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Mid-water zooplankton profiles from the temperate ocean and partially landlocked seas. A re-evaluation of interoceanic differences

Bathypelagic zooplankton
Interoceanic comparison
Vertical distribution
Vertical flux

Zooplancton bathypélagique
Comparaison inter-océanique
Répartition verticale
Flux vertical

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ABSTRACT

Differences in the vertical distribution of bathypelagic zooplankton in the open northeast Atlantic and in the partially landlocked Levantine and Red Seas were re-evaluated to provide an interoceanic comparison. The decrease in zooplankton abundance with depth was most pronounced in the Red Sea and least evident in the northeast Atlantic. The Levantine Sea showed intermediate characteristics. The data plotted on a semi-log scale against a linear change in depth revealed a reduced rate of decrease in the zooplankton concentration with depth in the deep bathypelagic zone of the northeast Atlantic and the Levantine Sea. This pattern was also found for vertical profiles of micronekton abundance in the southeast Pacific. In the Red Sea, the decrease was exponential. Possible ecological mechanisms are discussed which might be responsible for these distribution patterns.

RÉSUMÉ

Profils verticaux du zooplancton bathypélagique des océans de basse latitude et des bassins marins semi-fermés. Réévaluation des différences inter-océaniques.

Les différences dans la répartition verticale du zooplancton bathypélagique entre l'océan ouvert (Atlantique Nord) et les bassins semi-fermés (Mer Levantine et Mer Rouge) ont été réévaluées à fin de comparaison inter-océanique. La diminution de l'abondance du zooplancton en profondeur est plus forte en Mer Rouge et moins forte dans le nord-est de l'Atlantique, tandis que la situation en Mer Levantine est intermédiaire. Les données portées avec une échelle semi-logarithmique en fonction de la profondeur indiquent une diminution plus faible de la concentration du zooplancton dans les zones bathypélagiques plus profondes de l'Atlantique nord-est et de la Mer Levantine. Un schéma identique fut observé sur les profils verticaux de micronecton dans le sud-est du Pacifique. En Mer Rouge la diminution est exponentielle. Certains mécanismes écologiques sont discutés qui pourraient être responsables des répartitions décrites.

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INTRODUCTION

The vertical distribution of pelagic animals in the deep sea is related to the flux of organic matter from the euphotic surface layer, the *in situ* production and consumption of organic particles in deep water, their loss due to dissolution and their sedimentation to the sea floor. In the past, the zooplankton abundance in the bathypelagic zone, below 1000 m, was believed to decrease exponentially with depth (Vinogradov, 1968; Wishner, 1980; Angel and Baker, 1982; Scotto di Carlo *et al.*, 1984; Roe, 1988; Weikert and Trinkaus, 1990). By evaluating vertically fine-spaced samples taken in the northeast Atlantic in 1988, we found that the decrease with depth in bathypelagic zooplankton abundance, determined as biomass and numbers, is relatively slight below 2500 m and thus better fitted to a power regression in the open ocean at lower latitudes. We have offered tentative ecological explanations for this distribution pattern (Koppelmann and Weikert, 1992). In the present study, we evaluated a set of profiles from different seas to test the proposed pattern and re-evaluate the hypotheses by comparing the expanded set of data from the Atlantic with those from deep, semi-landlocked warm-water seas, specifically the Levantine and central Red Seas. Possible qualitative differences in the vertical flux were considered.

There is a lack of data sets from net hauls, observations, and experiments at depths below 2000 m that are suitable for providing information on functional ecological processes occurring in the deep-sea ecosystem, except for a few findings from initial studies (*e.g.* Hargreaves, 1985 and refs.; Shushkina *et al.*, 1991). Consequently, the ecological implications relevant to oceanic systems outlined in this paper are rather speculative and general. They are meant to stimulate future studies on the structure and function of the deep-sea pelagic ecosystem.

MATERIAL AND METHODS

Consecutive, discrete zooplankton samples were taken throughout the water column during oblique tows at closely spaced depth intervals (Table 1) using a 1 m^2 MOCNESS with a 0.33 mm mesh size (Wiebe *et al.*, 1985) in the Levantine Basin of the Eastern Mediterranean southeast of Crete in January 1987. Similar samples were obtained in the central Red Sea during July 1987 and at the BIOTRANS site (47° N, 20° W) in the northeast Atlantic during March and April 1988 and 1992. The first two of these seas are generally characterized as semi-landlocked basins and are distinguished from the open ocean by their warm, saline deep-water mass. The temperature and salinity are 13.6 °C and > 38.65 in the Levantine Sea, respectively (*e.g.* Malanotte-Rizolli and Hecht, 1988), and 20.6 °C and > 40.50 in the Red Sea (*e.g.* Morcos, 1970). The environmental conditions are most extreme in the Red Sea. The difference in temperature above that in the ocean, for example, increases from 10.0 °C at 200 m to 18.5 °C at 2000 m depth. In the Levantine Basin, the increase is from 1.0 °C at 200 m to 10.0 °C at 4000 m depth.

In addition, we analysed a vertical micronekton profile from the tropical southeast Pacific, sampled during April and May 1992, to expand the set of vertical profiles (Tab. 1). These samples were collected using a 10 m^2 MOCNESS with a 1.6 mm mesh size, employing the sampling strategy described above. All the material was preserved in a 4 % formaldehyde-sea water solution buffered at a pH of 8.0 to 8.2. In the laboratory, the material was wet weighed using the method of Tranter (1962) and then transferred to a fluid composed of 0.5 % propylene phenoxetol, 5.0 % propylene glycol, and 94.5 % water (Steedman, 1976). Exoskeletons and carcasses were distinguished according to the methods of Wheeler (1967) and Weikert (1977) and excluded from the counts. All of the specimens in each sample were counted. The data were obtained for the zooplankton in the size range from 1 to 5 mm (Weikert and Koppelmann, 1993). Detailed information on the hydrographical conditions at the sampling sites, the hauls completed during the cruises, and the analysis of the material was previously described by Weikert and Koppelmann (1993) and Twest (1993). For the present study, only the water column below 1000 m is considered, to avoid influences on the conclusions from the mass of organisms that participate in daily vertical migrations (*see* Angel, 1989).

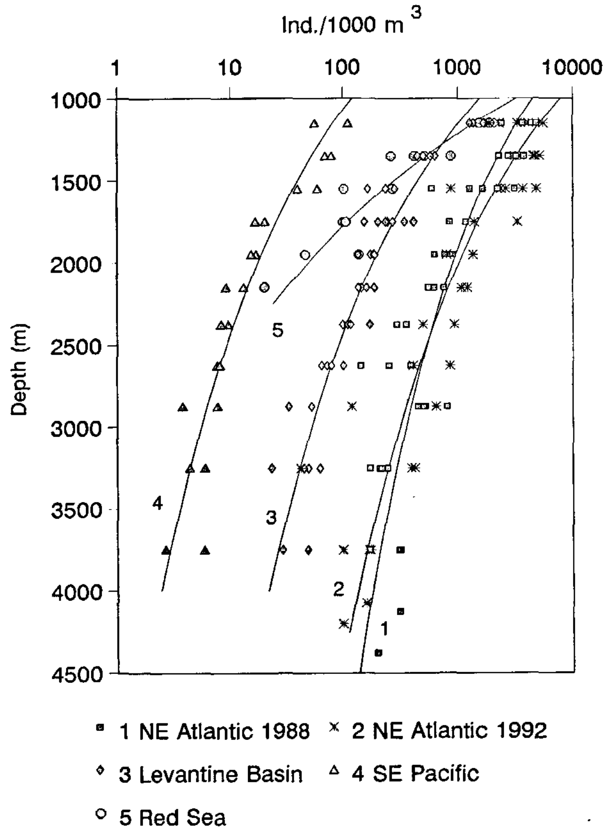

Figure 1

Vertical distribution of bathypelagic zooplankton and power regression lines at the sites investigated.
(1) $N = 10^{10.6} D^{-2.315}$, $r^2 = 0.837$.
(2) $N = 10^{12.6} D^{-2.918}$, $r^2 = 0.821$.
(3) $N = 10^{12.5} D^{-3.101}$ $r^2 = 0.925$.
(4) $N = 10^{10.5} D^{-2.811}$, $r^2 = 0.909$.
(5) $N = 10^{21.7} D^{-6.063}$, $r^2 = 0.814$.
N = Individuals per 1000 m^3,
D = Depth.

Table 1

Cruise and sampling data. A = Number of samples. B = Mean filtred volume (m^3).

No.	Cruise name	Date	Location
1	Meteor 6/7	11.04. – 10.05.88	NE Atlantic, 47°N, 20°W
2	Meteor 21/1	21.03. – 05.04.92	NE Atlantic, 47°N, 20°W
3	Meteor 5/1	14.01. – 21.01.87	Levantine Basin, 34°N, 26°W
4	Sonne 79	28.04. – 13.05.92	Tropical SE Pacific, 07°S, 90°W
5	Meteor 5/5	24.07. – 29.07.87	Central Red Sea, 19-21°N, 38°W

Strata. (m)	Sample interval (m)	Meteor 6/7		Meteor 21/1		Meteor 5/1		Sonne 79		Meteor 5/5	
		A	B	A	B	A	B	A	B	A	B
1050-2250	200	21	1370	21	620	28	1275	12	8670	15	1295
2250-3000	250	11	1930	6	840	10	1450	6	12100		
3000-4500	250 or 500	11	2270	8	1350	6	3300	4	15500		

RESULTS AND DISCUSSION

Vertical distribution

The vertical distribution patterns of the mesozooplankton and micronekton abundance are depicted in Figure 1. A power curve is fitted to the data points for each region investigated. As shown for the data from the northeast Atlantic in 1988, the power function fits better when the rate of decrease in deep-living zooplankton biomass and numbers with depth below 2500 m is reduced in comparison with the stronger decrease between 1000 and 2500 m (Koppelmann and Weikert, 1992). This pattern was also observed in the Levantine Sea, and it also corresponds to the profiles obtained in 1992 for zooplankton from the northeast Atlantic and for micronekton from the southeast Pacific (Fig. 1). In addition, zooplankton profiles prepared from closely spaced samples down to 4500 m in the northeast Atlantic presented by Angel and Baker (1982) have a similar shape. All these data indicate that the observed pattern of distribution is a frequently observed feature. As an exception to this pattern, the nearly constant zooplankton concentrations could not be observed in the deep water of the Red Sea, where the maximum depth is 2500 m. These data fit an exponential regression well, according to the test for linearity, $p > 0.1$. It seems unjustified to suggest that the exponential decrease in the Red Sea below 1000 m is homologous to that in the other seas at similar depths. Wiebe *et al.* (1988) reported that zooplankton biomass was relatively constant at depths below 1200 m in the Guaymas Basin (27° N, 111° W), Gulf of California, which is about 2000 m deep. Their samples were also obtained using a 1 m^2 MOCNESS with a 0.33 mm mesh size for sampling at close intervals.

To make data on the zooplankton from the Red Sea comparable with those from the northeast Atlantic and the Levantine Sea (Fig. 1), we used a power regression. The methods and feasibility of this test were described by Koppelmann and Weikert (1992). The slopes of the regressions indicate that there are overall differences between the regions, as determined by an analysis of covariance, $p < 0.001$, and significant differences were also observed in the results of an *a posteriori* test (Tab. 2) of the slopes of every pair of regions, except for the Atlantic in 1992 and the Levantine Sea. The overall decrease in the zooplankton concentrations with depth was greatest in the Red Sea and least in the northeast Atlantic, while the Levantine Sea showed an intermediate decrease. Tests employing exponential regressions incorporating data from the literature obtained using different devices yielded similar results (Weikert and Trinkaus, 1990). However, unlike the data from wide interval sampling in the literature, differences among the slopes of the profiles are evident in the upper bathypelagic zone when the water column is sampled at close intervals (Fig. 1). Actually, below 2500 m, where the zooplankton concentrations are nearly constant, there are no detectable differences among these slopes tested by exponential regressions ($p = 0.256$).

It is generally thought that the similarity in the overall slopes of the exponential regressions (Angel and Baker, 1982; Roe, 1988) and power regressions (Koppelmann and Weikert, 1992) of data from the subtropical and temperate oceans indicate that processes determining the distribution in the deep-sea are similar despite differences in the overlying surface production. The differences in slopes found by exponential regressions (Wishner, 1980; Weikert and Trinkaus, 1990) and by power regressions (present study) in the various seas are generally related to the elevated temperatures in the bathypelagic zone of the semi-landlocked seas, which affect the processes determining the distribution of zooplankton (Wishner, 1980; Weikert, 1982). Accelerated bacterial metabolism and increased activity of extracellular enzymes (*e.g.* Meyer-Reil and Köster, 1992; Bianchi and Garcin, 1993) enhance remineralization of biogenic material and diminish the supply of food with increasing depth. As reported for the Red Sea by Thiel *et al.* (1987) and Pfannkuche (1993*a*), the bathyal benthic fauna in the food-limited environment is characterized by high maintenance expenditure and low production.

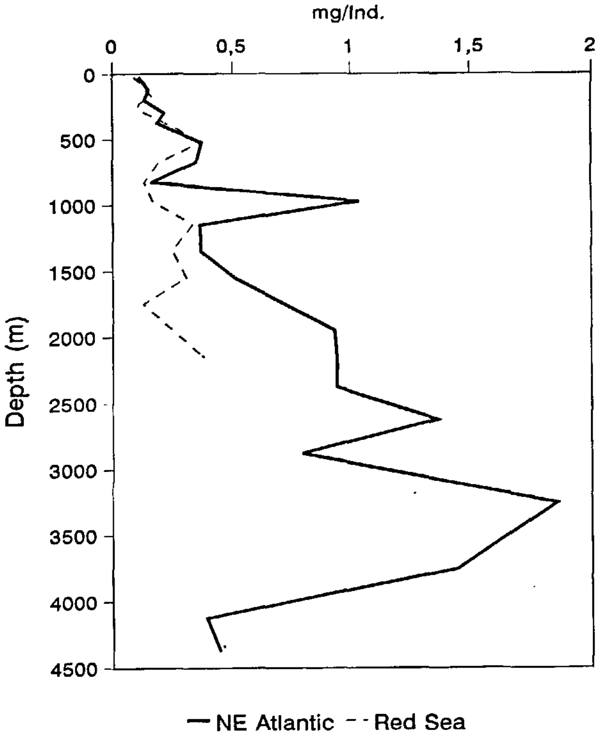

Figure 2

Wet weight profiles of individual zooplankton mean biomass.

The wet weight:number ratios for zooplankton show that the high metabolic demands are met at the expense of body size (Fig. 2). This does not imply, however, that there is a large standing crop of small zooplankters below 1000 m. Multiple nets with a 0.10 mm mesh size (Böttger, 1987) yielded ten times the number of metazoans collected using 0.30 mm mesh (Weikert, 1982), and the gradients of plankton abundance were similar (Böttger, 1987). On the other hand, the trend toward a relatively constant zooplankton biomass in the ocean at depths below 2500 m (Koppelmann and Weikert, 1992) is influenced to some extent by the increase in the mean individual weight with depth.

Evaluation of the hypotheses

The ambivalent differences between the regression coefficients of the profiles from the northeast Atlantic and the Levantine Sea may indicate that temperature is not the only factor which governs the processes in the water column (Tab. 2). The question arises whether there are other underlying ecological mechanisms which are responsible for the patterns of vertical distribution described. In discussing the power regression for the northeast Atlantic (Koppelmann and Weikert, 1992), we proposed that the following factors could theoretically compensate for the decreasing numbers of individuals and biomass: (1) resuspension, (2) faunistic changes, and (3) weak pressure by predators.

Table 2

Results of the a posteriori *test (Sokal and Rohlf, 1969). The sums of squares (SQ) of the slopes are presented in the upper right triangle, and the SQ of the y-intercepts, in the lover left triangle, if no differences were detectable in the slopes. SQ_{crit}; 0.05 = 0.303. Values in bold type denote significant differences.*

	NE Atlantic 1988	**NE Atlantic 1992**	**Levantine Sea**	**Red Sea**
NE Atlantic 1988	–	0.242	**0.429**	**2.696**
NE Atlantic 1988	0.141	–	0.20	**1.815**
Levantine Sea		**11.389**	–	**1.630**
Red Sea				–

Resuspension

Animals and organic particles, which could serve as a food source, can be resuspended from the sediment to more than a thousand metres above the seabed (Angel, 1990; Roe *et al.*, 1990; Geynrikh and Rudyakov, 1991; Gardner and Richardson, 1992). These can possibly sustain zooplankton at a nearly constant abundance in the lower bathypelagic zone. According to data from samples taken in reversed sediment traps, the upward flux of buoyant, resuspended particles from great depths can be considerable in comparison to downward mass transport (Smith *et al.*, 1989). Resuspension of small particles may occur due to currents at high velocity produced by energetic eddies (*e.g.* Hollister *et al.* 1984; Gross *et al.* 1988). In the BIOTRANS area and an adjacent site in the northeast Atlantic, which are about 4500 m deep, extensions of the benthic nepheloid layer high above the sea bottom, sometimes up to 1000 m, have been observed (Nyffeler and Godet, 1986; Auffret *et al.*, 1994). In this area, current velocities of 2 to 6 cm s^{-1} prevailed 10 m above the bottom. For 11 % of the deployment time, velocities were between 10 and 27 cm s^{-1} (Mittelstaedt *et al.*, 1986), due to the presence of high-speed currents and abyssal storms (*e.g.* Klein and Mittelstaedt, 1992). These currents are capable of resuspending fine particles and aggregates (Gardner and Richardson, 1992 and refs.). However, resuspended particles are poorer in nutrients than freshly sedimented ones. Honjo (1978) concluded that bathypelagic zooplankton prefers the fresh particles, thereby displaying coprophagic feeding habits. This conclusion cannot be denied on the basis of any information presently available. However, the richness of the pellets in aluminosilicates indicates that they originate as nepheloid layer particles (Spencer *et al.*, 1978). The influence of an increased availability of nutrients on bathypelagic plankton was studied at a hydrothermal vent plume site (Burd and Thomson, 1994). The conditions prevailing there supported an increase in the deep-sea zooplankton biomass, which was partly due to the invasion of animals from shallow water layers.

At first view, these arguments do not seem to be supported by the information from the two semi-landlocked seas. In the Levantine Sea, a significant upward movement of animals or their pelagic larval stages was not expected since appreciable amounts of macro- and megabenthos were not found at great bathyal depths (Tschukhtchin, 1963; Vinogradova *et al.*, 1982; Türkay, pers. comm.). The existence of several mesoscale eddies in the Levantine Sea has been reported by Özsoy *et al.* (1989) and Golnaraghi (1993), and we cannot exclude an ecologically relevant resuspension of sedimented organic matter. Evidence against the resuspension hypothesis seems to be provided by the exponential decrease of zooplankton concentrations observed in the bathypelagic zone of the Red Sea (Fig. 1). This contrasts to the situation described for the 2000 m deep Guaymas Basin by Wiebe *et al.* (1988), although the depth of the Red Sea basin (2500 m) resembles that of the Gulf of California and mesoscale eddies (Quadfasel and Baudner, 1993) as well as standing stocks of bathyal benthos are present (Thiel, 1979; Thiel *et al.,* 1987; Pfannkuche, 1993*a*). However, we believe that the exponential decrease in the zooplankton in the Red Sea can be explained by the impoverishment of the fauna below 1000 m. In fact, a true bathypelagic fauna is lacking, and the niches usually occupied by these species are only rarely occupied by species migrating from the mesopelagic zone (Weikert, 1987). Obviously, the use of resuspended organic material requires the presence of true bathypelagic animals capable of effective harvesting of suspended fine material (Weikert, 1990).

Occurrence of a new fauna

Re-evaluating data from Grice and Hülsemann (1965), Vinogradov (1968) described a well-defined faunistic succession of copepods between depths of 2000 and 3000 m in the northern subtropical region of the northeast Atlantic. Geptner (1973) and Markhaseva and Razzhivin (1992) observed a faunal shift in the species composition within a number of copepod families in the Kurile-Kamchatka Trench between 2000 and 4000 m, with the most pronounced change occurring at about 3000 m. This pattern appears to be typical for the fauna in general (Sagalevich *et al.,* 1991). In the Levantine Sea, *Lucicutia longiserrata* and *Candacia elongata* are the only genuine deep-sea copepods. They are endemic to the deep parts of the bathypelagic zone, where these two species constituted the bulk of its zooplankton (Weikert and Koppelmann, 1993).

A possible influence of resuspension on the establishment of nearly constant zooplankton concentrations when a bathypelagic fauna is present does not preclude the occurrence of differences among the bathypelagic species in the ability to filter and consume particles. This could increase the tendency toward constant abundance, even if it does not cause it. Koppelmann (1995) found significant seasonal fluctuations in mesozooplankton abundance within the upper bathypelagic zone, from 1000 to 2250 m, in the northeast Atlantic. This appeared to be associated with the transient input of phytodetritus. Unlike the situation in the upper bathypelagic zone, there was no observable reaction to the episodic influx of large food aggregates below 2500 m, in the zone of semi-constant zooplankton abundance. The term abyssopelagic, which is used for these great depths in some publications (*e.g.* Vinogradov, 1968), would then be ecologically defined.

Weak pressure by predators

Predation is thought to play a minor role in the bathypelagic zone for reasons related to energy and behavior (*e.g.* Childress *et al.,* 1980; Childress and Mickel, 1985). This may lead to less decrease in the amount of deep water zooplankton at depths below 2500 m than at shallower depths in the bathypelagic zone. In fact, strikingly similar zooplankton and micronekton biomass profiles in the bathypelagic zone of the northeast Atlantic (Roe, 1988), the absence of micronekton in the deeper bathypelagic zone of the Levantine Sea (Weikert, 1990), and data on feeding types among deep-sea zooplankton in the world ocean (Vinogradov, 1968; Vinogradov and Tseitlin, 1983; Sazhin, 1984) indicate that the animals are chiefly omnivorous or detritivorous at depths below 2000 m, and pressure by predation would thus be low. However, the data from the Red Sea do not support the conclusion that predation is of major importance. Although we did not encounter micronekton at depths below 1000 m in the Red Sea (Weikert, 1990 and unpubl. results), nearly constant zooplankton concentrations were not detectable below this depth.

In conclusion, the presence of a true deep-sea fauna with the ability to utilize the suspended particles in the bathypelagic zone, including the resuspended fraction, seems to be the most important factor responsible for the concentrations of mesozooplankton becoming nearly constant in the bathypelagic zone. However, predator-prey interactions and the upward flux of benthopelagic and benthic animals and their larvae cannot be ruled out as causative factors.

Ecological implications

If our findings are correct, the two bathymetric distribution patterns observed for the zooplankton may result from two main pathways of vertical flux in the deep-sea. The power curve pattern should be associated with a truly pelagic deep-sea fauna which is able to harvest small resuspended and slowly sinking particles. Their subsequent incorporation in fast-sinking fecal pellets is generally thought to increase the particle flux. In the oligotrophic Levantine Sea, the quantity of sedimented nutrients is not sufficient to support a benthic metazoan fauna.

In the Red Sea, which displays an exponential pattern, the flux of particulate organic matter through the bathypelagic zone would hardly be influenced by the strongly reduced numbers of metazoan consumers, thus allowing the existence of a bathyal benthos, though its biomass is less than that at similar depths in the ocean because of increased bacterial decomposition in the deep water column and for reasons related to the energy requirement of the fauna near and at the bottom (Thiel, 1979; Wishner, 1980). As a result of the conditions described above, the main source of nutrients reaching the bathyal zone of the Red Sea should be the epipelagic and mesopelagic layers. The nutrient material rapidly traverses the water column and thus consists of relatively fresh nutritive material. In the ocean, this second route is thought to be traversed by pulses of fast sinking macroaggregates and large organic particles, which contribute most to the mass flux toward the deep-sea floor (Wefer, 1989; Silver and Gowing, 1991; Walsh and Gardner, 1992).

However, unlike the northeast Atlantic (Billett *et al.,* 1983; Thiel *et al.,* 1988/1989; Riemann, 1989; Pfannkuche, 1993 *b*; Koppelmann, 1994 and others), no descent of macroaggregates has yet been observed in the two semi-landlocked basins. Nevertheless, we should look for potential causes of the strong pelago-benthic coupling. In the Red Sea, the transient import of material produced by *Oscillatoria* and salp blooms in the surface layers (Beckmann, 1984; Nacqvi *et al.,* 1986; Böttger-Schnack, 1991 and refs.) may be of great importance. Pellets produced by salps settle at rates of 320 to 2238 m/day (Madin, 1982), or even as rapid as 2700 m/day (Bruland and Silver, 1981), and reach the bathyal seabed in 1 to 14 days. Caron *et al.* (1989) reported that pellets of oceanic salps incubated for ten days at 22 °C, a temperature similar to that found in the deep water of the Red Sea, did not show significant changes in gross physical and chemical composition or in their sinking rates.

Additional substantial food input in the central trench of the Red Sea can be expected due to eddies. They may influence lateral transport processes from the narrow coastal zones surrounded by highly productive reefs that fringe the steep slope of the basin. Mud floats from the reef and drifting *Sargassum,* distributed by a strong cross-circulation, are typically encountered in the nutrient-rich pelagic waters of the southern half of the Red Sea (Thiel, 1979; Fedoryako, 1989), where a relatively large bathyal benthic stock has been observed (Thiel, 1979; Pfannkuche, 1993*a*).

The different nutrient sources apparently generate a mass flux of large, rapidly sinking aggregates which should reach the benthic community. This flux may be triggered by changes in the monsoonal circulation system and the winter cooling of the surface waters, and it may be superimposed on the permanent "rain" of very fine material which is scarcely exploited at all by metazoans in the bathypelagic zone (*see* above). In the ocean, the exploitation of the particle flux by the pelagic community is expected to occur to varying degrees, generally decreasing from low to high latitudes (Angel, 1989). The deep Red Sea is probably an exception, and exploitation by pelagic animals should be most efficient in the Levantine Sea.

In contrast to the Red Sea, the deep oligotrophic Levantine Sea lacks a productive coastal environment and a food-trapping, canal-like geometry. Blooms of salps have not yet been observed in the open waters (Godeaux, pers. comm.). However, the presence of bacteria and protozoa in the bathyal sediments (Boetius *et al.*, 1994; Hausmann *et al.*, 1994), which can survive long periods of starvation (*e.g.* Morita, 1988), suggests that the sedimentation of any kind of food within the entire size spectrum from the upper water layers must occur at rates too low to allow a development of an appreciable standing stock of bathyal metazoan animals.

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