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Copepod Carcasses in the Upwelling Region South of Cap Blanc, N.W. Africa

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Abstract

High numbers of copepod carcasses were found in zooplankton samples taken in the upwelling system off N.W. Africa. The validity of the measurements is discussed. It is suggested that rapid changes in the environment, caused by the pulsation of violent mesoscale upwelling at the shelf edge, result in an increased mortality in zooplankton. Considerations are made on the role of copepod detritus in the upwelling region.

Introduction

Information on the amount of dead organisms in zooplankton in the natural environment is still scarce. Farran (1926) reports that the number of mutilated copepods in relation to living individuals appears to increase with depth. In the oligotrophic Sargasso Sea, dead copepods are suggested to outnumber the living fraction in net tows from 2,000 to 4,000 m (Wheeler, 1967). Similar phenomena may also occur in surface waters (Weikert, 1975).

This paper presents, for the first time, data derived from the euphotic layer of a tropical area in the Canary Current system eutrophicated by upwelling processes. Some hypotheses are put forward concerning the cause of high numbers of copepod carcasses and the ecological consequences which might result from increased mortality of copepods in the upwelling region off N.W. Africa. A more detailed study will be published in the "Meteor" Forschungsergebnisse of the Deutsche Forschungsgemeinschaft.

Materials and Methods

In February-March 1972, during Cruise No. 26 of R.V. "Meteor", zooplankton was collected in the upwelling region off Mauritania. Samples were taken with a neuston katamaran (Hempel and Weikert, 1972) equipped with two 300 µm nets. At a towing speed of 2.5 knots, two layers (at about 0 to 13 cm and 15 to 30 cm depth) were sampled simultaneously for 20 min.

At the beginning and at the end of the cruise, towing occurred in oceanic waters and in the border area of a zone of older upwelled water, which was adjacent to the oceanic regime. Since in both regions there were no significant differences in the zooplankton, they will be referred to as "oceanic water". In the middle of the cruise, repeated transects were made from the oceanic water to the shelf water of the Bank d'Arguin, crossing the area of large-scale coastal upwelling and remaining several days at the same position. Thereby, zooplankton was collected near to and at the shelf break in a transition located within the upwelling area. This transition separated the older upwelled water from a zone of freshly upwelled water covering areas of the shelf and the shelf break (Fig. 1).

A total of 23 tows was made during the cruise. Seventeen tows, which were assigned to certain time intervals during broad daylight and at dusk, were suitable for a comparison between the oceanic and transitional waters.

All exoskeletons of copepods, as well as their fragments, were sorted from the original samples preserved in buffered 4% formalin. Depending on species, only those pieces of the chitinous integuments were counted which belonged either to the head or to the abdominal region of specimens, in order to avoid an overestimation of carcasses. The identifica-

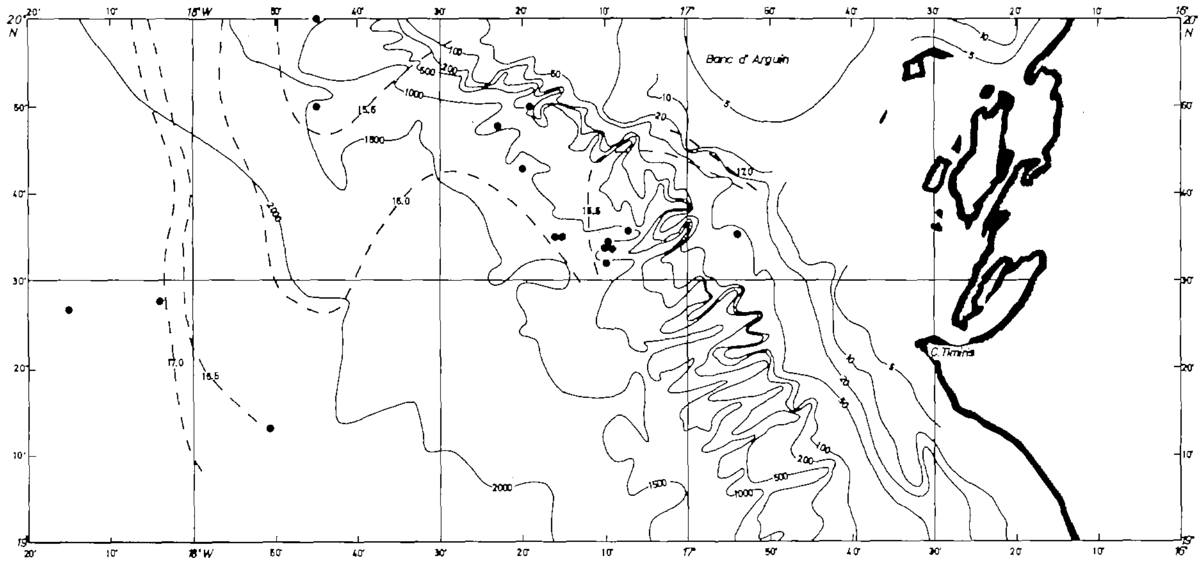

Fig. 1. Composite temperature distribution (°C) between February 29 and March 2, 1972 during first third of the zooplankton investigation of R.V. "Meteor". Temperatures <16°C indicate freshly upwelled water which is associated with two cores of violent mesoscale upwelling (<15.5°C) at the shelf break (after Shaffer, 1976). Filled circles: positions of zooplankton tows between February 26 and March 9, 1972. Seven tows from oceanic water, made on March 14, were located at 19°50'N, 19°11'W

tion of copepods which apparently were dead when captured was described by Wheeler (1967) and Harding (1973), who made similar observations. Individuals whose exoskeletons were split between the cephalic and thoracic regions were considered dead when parts of the dorsal muscle and internal tissue had collapsed and were partly lost. Often, in the swimming feet or in the body, degradation of internal structures as well as loss of tissue were plainly noticeable although the integument appeared intact. In contrast, copepods which had been damaged or mutilated during the sampling procedure exhibited well-structured tissue and jointed appendages in relatively good condition.

Results

Hydrographic Situation

During the investigation in the area between Cap Blanc and Cap Timiris, three main water masses existed: shelf water, upwelled water, and oceanic water. These water masses were separated by strong physical fronts (Fig. 1).

The warm bank water of high salinity (>16°C, >36.3‰) covering the shelf and the Bank d'Arguin, was separated from the upwelled water (<16°C, 35.5 to 36‰) at about the 17 m depth line. The position of this front was marked by an abrupt change in the water colour from a milky-green of the bank water to a green-blue of the upwelling water. Beyond the shelf edge, at a distance of 50 to 100 km off the bank front, a second, less pronounced front separated the regime of upwelled water from the clear blue oceanic water, which was characterized by temperatures of >17°C. There were no differences in salinity between the water masses (Mittelstaedt, 1976).

Within the coastal upwelling regime, violent upwelling occurred, ranging from the 17 m depth line of the Bank d'Arguin to about 20 km seaward. The seaward front of the intense blue, freshly upwelled water bordering the area of older upwelled water, was associated with a surface convergence (Tomczak and Miosga, 1976). This internal upwelling front, referred to as "transition or transitional zone", was marked by an increase of temperatures from 15.0° to 16.0°C over a distance of 2 to 4 km.

During the investigation, the fronts bordering the zone of intensive upwelling approached each other and simultaneously moved slowly landward. In the middle of the survey, the bank front collapsed, and a strong flow of bank water streamed seawards for approximately 5 h. Simultaneously, within a few hours the offshore front (= transition) was displaced about 10 km onshore. Thereafter, the bank front was re-established, whereas the transition receded westward

(Shaffer, 1976). Irregular bursts of bank water and events of intense mixing at the upwelling fronts are typical phenomena in the area off the Bank d'Arguin (Mittelstaedt, 1976; Peters, 1976).

Zooplankton Distribution

The bulk of net zooplankton consisted of copepods (75% of the total number of zooplankton), of which the calanoid family Temoridae was most abundant (34%).

The horizontal distribution of copepod numbers exemplified the general distribution of zooplankton: maximum numbers of specimens were found in the transitional zone separating the older upwelled water from the freshly upwelled water, i.e., in the vicinity of the shelf break. Their average density amounted to 27,646 specimens/100 m^3. In the oceanic water density was lower – 5,240 copepods/100 m^3.

Among the Temoridae, the distant neritic *Temora stylifera* was most abundant in the oceanic water. A mean density of 1,445 specimens/100 m^3 was calculated in comparison to 769 specimens/100 m^3 in the transition. The strictly neritic species *T. turbinata*, however, was obtained in maximum numbers from those tows made in the zone of the transition (9,123 specimens/100 m^3). Judging from the high amount of very young copepodite stages found in the transition zone and the low average of 207 specimens/100 m^3 encountered in the oceanic water, the internal upwelling front apparently functioned as a strong barrier, hampering the seaward distribution of this shelf-species.

Occurrence of Copepod Carcasses

In all samples, carcasses and exuviae of copepods at all ontogenetical stages were conspicuous. Up to 97% of the carcasses (in relation to the total number of copepods) coincided with the transition separating the upwelled waters of different age. Samples containing a minimum of copepod detritus (0.5%) were encountered in the oceanic water. In this latter water, with the exception of two tows, the amount of carcasses did not exceed the 20% level, but within the transition, near to the shelf break, 9 out of 11 tows yielded more than 25% copepod detritus. On an average, carcasses amounted to about 16 and 28% of the total copepods in the oceanic and transitional zones, respectively.

Of the amounts of copepod carcasses present in the oceanic area and the transition zone, temorids contributed 18 and 39%, respectively. The portions of the dead fractions for both the above-mentioned species have a similar range of magnitude: for *Temora stylifera* from 9 to 40%, and for *T. turbinata* from 12 to 30%. The values obtained for the latter species suggest that mortality of *T. turbinata* is more pronounced at the shelf break, which constitutes part of the species reproductive area, than in its distribution area, i.e., in the realm of the oceanic water.

Discussion and Conclusions

The author realizes that counts of carcasses are somewhat ambiguous due to inadequate techniques. Numbers, in part, are biased by the fact that identification of specimens (dead prior to the tow) from the living fraction of the sample, is not absolutely objective. Another, unalterable, source of bias is the disintegration of older copepod carcasses during collection by nets and water bottles (Harding, 1973).

Nevertheless, there is clear evidence that dead copepods constitute a significant part of the copepod plankton off the Banc d'Arguin. In comparison to investigations made in the Sargasso Sea, mean numbers of carcasses found in the surface waters of N.W. Africa exceeded the values evaluated from single deep-water tows by Wheeler (1967) by one or two orders of magnitude. It is further significant that the number of carcasses is correlated with the properties of definite water masses.

The question is, however, whether these observations are valid for the entire upwelling system off N.W. Africa. Firstly, high concentrations of carcasses may be effected by accumulation at the air-sea interface as well as by crowding at the internal upwelling front which is associated with a convergence. Such an accumulation is a well known phenomenon in the sea. Secondly, the enormous variability in the hydrographic conditions of the N.W. African upwelling region will cause manifold phenomena in its plankton distribution. In particular, the high proportion of dead copepods of all developmental stages in the transition zone separating the upwelled waters of different age may have been locally generated. With respect to the upwelling system as a whole, however, events of violent mesoscale upwelling at the shelf break, such as those observed during this investigation, are considered a common feature of N.W. African upwelling waters. These events are caused by internal surf along the shelf edge (Tomczak, 1973) or by submarine canyons (Shaffer, 1976).

On the basis of the arguments presented above, I would like to put forward some working hypotheses to stimulate intensified studies on zooplankton detritus in the light of the N.W. African upwelling system (or of any other upwelling region).

(1) The pulsation of mesoscale upwelling events associated with the dramatic build-up and the collapse of sharp transitions, as well as their rapid horizontal shift over some 10 km, will increase stress upon the zooplankton inhabiting the Ekman layer and the zone of downwelling. This, in turn, will lead to increased mortality in the zone of violent upwelling at the shelf break.

(2) Increased mortality compensates, to some extent, for a surplus in the standing stock of secondary producers which obviously are preyed upon by only a small stock of invertebrate carnivores. There is reason to suppose that the horizontal and vertical distribution of the carnivorous copepod *Euchaeta marina* in the region of Cap Vert (Khromov, 1973) may be negatively affected by ascending water. In spring, this dominant carnivore apparently avoids the shelf slope where intensive upwelling occurs.

(3) Downwelling in the offshore front of mesoscale upwelling (Keunecke and Tomczak, 1976) and advection (Mittelstaedt, personal communication) facilitate rapid transport of carcasses to the deeper water and to the upper slope sediments. The shortened residence time of carcasses in the shallow-water layers also leads to enrichment of the water below 200 m depth with a less decomposed, i.e., higher energetic material, on which relatively large stocks of deep-water zooplankton and deep-sea benthos can feed.

The pelagic and the benthic realms are intimately linked by the "rain" of organic matter produced by the phytoplankton (Steele, 1974), or by food transport to the sea bottom in general (Thiel, 1975). In the upwelling region off N.W. Africa, where mesoscale upwelling occurs, detritus of the secondary producers is considered an important mediatory matter. Downwelling, however, is only one mechanism in the system of vertical transport which is by no means fully understood.

The downward transport of carcasses suggested near the shelf break appears to be supported by the investigation of Khromov (1973): above the slope, surface-dwelling copepods such as *Temora* species were collected in considerable numbers (1 specimen/1 m^3) down to 200 m depth. There are further indications that, besides phaeopigments, chlorophyll *a* is carried into the upper slope sediments (Thiel, in preparation).

(4) Primary producers are considered to "condition" freshly upwelled water through the release of organic metabolites (Barber *et al.*, 1971). In the N.W. African upwelling region, the decay of copepod carcasses contributes to the amount of biogene chelators. The problem of conditioning calls for very careful study, however, since recent results from cultivation of N.W. African phytoplankton in virgin upwelled water (Jacques *et al.*, 1976) are somewhat contrary to those reported in the investigations of Barber *et al.*

(5) The beneficial effects of copepod detritus suggested for the N.W. African upwelling region off Mauritania, however, appear to be valid solely in systems of moderate productivity. Upwelling systems, or particular regions within them, exhibiting excessive production, may result in mass mortality induced by adverse hydrographical and biological conditions. This, in turn, may lead to burial and fossilization of the organic material deposited on the sea floor (Baturin, 1974), thus prohibiting its recycling into the marine biosphere.

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