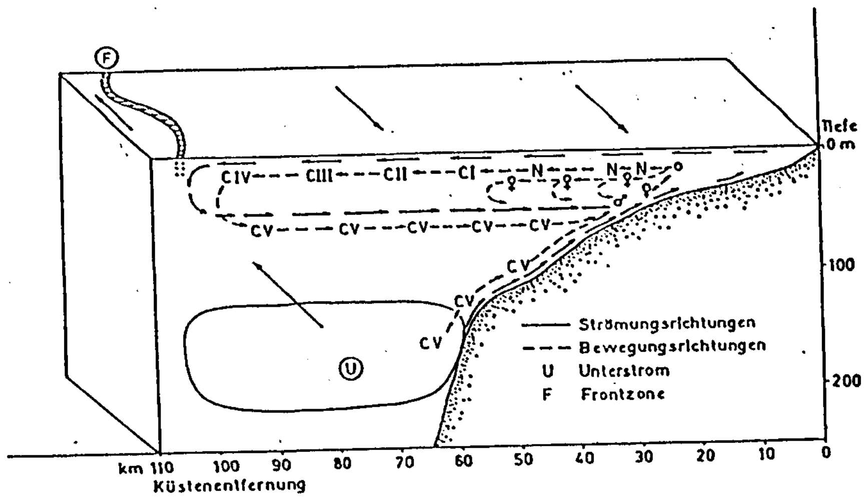

Fig. 9: Tentative diagram to demonstrate maintenance mechanisms of *Calanus carinatus* (Kroyer, 1849) in the near coastal area off Northwest Africa by a coupling mechanism of the development and current velocities in the system of main currents parallel and perpendicular to the coast according to Chagouri (1989); "Strömungsrichtungen" means current directions, "Bewegungsrichtungen" = transport direction of calanoids, U = undercurrent, F = upwelling front, "Küstenentfernung" = distance to the shore .