

## Zoobenthos of the CINECA area and other upwelling regions

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Standing stock (and production) of benthic communities depend on the food supply to bottom water layers and on sedimentation conditions and are thus related to primary productivity in surface waters, altered by subsequent degradation processes. A high standing stock of benthic animals is to be expected in upwelling regions.

Studies off the coast of Northwest Africa at 17°, 21°, and 25°N confirm this hypothesis for the macrofauna and for chloroplastic pigment equivalents in the sediment, but not for the meiofauna. Latitudinal differences seem to be related to upwelling intensity.

Off Cape Blanc a low faunal density and a low content of organic matter are encountered on the upper slope, while high values characterize the lower slope area. These deviations from an expected decrease with water depth are related to downwelling processes, accelerating the transport of energy-rich food particles into deeper water layers.

The sedimentary environment of the organisms is largely determined by its organic matter content. Off Chile, Peru, and Southwest Africa, negative redox potentials at the sediment surface are present in some regions and sulfide biomes are developed with intense microbial populations, but a reduction in macrofaunal elements. Those cases seem to be absent or rare off Northwest Africa. This may partly be explained by a downslope transport of organic matter, and its concentration in depths of about 1000 to 2000 m.

Off Northwest Africa the benthos develops in dense populations. However, they constitute low food resources for demersal fish. Most larger organisms belong to filter-feeding taxa, like Octocorallia, Crinoida, Actiniaria, and Porifera, none of which are strongly preyed on by fish. The abundant infauna made up by polychaetes, crustaceans, molluscs, and other less important taxa may constitute some fish food.

Thus, high production in surface water layers and high transport of organic matter down to and along the sea floor do not necessarily lead to a high standing stock of demersal fish and to favorable fishing yields.

### Introduction

Benthos investigations in upwelling areas are rare, which seems to be related to the fact that the benthos is considered to be of little importance in this kind of ecosystem. As in many other environments the benthos, including demersal fish, constitutes the final steps of living organic matter in offshore food webs, recycling inorganic nutrients back into the water column for further use in photosynthesis.

Since benthic standing stock (and production) depend on food availability, high benthic biomass values are expected in upwelling regions. Ultimately, the benthos is related to primary production, yet intermediate processes, such as total conversion rates depending on the number of trophic levels, feeding habits in relation to food density, short circuits, recycling of organic matter in the water column, and hydrographic plus sedimentary conditions, alter the local benthic production (Thiel, 1978). The few recent publications on the benthos from upwelling regions (Christensen and Packard, 1977; Gallardo, 1976; Nichols and

Rowe, 1977; Rowe, 1971a; Rowe et al., 1977; Thiel, 1978; and Watson, 1978) permit some general statements on benthic communities and can help in the interpretation of processes and in understanding fishing potentials in upwelling systems.

The publications on the benthos from upwelling regions are too few to form a base for a review paper. Therefore, this paper contains some original data and summarizes what is known on the benthos of upwelling areas. The present results originate from "Meteor" cruises 26, 36, and 44 (Fig. 218).

### Benthos in the upwelling region off Northwest Africa

Chloroplastic pigment equivalents, microorganisms, and sediment properties

Looking for some indication of sedimentary processes of primary organic matter, the distribution of chloro-

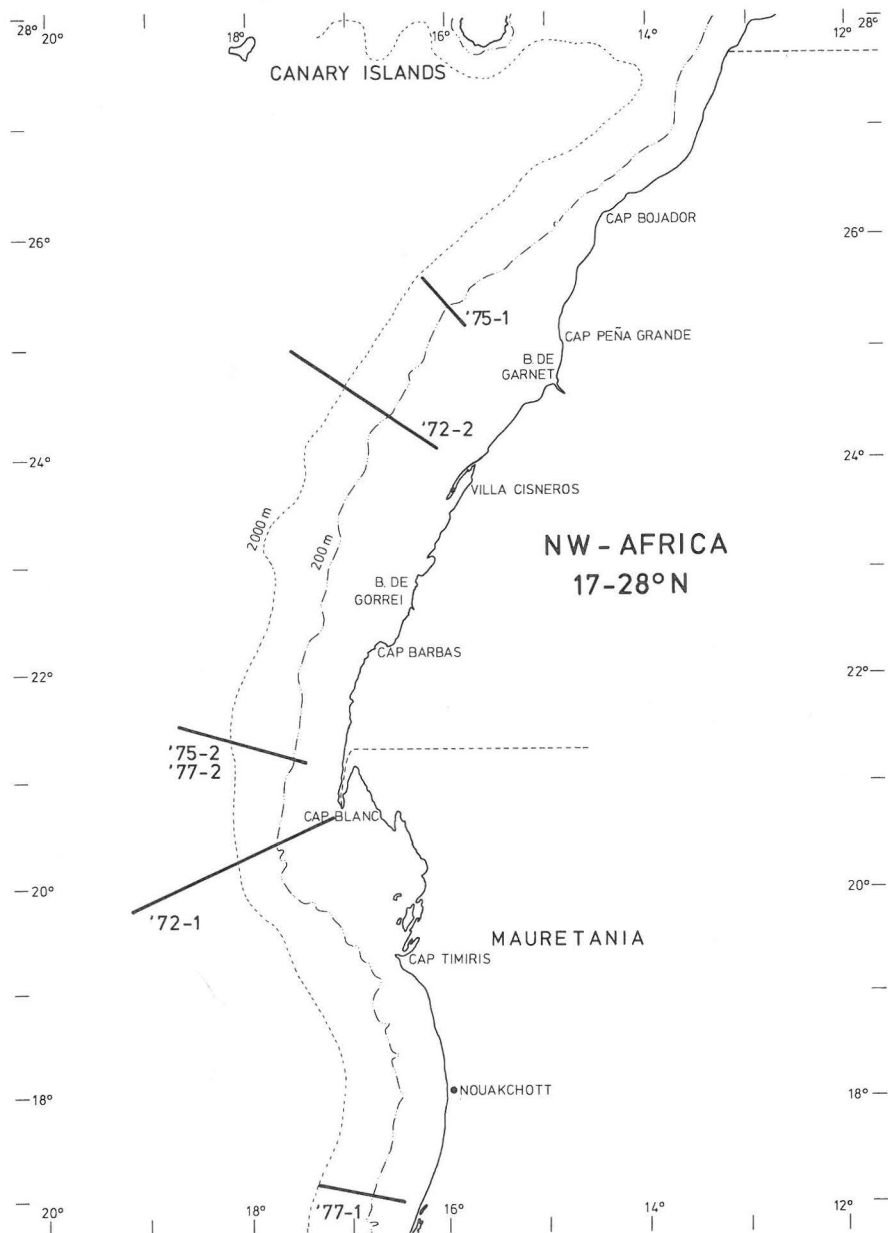


Figure 218. Northwest Africa between 17° and 28°N, with the location of the transects: '72-1 and '72-2 ("Meteor" 26); '75-1 and '75-2 ("Meteor" 36); '77-1 and '77-2 ("Meteor" 44).

plastic pigments in the sediment surface was studied. Subsamples for the determination of pigments were taken with medical syringes from 600 cm<sup>2</sup> box grab samples. Each three such microcores were used for the analyses and the graph is based on means.

Chlorophyll *a* is not expected to concentrate in high amounts in sediments, because of its fast degradation soon after the organism's death, but its disintegration products are more stable. For the determination the method of Lorenzen (1967) and Shuman and Lorenzen

(1975) was used. A few chromatographic tests revealed that the pigment composition in the sediment is not well understood and therefore the term "chloroplatic pigment equivalents" is used for what was measured.

The distribution of these chlorophyll derivatives on a depth transect off Cape Blanc shows some interesting features (Fig. 219): minimum values on the upper continental slope and a maximum at a depth range of 1000 m or even more. The exact position of the minimum is not known, owing to the low number of samples taken

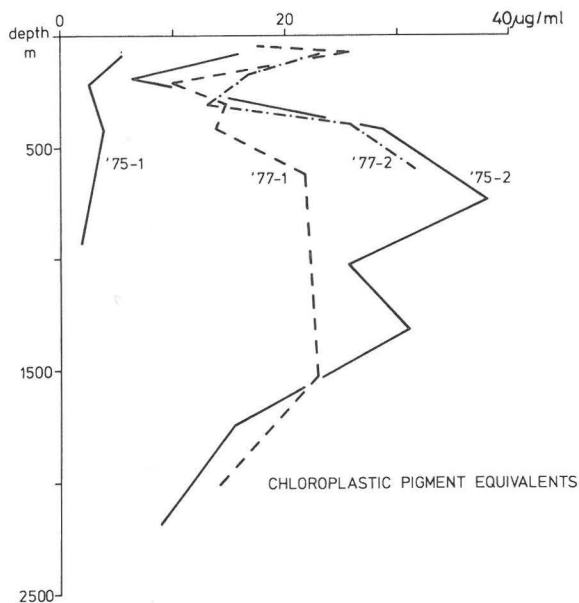


Figure 219. The distribution of chloroplasic pigment equivalents ( $\mu\text{g/ml}$ ) in the sediments of the '75 and '77 transects.

on the upper slope. In the '77-2 profile more samples were taken to improve the location of the minimum, and it was found somewhat deeper down. The curves of the '75-2 and '77-2 transects show a similar pattern, which is also found in other regions (Fig. 219), i.e. in the transects '75-1 and '77-1, located roughly 240 miles north and south, respectively. The between-transect differences in general level can be taken as indicative for areal productivity. However, the within-transect distribution with its minima and maxima is not necessarily an upwelling characteristic. It points to some sedimentation patterns not correlated primarily with water depth, but with hydrographic conditions.

Similar depth profiles were encountered during the '75 cruise ("Meteor" 36) for bacteria from plated cultures by R ger (1975) and Weyland (personal communication), for pollen baited fungi by Gaertner (personal communication), for organic carbon by Weyland (personal communication), and for energetic content measured as calories by Hansen (personal communication). Maximum values of organic carbon were found by Ruehl (personal communication) on transects '72-1 and '72-2 at depths of 1000 and 2000 m (Diester-Haass et al., 1973), by Rowe et al. (1977) at 880 and 1830 m, and by Miro Orell (1973) between 680 and 1125 m depth. Therefore, information from various sources seems to confirm the existence of the upper slope minimum and the deep slope maximum. However, the American cruise JOINT-I on RV "Atlantis II" in 1974 returned with partly deviating results. The stations worked are located on four transects between 21°N and

22°N with two to six sampling depths. Work concentrated on the inner and the outer shelf and on a few stations on the continental slope.

Nichols and Rowe (1977) present data on organic carbon with values of less than 1 %  $C_{\text{org}}$  of dry sediment for most shelf areas, with 1–2 or 2 % on the upper slope and more than 2 %  $C_{\text{org}}$  of dry sediment for their two deep stations at 880 and 1830 m depth. Christensen and Packard (1977) measured ETS activities and protein (primary amino nitrogen), while rates of oxygen utilization and carbon dioxide production were calculated from ETS. For both ETS and protein a steady decrease was found with depth and this is reflected in the calculated values of oxygen utilization. Watson (1978) compares total and bacterial biomass in the water column and in the sediment from the same stations of the JOINT-I cruise. In his Table 10, bacterial and total biomasses for the sediments are given, and they tend to decrease with water depth, although the values for the depths of 469 and 480 m are lower than those for 800 m. At first glance the "Atlantis II" data look somewhat contradictory to the above-mentioned "Meteor" results. However, sampling in the range of the upper slope is rather limited in the JOINT-I programme. Sediment bacteria are not evaluated from upper slope depths above 469 m, and for ETS and protein only one sample is available from 140 m depth, with 90 and 480 m being the adjacent stations. Only the organic carbon shows very low values around 100 m and higher ones around 200 m, but organic carbon cannot be expected to correlate with the different faunal components, because of the variable conditions of sedimentation and burial of refractory and non-refractory organic matter. Thus, the JOINT-I results are too incomplete to indicate the upper slope minimum, but together with the other material they allow a general interpretation.

### Meiofauna

Meiofauna was collected by subsampling a box grab sample of 600  $\text{cm}^2$  total area, using a 10  $\text{cm}^2$  meio-stecher. Each subsample was sorted to a sediment depth of 4 cm, and in a second uppermost 1 cm layer the meiofauna was counted to check for the variability in density. Because deviation did not exceed the normal range no further sorting was carried out.

The distribution of meiofauna seems to depend on the settled organic matter as a source of food. It shows a depth gradient comparable to the chloroplasic pigment equivalents and organic matter (Fig. 220). These meiofauna counts originate from a cruise in 1972, and again, the upper slope minimum and the maximum on the deeper slope are well established.

Compared with other regions of similar depth, meiofauna densities are high, indicating the influence of upwelling and high productivity on this faunal component off Northwest Africa (Thiel, 1975; 1979).

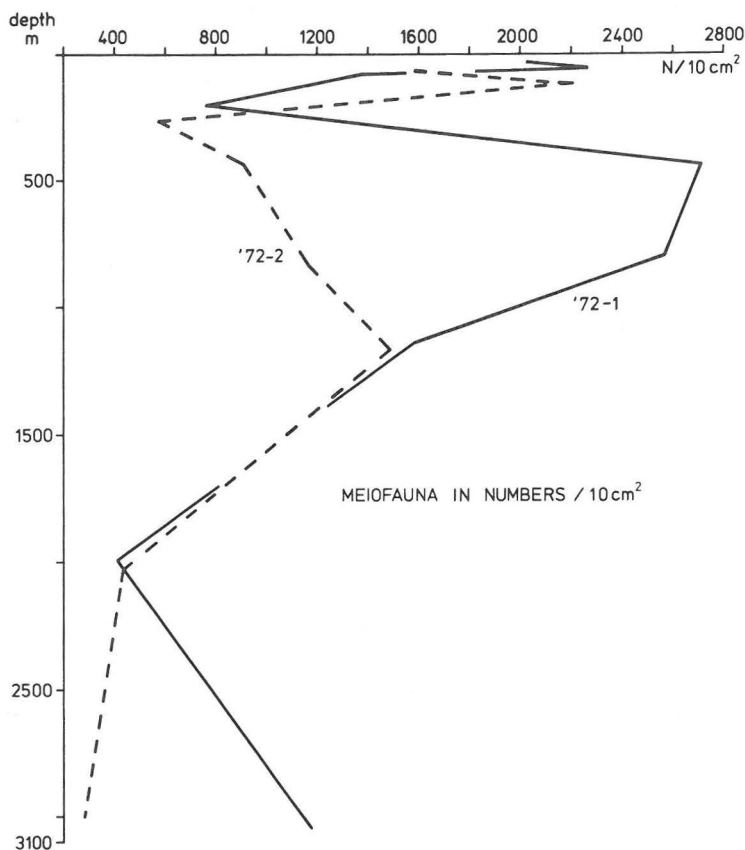


Figure 220. The density of meiofauna (numbers/10 cm<sup>2</sup>) in the '72 transects.

### Macro-infauna

These macro-infauna studies are based on box grab samples with a surface area of 600 cm<sup>2</sup>, and three samples were taken at each station. The smallest sieve mesh size used was 0.5 mm.

The results are not fully comparable with the data reported above since the information on macro-infauna does not cover the same depth range. Comparing the two transects '77-1 and '77-2 (Fig. 221), the latter sampled off Cape Blanc shows higher mean values. The difference in standing stock between the two transects may be attributed to food availability and upwelling-enhanced productivity in the area of transect '77-2.

The infaunal component, which could better be termed "grab-fauna" since small epifauna is included, does not show in either of the two transects the upper slope minimum as demonstrated by the data on chloroplastic pigments and meiofauna. The reason could be different food requirements of macro- and meiofauna, suspended or deposited organic materials, respectively. A high concentration of suspended organic particles, unable to settle permanently, forms a good food source for filter-feeding organisms, while bottom dwellers

(*viz.* meiofauna) find a poorer food supply under such conditions. Species analysis has not been conducted so far, but most macrofaunal species caught seem to be filter feeders, which would explain their large numbers on the upper slope.

Infaunal macrobenthos mainly on the shelf was sampled by Nichols and Rowe (1977) off Cape Blanc. They found higher densities at the stations of the outer shelf (57–90 m) than on the inner shelf (30–39 m), the latter not sampled in the present study. At the shelf break (100 m), faunal density was low and comparable to that at 1800 m, while higher numbers were encountered at 180 and slightly less at 480–556 m depth. Their biomass data show a similar trend, but exhibit a much wider range. The low values at 100 m depth, and the comparable high numbers from the slope, are remarkable. The actual figures show a poor correspondence with the numbers I counted, and this can only partially be attributed to methodological differences, *i.e.* the use of 0.42 mm mesh by Nichols and Rowe and 0.5 mm in my studies, since no general trend is visible for comparable depth strata.

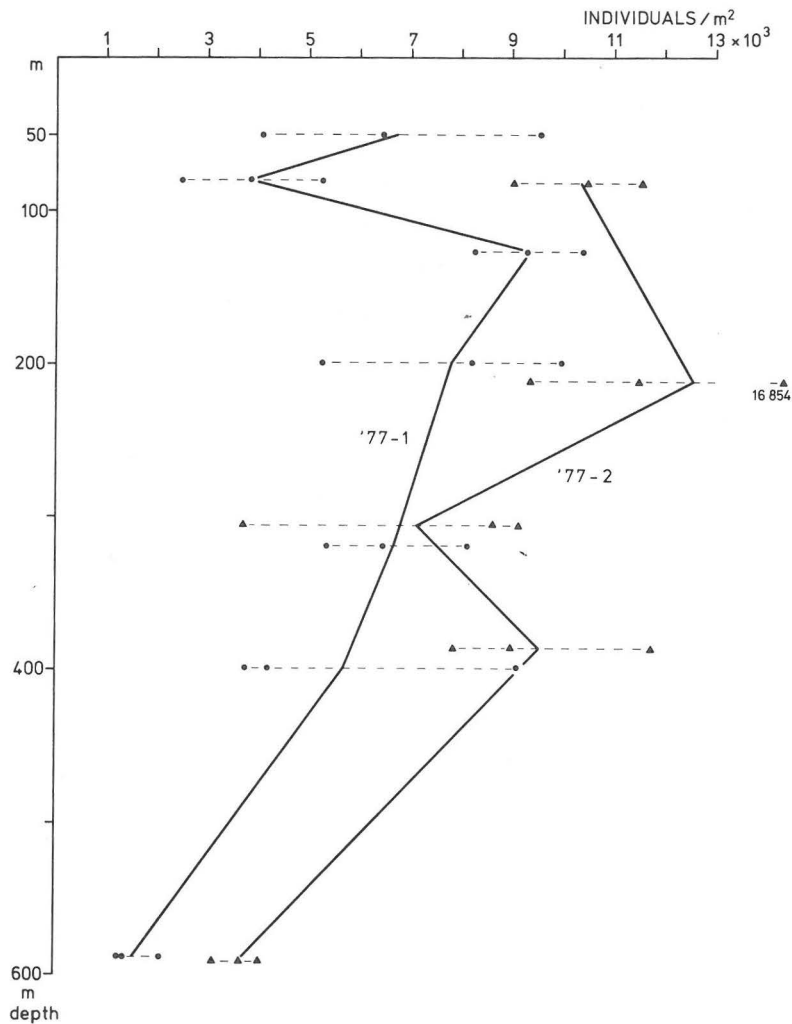


Figure 221. The abundance of macro-infauna ("grab-fauna") in the '77 transects (numbers/m<sup>2</sup>). Hatched lines connect the three absolute values used for each mean. Circles denote transect '77-1. Triangles denote transect '77-2.

Production rates off Northwest Africa have been deduced from biomass estimates by Nichols and Rowe (1977), and assumed to be 40–60 g wet weight/m<sup>2</sup>/yr, which are high values for shelf and upper slope regions. These rough estimates do not include the larger filter feeders, whose productivity is not known.

Nichols and Rowe do not describe an upper slope minimum. As mentioned above, their sampling did not cover the upper slope and their results from 100 m and around 500 m depth are not sufficient to elucidate it. North of the Canary Islands, off South Morocco, Boucher and Glemarec (1974) discovered an increase of infauna down to about 50–60 m, followed by a decrease to a depth of 140 m. At 300 m depth a new faunal maximum was found and from there on a steady decline.

### Megafauna

In comparison with the "grab-fauna" the megafauna should be termed "photo-fauna". Their large size and relatively low density do not allow them to be gathered quantitatively with grabs. The only method for receiving information on their density and distribution is the photographic record, and Figures 222–228 demonstrate their photogenous character.

The entire area between 50 m and 350 m depth is dominated by filter-feeding organisms. On the shelf off Cape Blanc the octocorallian *Pennatulula rubra* (Fig. 222) is a conspicuous member, and at the outer shelf the featherstar *Antedon bifida* (Fig. 223) and solitary corals like *Caryophyllia* sp. (Fig. 224) are prominent species. At the shelf edge a rather sharp break occurs



Figure 222. *Pennatula rubra*. 103 m depth, frame 546.

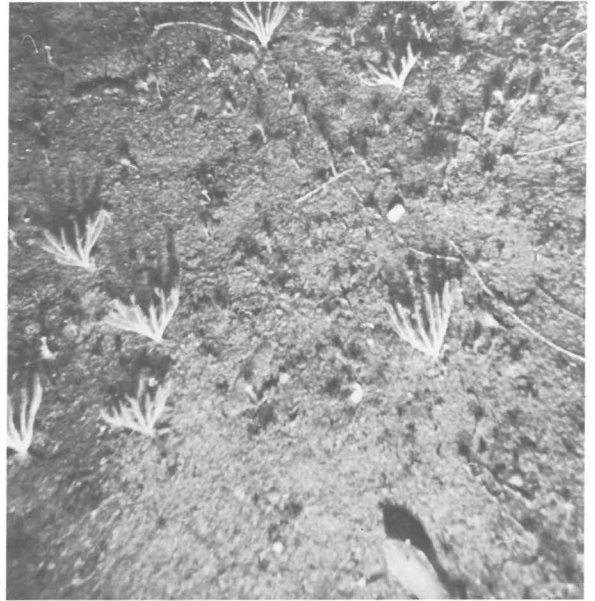


Figure 223. *Antedon bifida*, some lying gorgonariids, *Lanice conchilega* tubes, and two small flatfishes. 230 m depth, frame 871.



Figure 224. Dense cluster of *Caryophyllia* sp., solitary corals in a dense patch, and *Pennatula rubra*. 92 m depth, frame 417.

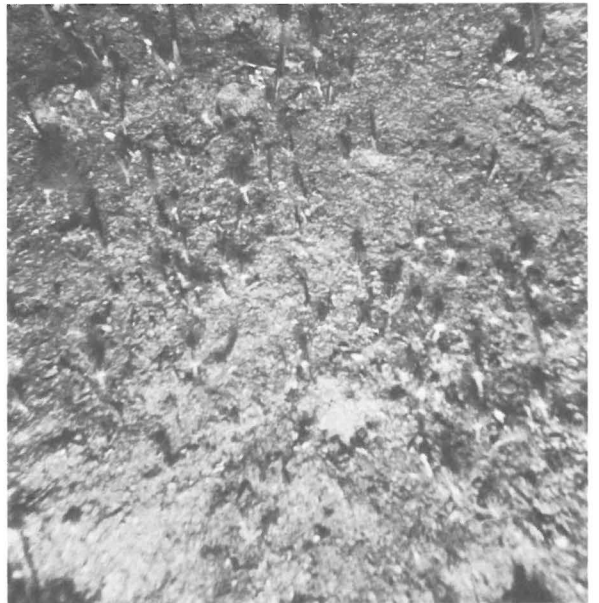


Figure 225. Several tubes of *Lanice conchilega* (Hartmann-Schroeder, personal communication). 135 m depth, frame 708.



Figure 226. Nine *Pinna ramulosa*, with only the shell and the mantle margin near the siphons to be seen. 255 m depth, frame 983.



Figure 227. Three *Munida speciosa* from the shelf population. 88 m depth, frame 282.



Figure 228. Several specimens of *Jullienella foetida*, large leaf-like Foraminifera. "Meteor" 44, station 192, transect '77-2, 67 m depth, frame 161, 16 February 1977.

Figures 222-227. "Meteor" 44, station 245 off Cape Blanc, 27 February 1977.

and the stock building species are the polychaete *Lanice conchilega* (Fig. 225) together with ascidians, actinians, large tube-dwelling polychaetes, sponges, and the large bivalve *Pinna ramulosa* (Fig. 226). This list of photogenous filter feeders could be prolonged, while sediment-feeding organisms like the holothurian *Stichopus disticha*, ophiuroids, or preying decapods are rare. Only at a depth of 200 to 350 m is *Munida speciosa* (Fig. 227) abundant in some places (Türkey and Thiel, 1977). Small, unexploitable fish are regularly seen on the photo-transect (i.e. Fig. 223).

Filter feeding seems to be the dominant style of life in this upwelling area. Newton et al. (1973) describe dense fields of *Pinna ramulosa* on the shelf off Cape Barbas at 48-57 m depth. According to Gosselck (1975), Flood et al. (1976), and Flood et al. (1982), some 6000 km<sup>2</sup> of the shelf have a population of probably more than 2000 specimens of *Branchiostoma senegalense* per m<sup>2</sup>, accounting for 450 g/m<sup>2</sup> wet weight (Thiel, 1978) or even 500 g/m<sup>2</sup> (Gosselck, 1974).

Judging from the photographic record, there seems to be a gradual decrease in the megafauna with depth from the outer shelf down the upper slope. The minimum zone in the region of the upper slope as detected for sediment properties and for meiofauna is not visible, a result comparable to that for the macrofauna. However, some indication for the deeper slope maximum is exhibited by at least one megafaunal species, the actinian *Actinoscyphia aurelia* (Aldred et al., 1979). Large masses of this species were trawled by "Discovery" and by "Meteor" at about 1000 and 2000

m depth in the central upwelling region off Cape Blanc. Trawl catches are not considered to be quantitative, but some of the samples are the largest ever hauled on board. Taking into account that a trawl never collects all animals in its path, the calculated densities of up to 5.5 individuals/m<sup>2</sup> are the highest ever recorded for that depth.

The populations of the "photo-fauna" are less well developed on the southern transect (17°N). Further, another component is dominant on the shelf at 60 m depth, i.e. the leaf-like foraminifer *Jullienella foetida* (Nørvang, 1961) (Fig. 228), a "photogenous protozoan". In some areas they cover up to 10 % of the sandy bottom. Also, on the northernmost transect '75-1 at 25°N the fauna of large filter feeders is less well developed than in the central (Cape Blanc) area.

The importance of filter feeders, of preying and sediment-dwelling animals, as well as of fish in the Cape Blanc region, is apparent when compared with an area of little or rather no upwelling off Cap Blanc du Nord, 33°30'N (Morocco). Fine-grained sediments cover the sampling area at a depth of 200 m and not much activity of organisms is seen. The community is dominated by sediment dwellers with a few additional epifaunal species. There are no filter feeders, which indicates the low concentration of food particles suspended in the bottom water. Differences in water movement, in the food particle load, and finally in production, are essential for an understanding of the bottom communities in shelf and slope upwelling and non-upwelling benthos communities.

Looking at the benthic species in the Northwest African areas sampled or observed in the bottom photographs, not much food for demersal fish seems present. The overwhelming part of the benthic biomass is made up of filter feeders like Octocorallia, Actiniaria, Madreporaria, tube-dwelling Polychaeta, Crinoidea, and Ascidia. These species do not appear to be preferred food organisms for nourishing good fish stocks.

## Benthos observations from other upwelling regions

Since the benthos in general depends on the production of primary organic matter and its transport to the near-bottom water and to the sediment, high standing stocks of benthic organisms should be expected in all upwelling regions. However, several factors (physical, biological) may disturb this picture.

The world's most important upwelling area is the one off Peru and Chile. Surface productivity is high and sedimentation of organic matter even more so. The standing stock of benthic animals is high, but shows a pronounced minimum, varying in depth between 150 and 500 m. While currents and water movement sys-

tems are principally similar, the explanation for the minimum differs from that off Northwest Africa. Off Peru the Subsurface Countercurrent, at depths of 50 to about 400 m, shows a very low oxygen content with less than 1 ml O<sub>2</sub>/l (Gallardo, 1976, 1977; Zuta et al., 1978). This in conjunction with a high amount of digestible organic matter causes oxygen deficiency and extensive sulfide biomes on the seabed. Most of the benthic organisms are not able to withstand the deoxygenated waters and the H<sub>2</sub>S conditions. Only a limited number of species can survive. Gallardo (1976) mentions meiofauna-sized polychaetes and nematodes with a biomass of only 0.17 g/m<sup>2</sup> wet weight at depths of 45–50 m. Low values for the standing stock of macrofauna were observed by Savilov et al., (cited by Khusid), while Khusid (1974) found low numbers of foraminifers in the sediments of the upper slope off Peru.

However, the sulfide biome is characterized by microbial life consisting of many kinds of prokaryotes. There is *Thioploca*, a gliding species with long filaments, *Ocellularia*-types of the cyanobacteria, flexibacteria, and many others. In considerable areas the filamentous microbes are interwoven, forming blankets which may be so thick that they can reduce the efficiency of fishing nets (Gallardo, 1976).

This is of importance, as some fishing on penaeid and galatheid shrimps and on hake is conducted off Chile in the area of these microbial communities. Gallardo (1977) suggests a possible trophic relationship between these commercially exploited crustaceans and fish stocks and the filamentous bacteria.

Independent of community type, oxygen or sulfide biome, total biomass is high throughout, while macrofauna is low under oxygen-deficient conditions. Frankenberg and Menzies (1968) report a minimum of 6.5 g/m<sup>2</sup> of macrofauna wet weight at 519 m, and between 112 g/m<sup>2</sup> at 126 m and 28 g/m<sup>2</sup> at 995 m, off Peru at 8°N. For an area between 15° and 18°N, Rowe (1971a) reports a wet weight of less than 1–10 g/m<sup>2</sup> for the macrofauna in the sulfide biome but more than 200 g/m<sup>2</sup> at about 1000 m, where below the Subsurface Countercurrent enough oxygen is available. Biomass of the filamentous microbes seems to be much higher than metazoan biomass in some places. Gallardo (1977) encountered more than 1 kg/m<sup>2</sup> wet weight for the filamentous microbes at 60 m depth outside Concepción Bay, while the macro-infauna biomass amounted to about 115 g/m<sup>2</sup> (0.25 mm<sup>2</sup> sieve).

The information on the benthic fauna off the coasts of Peru and Chile is in fact insufficient to give a complete picture of the situation. Several transects within an upwelling intensity gradient should be sampled in order to understand the benthic system. In addition it would be of great interest to conduct fotosed surveys from about 1000 m depth up the slope and the shelf, passing the sulfide biome, to learn about the coverage of the filamentous bacteria and about the benthos component of the filter-feeding megafauna.



Off Walvis Bay, Southwest Africa, a similar sulfide biome covers a smaller area, on the inner shelf in the depth range between 50 and 200 m, where the sediment contains between 5 and 26 % of organic carbon (Calvert and Price, 1971). Upwelling off India occurs in a half-year cycle and is driven by the monsoon winds. Productivity and sedimentation are not exceptionally high, but the oxygen-deficient water impinging on the slope at more than 200 m depth is sucked up onto the shelf when the monsoon blows. During June – September, fishery breaks down to less than 25 % owing to an avoidance reaction of fish and shrimps to the low oxygen content (0–0.5 ml O<sub>2</sub>/l) of the water (Banse, 1964; Kinzer, 1967; Sankaranarayanan and Qasim, 1968).

The northern hemisphere upwelling regions of the Atlantic and the Pacific seem to have no sulfide regions. Khoo (personal communication) encountered lower Eh-values in surface sediments at 21°N than on the transects at 25° and 33°30'N along the North African coast. However, all values were still positive and became negative at only a few centimetres deep in the sediment. The only hypothetical note on the influence of upwelling on the benthos off the California–Oregon–Washington coasts is by Carey (1972): Benthos standing stock decreases from the south to the north, with probably a factor of 2 between Oregon and Washington.

From the same region, information on commercially important benthic species is provided by Peterson (1972) and by Peterson and Miller (1975). These authors suggest a relation between upwelling intensity and catches of the shrimp *Pandalus jordani*, of the razor clam *Siliqua patula*, and of the dungeness crab *Cancer magister*. Upwelling indices were computed, taking into account the volume of upwelled water (calculated from wind data), time, and units of coastline. For *C. magister* a time lag of upwelling events and catches of 1.5 years for northern California and Oregon and of 0.5 years for Washington were indicated.

## Upwelling and benthos

Summarizing the results of benthos studies in upwelling regions so far available, a latitudinal and a depth aspect have to be considered. While the first is directly related to primary production, physical parameters are of major importance for the second.

### Latitudinal aspects

Comparing the benthos under the latitudinal aspect, standing stock should change in relation to primary production, which in itself depends on nutrient supply and on nutrient exploitation. Nutrient supply is related to upwelling intensity, which may change with season, and nutrient recycling.

The highest benthos standing stock in the Northwest African region is to be expected off Cape Blanc, where upwelling occurs throughout the year, while to the north and to the south benthos biomass should decrease according to shorter upwelling periods during the year (Wooster et al., 1976). This is supplemented by the productivity data given by Schulz and Kaiser (1974) and by Schulz et al. (1978).

The data on macro-infauna and on macro-epifauna seem to confirm this expectation. However, this does not hold so far for the meiofauna, but as pointed out above, we cannot generally expect the same reaction of macro- and meiofauna to environmental conditions. In addition, macrofaunal feeding pressure on meiofauna may vary between areas.

It is still an unsolved question, whether and to what extent benthic biomass reacts to within-year variations in primary production. While Rowe (1971a) relates biomass of benthos to yearly averages of primary production, Hargrave and Peer (1973) found a correlation of benthic standing stock only with spring primary production. Therefore, not only primary production per unit of time seems to be of importance for the benthos, but also the timing of this production. Local differences in the transfer of organic matter to the bottom are introduced through the number of trophic steps with their respective loss of energy, through feeding habits in relation to food availability, and through the intensity of recycling with regard to productivity (Nakajima and Nishizawa, 1972). Our knowledge of these energetic connections is still very limited.

### Depth aspects

Benthos standing stock within each depth transect, from the shelf down the continental slope and rise, depends ultimately on the average primary production in the surface waters of an area. Rowe (1971a, b) considered benthos to be directly related to primary production and inversely to depth on a logarithmic scale. As a first approximation this may be correct (see above), but local hydrographic conditions may introduce deviations from this pattern (Thiel, 1979). Some of these deviations may be connected with upwelling processes, while others are of a more general nature.

Although still incomplete, our best knowledge of physical conditions and benthic life is available for the Cape Blanc area. Explanations are wanted for the deviations from the apparently “normal” benthos distribution, i.e. for the upper slope minimum and for the lower slope maximum in faunal densities.

#### *The upper slope minimum*

The upper slope minimum is situated at 200–300 m depth, i.e. the depth range of the counter current. At the upwelling symposium in Kiel in 1975 I stated my opinion (Thiel, 1978) that this current might not allow

organic matter to settle or that it might erode potential food sources. In the meantime it has become evident that the counter current is too weak for such action. Observations on tides and internal waves by Fahrbach and Meincke (1978 and personal communication) have shown that the interactions of water movements due to dissipation of tidal and internal wave energy at that depth range are much stronger. Therefore, non-sedimentation of organic particles on the upper slope is probably due to tides and the impinging of internal waves on the bottom of the oceanic basin at the depth range around the shelf break. This is a world-wide phenomenon known to geologists (e.g. Swift et al., 1971; Kudrass, 1973). Yet, it is not primarily related to upwelling. In upwelling regions the non-sedimentary or eroding power may be somewhat intensified by the counter current, which on its own would rarely be strong enough to change the sediments, the sedimentation, and with them the animal communities. These conditions may indicate a downslope transport of organic matter into the region of the lower slope maximum.

#### *The lower slope maximum*

While theoretically a gradual decrease of faunal density is expected with increasing depth, in the upwelling off Cape Blanc below the upper slope an increase was discovered with a maximum around 1000 m and deeper. Feeding-type analysis will probably indicate this faunal maximum to consist of suspension and sediment feeders. This appears from high densities of *Actinoscyphia aurelia* (Aldred et al., 1979) and of meiofauna and is further supported by bacterial counts, estimates of chloroplastic pigment equivalents, organic energy and organic carbon measurements, and by grain-size distribution (Lange, 1975; Bein and Fütterer, 1977). All facts point to a strong sedimentation regime and to a decrease in the carrying capacity of the water masses for hydrodynamically light particles in this depth range. Inert materials and food particles, which normally settle out on the upper slope, showing a sedimentation decreasing with depth, come to rest and concentrate around 1000–2000 m depth in the Cape Blanc area. Mittelstaedt (1976) in his model concludes a near-bottom downslope water movement, Horn and Meincke (1976) and Fahrbach and Meincke (1978) describe internal waves and tidal current velocities of 30 cm/s; and up to 50 cm/s are recorded 8 to 10 m above the bottom by Meincke et al. (1975) and by Brockmann et al. (1977). Kullenberg (1978) encountered turbid bottom water layers, and Bein and Fütterer (1977) found indications of downslope transport of sediments. All these facts point to food transfer into deep water, where a relatively high food supply allows dense populations to thrive.

It is an open question whether sedimentation conditions depend on processes related to upwelling or to shelf-edge hydrography. The truth seems to be a mix-

ture of both. Shelf-edge hydrography is, however, involved to the extent that many of the food particles are prohibited from settling out from the water column at the upper slope, and are thus possibly transported to greater depths.

However, good or even better arguments speak for a connection with the upwelling system. Organic matter originating from local primary production is transported offshore in the Ekman layer, and this material will ultimately sink to the bottom. Mortality and sinking may be higher in slope regions than in the reaches of the continental shelf. Weikert (1977), in his discussion on observations of copepod carcasses, points to the stress upon plankton populations living near the frontal zones between water masses. Variability in the position of these zones, shifting over the outer shelf and the inner slope in relation to wind conditions, causes high mortality rates among planktonic organisms.

Besides pure gravity sinking, the transport into deeper water may be enhanced by downwelling processes (Fraga, 1974; Hagen, 1974; Johnson et al. 1976; Walsh, 1976). Depending on shelf and slope inclination angle and on wind stress and currents, a double-celled hydrographic system may develop. Theoretical considerations show a frontal zone, more or less vertical, or with a tilted discontinuity layer, in which organic particles, originating from areas of high production, may be carried to greater water depths. From there they will tend to sink to the deeper slope. The horizontal distances from the shelf edge at 100 m depth to the 1000 and 2000 m isobaths are only 30 and 40 km, respectively, which are covered by the double-cell upwelling system. It is not known how far these downwelling fronts penetrate into the ocean and how fast water and matter transport takes place. But it seems plausible that downwelling-enhanced sedimentation is an important process in the transport of food to the organisms comprising the lower slope maximum.

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