Vol. 77: 301–306, 1991 | MARINE ECOLOGY PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published November 26

NOTE

Zooplankton community metabolism in the upper 200 m of the central Red Sea and the Gulf of Aden

Gerald Schneider*, Jürgen Lenz

Institut für Meereskunde an der Universität Kiel, Düsternbrooker Weg 20, W-2300 Kiel, Germany

ABSTRACT: A comparative study was conducted between the central Red Sea and the Gulf of Aden during spring in February/March 1987. Zooplankton (> 100 µm) standing stock, determined as carbon and nitrogen content, and community respiration were measured in 2 layers: in the euphotic zone and in the underlying layer, the so-called lower epipelagic zone, down to 200 m. The euphotic zone exhibited a significantly higher biomass and respiration rate than the layer below. Standing stock and respiration in the Gulf of Aden exceeded those in the Red Sea by factors of 3 and 2 respectively (station means for the euphotic zone: 10.3 ± 1.3 mg C m^{-3} and 3.4 ± 0.6 mg O_2 m^{-3} d^{-1} in the Gulf of Aden; 3.4 ± 1.4 mg C m^{-3} and 2.6 ± 0.9 mg O_2 m^{-3} d^{-1} in the Red Sea). However, weight-specific respiration was highest in the Red Sea euphotic zone, amounting to an average of 0.57 ± 0.13 mg O_2 mg C^{-1} d^{-1}. This corresponds to a daily carbon turnover rate of 17.2% body carbon per day whereas in the Gulf of Aden turnover averaged only 11.4% C d^{-1}

Zooplankton research in the Red Sea has so far dealt mainly with species composition (Halim 1969), vertical distribution and abundance (Weikert 1982, Beckmann 1984, Böttger 1987). Existing biomass data are based only on wet weight values or displacement volumes (summarized by Weikert 1987). There are difficulties in converting these into carbon values, which is prerequisite to relating biomass to metabolism and comparing different compartments in ecosystem studies. Moreover, carbon values are a key to recognizing principal differences in biomass composition between crustaceans and gelatinous plankton – the former with a high carbon content and the latter with a low carbon content (Schneider 1989). So far no data exist, to our knowledge, on zooplankton metabolism in the Red Sea and adjacent areas.

In this note we present data on carbon and nitrogen biomass and community respiration for zooplankton (> 100 µm) in the upper 200 m of the central Red Sea and the Gulf of Aden. These data are part of a comprehensive study on primary and secondary production within the euphotic zone and the layer below down to 200 m (Lenz et al. 1988, Weisse 1989, Schneider et al. 1991). Data on ultra- and microplankton metabolism measured in water-bottle samples and details on species composition of the mesozooplankton dealt with here will be reported elsewhere.

Material and methods. The investigation was carried out during Cruise 5/2 of RV 'Meteor' in February/March 1987. Eleven stations were occupied in Sudanese waters (central Red Sea) and 4 in the Gulf of Aden (Fig. 1).

The upper 200 m of the water column was divided into 2 layers, the euphotic zone defined by the 1% light level and the lower epipelagic zone (1% light level down to 200 m). The depth of the 1% surface light level was determined by a LI-COR LI-193 SB quantameter with a spherical sensor (400 to 700 nm). Zooplankton was sampled in vertical hauls with a 100 µm Bongo net fitted with a Nansen closing device. Hauling speed was 0.5 m s^{-1}. The volume of water filtered ranged between 12 and 20 m^3 for the euphotic zone and between 28 and 37 m^3 for the layer below. The catch of one net bag was used for standing stock analysis and that from another, which was fitted with a non-filtering beaker, for respiration measurements.

Zooplankton samples were split by means of a Folsom splitter into ½ to 1/64 volume subsamples according to sample size. For biomass estimations, subsamples were filtered onto precombusted Whatman GF/C glass-fibre filters. These filters were deep-frozen, and carbon and nitrogen determined after the expedition by means of a Perkin Elmer CHN elemental analyzer model 240 C. Precision was ± 0.5% for both elements with acetanilide as reference.

* Present address: Biologische Anstalt Helgoland – Wattenmeerstation, W-2282 List/Sylt, Germany

© Inter-Research/Printed in Germany

0171-8630/91/0077/0300/$ 03.00

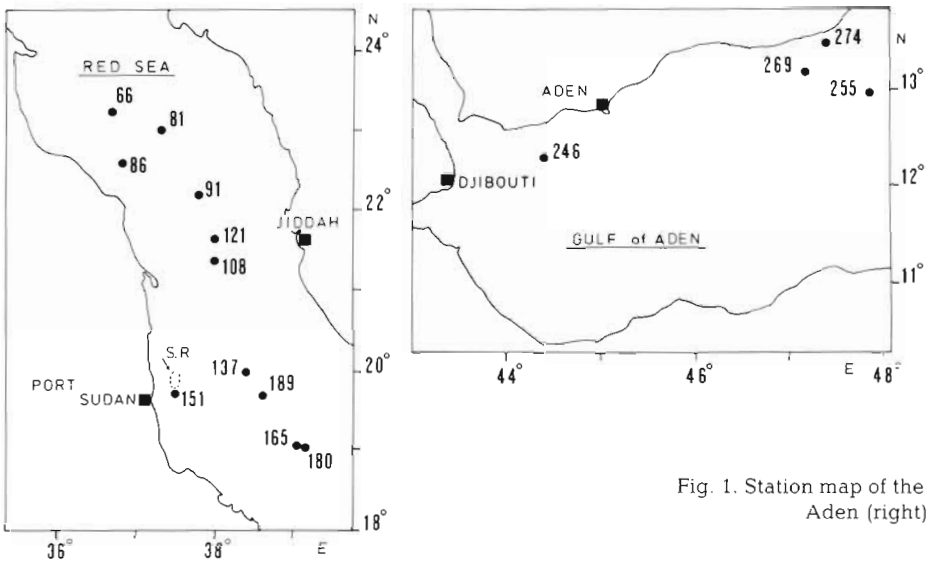

Fig. 1. Station map of the central Red Sea (left) and the Gulf of Aden (right). S.R. = Sanganeb Reef

For respiration measurements 2 subsamples of each layer were transferred individually into 1.2 l glass bottles filled with 0.45 µm filtered natural seawater. The bottles were placed in 2 incubators on rotating discs (3 rpm), to prevent settling of plankton organisms. One incubator served for the euphotic zone samples and the other for those of the layer below. The temperature in each incubator was adjusted to the average in situ temperature for the zone sampled. The samples were incubated for a period of 3 h in the dark. The experimental temperature deviated from the average in situ temperature (Table 1) by not more than 0.5 C°.

At the beginning and end of the experiments, two 120 ml subsamples were taken and oxygen content measured according to the Winkler method. Oxygen saturation values at the beginning and end of the experiments varied between 96 and 102% and between 57 and 74%, respectively. Deviation in the results of both subsamples averaged ± 10%. Two bottles filled with only 0.45 µm filtered seawater served as controls for the experiments.

Table 1. Average in situ temperatures (°C) at the stations investigated. A: Euphotic zone; B: lower epipelagic zone (1% light level to 200 m)

Stn	A	B
Central Red Sea		
66	23	22
81	23	22
86	23	22
91	24	22
108	24	23
121	24	22
137	26	23
151	25	23
165	26	23
180	26	23
189	26	24
Gulf of Aden		
246	25	20
255	25	19
269	26	19
274	25	19

Results. The results of the measurements are summarized in Table 2. Zooplankton carbon in the euphotic zone of the central Red Sea ranged from 1.2 to 5.6 mg C m^{-3}. The exceptionally high value of 8.3 mg C m^{-3} at Stn 151 approaches the higher values obtained in the Gulf of Aden (9.0 to 12.1 mg C m^{-3}). It was excluded from further analysis because of non-typical hydrographic conditions at this station (see below). Station means were 3.4 ± 1.4 mg C m^{-3} in the Red Sea (without Stn 151), and 10.3 ± 1.3 mg C m^{-3} in the Gulf of Aden; thus zooplankton carbon in the euphotic zone was about 3 times higher in the Gulf of Aden than in the central Red Sea. A similar disparity was observed for nitrogen. In both areas, the decrease of zooplankton biomass with depth is indicated by reduced values in the lower epipelagic zone; the biomass was never more than quarter of that in the euphotic zone.

The C:N ratio was uniformly 4.2 ± 0.5 in the euphotic zone, with no significant differences between the 2 areas. The difference in the ratios obtained for the lower epipelagic zone, 4.4 ± 0.2 for the central Red Sea and 5.6 ± 0.6 for the Gulf of Aden, cannot be regarded as significant since only 2 measurements were taken from the latter region. The similarity in the C:N ratios thus points to a comparatively uniform chemical composition of the zooplankton community.

In contrast to the 3-fold difference in biomass, zooplankton respiration in the euphotic zone of the Gulf of Aden was only about twice as high as in the Red Sea.

Table 2. Carbon and nitrogen biomass (mg m^{-3}) and respiration (mg O_2 m^{-3} d^{-1}) of the zooplankton community > 100 µm in the euphotic zone (A) and the lower epipelagic zone (B) of the Red Sea and the Gulf of Aden ($\bar{x}$: mean; SD: standard deviation)

Stn	Carbon		Nitrogen		Respiration		Depth range (m)	
	A	B	A	B	A	B	A	B
Red Sea								
66	1.21	–	0.40	–	0.92	–	0–80	
81	2.20	0.96	0.53	0.23	–	0.17	0–80	80–200
86	2.13	–	0.51	–	1.33	–	0–85	
91	3.23	0.93	0.95	0.23	2.26	0.25	0–60	60–200
108	–	1.19	–	0.28	3.84	0.24	0–60	60–200
121	2.80	1.04	0.79	0.23	1.54	0.17	0–70	70–200
137	4.07	1.11	0.91	0.24	2.78	0.24	0–75	75–200
151[a]	8.26	1.41	2.10	0.34	4.65	0.47	0–48	48–200
165	4.69	1.07	1.10	0.24	2.20	0.22	0–68	68–200
180	5.55	1.37	1.13	0.29	1.93	0.32	0–65	65–200
189	4.50	0.63	1.03	0.14	2.08	0.29	0–70	70–200
$\bar{x}$	3.38	1.04	0.82	0.24	2.10	0.24		
SD	1.42	0.22	0.27	0.05	0.86	0.05		
Gulf of Aden								
246	9.91	–	1.99	–	3.16	–	0–60	60–200
255	10.20	1.24	2.32	0.24	4.24	0.21	0–57	57–200
269	12.10	3.93	2.73	0.66	3.56	0.30	0–63	63–200
274	8.99	–	2.06	–	4.43	–	0–55	55–200
$\bar{x}$	10.30	2.59	2.28	0.45	3.85	0.26		
SD	1.31	1.90	0.33	0.30	0.59	0.06		

[a] Not included in means because of exceptionally high values

excepting Stns 108 (excluded because of its anomalously high respiration value) and 151, whereas in the lower epipelagic zone respiration decreased considerably by a factor of roughly 10 in both areas (Table 2). Integrated respiration rates for the upper 200 m ranged from 130 to 294 mg O_2 m^{-2} d^{-1}, 83 % of these values being respired within the euphotic zone. Assuming a respiratory quotient of 0.8 (for a mixed protein-lipid dominated metabolism), the integrated daily carbon demand of the euphotic zooplankton community averaged 45 ± 16 mg C m^{-2} d^{-1} in the Red Sea and 68 ± 8 mg C m^{-2} d^{-1} in the Gulf of Aden (Fig. 2). Below the euphotic zone carbon demand decreased to 10 mg C m^{-2} d^{-1} in both areas. Zooplankton biomass and respiration were higher in the Gulf of Aden than in the Red Sea, but the situation was reversed for weight-specific respiration and carbon turnover (Fig. 2). In both layers metabolic activity was higher in the central Red Sea than in the Gulf of Aden. Carbon turnover averaged 17.2 ± 3.9 % and 11.4 ± 2.8 % C d^{-1} in the euphotic zone of the central Red Sea and the Gulf of Aden, respectively, and 7.5 ± 2.8 and 3.7 ± 2.0 % C d^{-1} in the lower epipelagic zone.

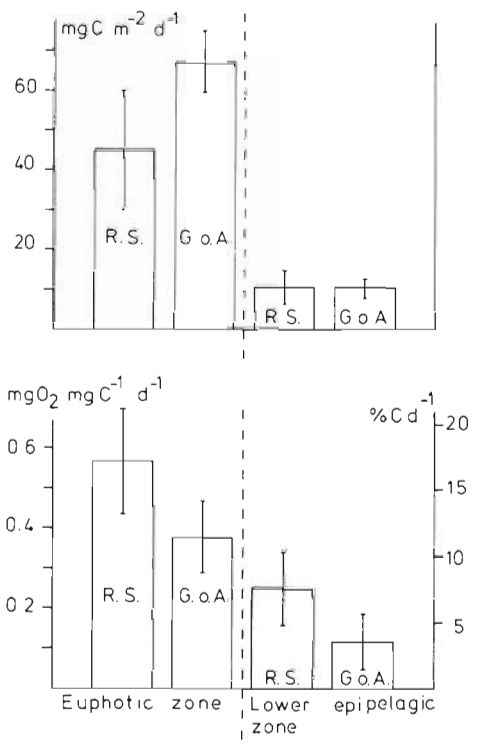

Fig. 2. Zooplankton metabolism in the Red Sea (R.S.) and Gulf of Aden (G.o.A.). Above: Calculated daily community carbon demand (mg C m^{-2} d^{-1}). Below: Weight-specific respiration rate (mg O_2 mg C^{-1} d^{-1}) and turnover rate (% C d^{-1})

Discussion. There are a number of methodological problems related to metabolism studies. To obtain measurable metabolic rates, zooplankton concentrations in incubation bottles usually exceed natural densities several times over. Confinement and crowding may lead to stress, influencing metabolic rates.

However, general conclusions on this problem are difficult to draw since different studies revealed somewhat contradictory results (summarized in Omori & Ikeda 1984). Nevertheless, at quite high zooplankton densities experimental results seem to lead to underestimates. Alternatively, to minimize the effect of crowding, experiments can be performed with a small number of individuals and a prolonged incubation period. Errors may result from starvation of individuals during incubation in this case, thus again leading to underestimates of metabolic activity. This is especially true for tropical and subtropical zooplankton with high turnover rates (Omori & Ikeda 1984). The same problem arises when maintaining zooplankton without food for a few hours prior to experiments to reduce stress from catching and handling. The addition of any kind of food may introduce other errors. Finally, metabolic rates are not well defined in zooplankton ecology since individuals' activity in the incubation bottle is uncontrolled. Ikeda (1985) suggested that metabolic rates of non-feeding individuals showing uncontrolled activity are close to routine metabolism. However, this term will become obscured if crowding and/or starvation affect metabolic rates during incubation.

In view of these drawbacks, inherent to the incubation method, the accuracy of metabolic rates obtained from incubation experiments can hardly be checked. The problems described above suggest that in all probability rates are underestimates rather than overestimates.

Another problem is the separation of zooplankton from phytoplankton with its interfering metabolic activity. The interference may be considerable in areas in which the size distribution of phytoplankton overlaps that of zooplankton (e.g. systems with high new production associated with large-sized phytoplankton). However, the bias due to phytoplankton appears to be low in oligotrophic areas like the Red Sea, since most phytoplankton species are rather small here. During our expedition, Pillen (1989) determined roughly 90% of total chlorophyll *a* ranging from 70 to 550 ng dm^{-3} to be associated with cells smaller than 20 µm in the Red Sea as well as in the Gulf of Aden. Among the remaining 10%, exceeding 20 µm in size, probably very few cells were larger than 100 µm, so that phytoplankton interference can be assumed to be insignificant in our study.

Zooplankton biomass and respiration were found to be lowest at the 3 northernmost stations in the central Red Sea (Table 2, Fig. 1), probably reflecting the general decrease in productivity from south to north (Halim 1969, Weikert 1987) within the Red Sea.

Exceptionally high values were observed at Stn 151 situated near the southern edge of Sanganeb Reef. ^{14}C assimilation here was also found to be almost double that at the other stations (0.6 g C m^{-2} d^{-1}; Moigis in Lenz et al. 1988). This higher productivity is probably due to a doming or upwelling of deeper water masses in the vicinity of the reef, as indicated by a shallow nitrocline at 30 m depth (Verch et al. 1989). Such exceptional conditions at Stn 151 were probably due to the island effect (Lafond & Lafond 1971). At all other stations within the central Red Sea, the nutrient-depleted layer ranged from the surface to at least 60 to 80 m, extending sometimes to more than 100 m (Verch et al. 1989), and primary production values of ca 0.3 g C m^{-2} d^{-1} were obtained (except Stn 108; Moigis in Lenz et al. 1988). The higher zooplankton biomass in the Gulf of Aden as compared with the central Red Sea probably reflects a generally higher productivity of the Gulf of Aden. Data on ^{14}C assimilation range from 0.2 to 1.6 g C m^{-2} d^{-1} in the Gulf in contrast to between 0.05 and 0.5 g C m^{-2} d^{-1} in the central Red Sea (Ryther et al. 1966, Khmeleva 1967, 1970, Krey 1973, Petzold 1986, Moigis in Lenz et al. 1988, Weikert 1988). These differences can be attributed to the hydrographical regime in the Gulf of Aden with its much shallower (40 to 50 m) and more pronounced nutricline. During our cruise, nitrate values between 0.2 and 0.4 µmol dm^{-3} were found in the 'nutrient-depleted layer' in the Gulf of Aden, whereas values near the limit of detection (0.05 µmol dm^{-3}) were obtained in the central Red Sea. Inorganic phosphate phosphorus levels were twice as high in the Gulf of Aden than in the central Red Sea (Verch et al. 1989). Similar observations were reported by Grasshoff (1969). However, high production rates were also obtained in the Red Sea. At Stns 151 and 108 values of about 0.6 g C m^{-2} d^{-1} were measured by Moigis (in Lenz et al. 1988). In the case of Stn 151 – as mentioned above – some doming of deeper water masses may be responsible for the increase in ^{14}C assimilation, whereas at Stn 108 no reasons can be found in the hydrographic data. Shaikh et al. (1986) determined ^{14}C assimilation rates exceeding 1 g C m^{-2} d^{-1} with annual values of roughly 400 g C m^{-2} at 2 stations off Saudi Arabia. Since these values are similar to those of upwelling areas we do not believe that these rates are characteristic for the entire central Red Sea. These observations, however, point to the importance of local conditions and caution against severe generalizations.

In Table 3 the weight-specific respiration rates obtained in this study for the zooplankton community of the euphotic zone are compared with similar studies in other tropical regions. The Red Sea data fit well into the range of the other data. The Gulf of Aden rates, however, are considerably below average. This deviation is difficult to explain, as the environmental conditions were quite similar within the euphotic zone of both areas. However, since only 4 stations were

Table 3. Comparison of weight-specific respiration rates (mg O_2 mg C^{-1} d^{-1}) in tropical epipelagic zooplankton. The following conversion factors were used: C = 40 % of dry weight, 4.86 mcal = 1 µl O_2 respired, 14.6 mcal = 1 µg C. n: number of data points

Area	Range	Mean ± SD	n	Source
Sargasso Sea	0.31–1.51	0.68 ± 0.36	8	Menzel & Ryther (1960)
Tropical N. Atlantic	0.09–0.79	0.50 ± 0.20	15	Schneider & Lenz (1987)
Tropical N. Pacific	0.29–0.75	0.56 ± 0.13	14	King et al. (1978)
Equatorial Pacific	0.19–1.42	0.65 ± 0.28	32	Shushkina & Pavlova (1973)
Tropical seas[a]	0.19–1.13	0.60 ± 0.24	28	Ikeda (1974)
Red Sea	0.35–0.76	0.57 ± 0.13	9	This study
Gulf of Aden	0.29–0.49	0.38 ± 0.09	4	This study

[a] Copepods

occupied in this region, this finding must be regarded with reservation.

Another possibility of explaining this deviation is the difference in the size structure of the zooplankton community in the 2 areas. Larger organisms have a lower weight-specific respiration rate than smaller ones due to the allometric relationship between body size and respiration rate (e.g. Peters 1983). A microscopical analysis of the zooplankton samples, the results of which will be published elsewhere, showed in fact that larger organisms were more abundant in the Gulf of Aden samples than in those of the Red Sea. Between 30 and 37 % of all specimens fell into the size class > 500 µm as opposed to between 15 and 26 % in the Red Sea. The higher share of large organisms associated with low weight-specific metabolic rates in the Gulf of Aden would decrease the average weight-specific rate of the zooplankton community.

The decline in weight-specific respiration rate for the lower epipelagic zone by a factor of 3 as compared with the euphotic zone (Fig. 2) can be partly attributed to the decreasing temperature according to the Q_{10} law. Other factors, however, must also have played a part, since the difference in incubation temperature for both layers was far less pronounced in the Red Sea (1 to 3 °C) than in the Gulf of Aden (5 to 7 °C). An increase in average organism size may be mentioned here, too (see above). Another factor which could not be checked under experimental conditions is a possible adaptation of the zooplankton community to the lower oxygen content in the deeper layers, leading to reduced respiration (Ikeda 1977). Oxygen decreased below the thermocline, which in both areas lay at the same depth range as the 1 % light level. At 200 m depth oxygen content averaged 2.2 mg l^{-1} in the Red Sea and 0.5 ml l^{-1} in the Gulf of Aden (Verch et al. 1989).

More than 80 % of total respiration by the zooplankton community in the upper 200 m, depicted as carbon demand in Fig. 2, took place in the euphotic zone. A comparably high degree of metabolic activity within the euphotic zone was also observed by King et al. (1978) in the tropical North Pacific. Studying ETS activity within different water layers, values of 100 to 270 µl O_2 m^{-3} h^{-1} were obtained for the 68 to 70 m deep euphotic zone, corresponding to 7.1 to 18.2 mg O_2 m^{-2} h^{-1}. In the lower epipelagic zone between 1 % light level and 200 m ETS activity amounted to only 0.24 to 0.46 µl O_2 m^{-3} h^{-1} and 0.24 to 0.46 mg O_2 m^{-2} h^{-1}, respectively.

A high metabolic activity is further demonstrated by the high turnover rate of zooplankton carbon within the euphotic zone (Fig. 2). Turnover time was 5.8 d for the central Red Sea and 8.7 d for the Gulf of Aden. Weisse (1989) measured bacterial standing stock and growth rate at the same stations during the same expedition. He found an average turnover time of 0.5 d for the Red Sea and 1.2 d for the Gulf of Aden. Although carbon turnover times measured as respiration and biomass doubling time cannot be compared directly, the latter being about twice as long as the former in the case of bacteria, they show the same difference between the Red Sea and the Gulf of Aden. This observation stresses the fact that the central Red Sea is distinguished by a very high metabolic activity within the plankton compartments and may thus be taken as an excellent example for the rapid cycling of matter in oligotrophic tropical seas.

The metabolic role of metazooplankton (> 100 µm) is a minor one with respect to total metabolism within the plankton community, as both areas were dominated by small organisms during the time of investigation. This is borne out by the fact that ultraplankton (0.45 to 20 µm) and microplankton respiration together ranged from 50 to 120 mg O_2 m^{-3} d^{-1} with an average of slightly more than 70 mg O_2 m^{-3} d^{-1} (Schneider et al. 1991) and that about 80 % of primary production was found in the size class < 2 µm (Moigis in Lenz et al. 1988). Since this small phytoplankton is not directly accessible to most filter-feeding copepods, which made up the bulk of metazooplankton within the euphotic zone (Schneider et al. 1991), the conclusion seems obvious that both phytoplankton and heterotrophic

protists served as food for metazooplankton as proposed by the concept of Sherr & Sherr (1988), where a microbial food web is connected with the metazoan food web.

Acknowledgements. We gratefully acknowledge the financial support from the 'Deutsche Forschungsgemeinschaft' through a grant given to the second author (Le 232/16). We thank Prof. W. Nellen, coordinator of the expedition, and Prof. H. Thiel, chief scientist of leg 2, as well as the captain and crew of RV 'Meteor' for their support. Finally, we also thank 4 anonymous referees for improving an earlier version of this paper

LITERATURE CITED

Beckmann, W (1984). Mesozooplankton distribution on a transect from the Gulf of Aden to the central Red Sea during the winter monsoon. Oceanol. Acta 7: 87–102

Böttger, R. (1987). The vertical distribution of micro- and small mesozooplankton in the central Red Sea. Biol. Oceanogr 4: 383–402

Grasshoff, K. (1969). Zur Chemie des Roten Meeres und des inneren Golfes von Aden nach Beobachtungen von FS 'Meteor' während der Indischen Ozean Expedition 1964/65. 'Meteor' Forsch.-Ergebnisse A (6): 1–76

Halim, Y (1969). Plankton of the Red Sea. Oceanogr mar. Biol. A. Rev. 7: 231–275

Ikeda, T. (1974). Nutritional ecology of marine zooplankton. Mem. Fac. Fish. Hokkaido Univ. 22: 1–97

Ikeda, T (1977). The effect of laboratory conditions on the extrapolation of experimental measurements to the ecology of marine zooplankton. II. Effect of oxygen saturation on the respiration rate. Bull. Plankton Soc. Japan 24: 19–28

Ikeda, T (1985). Metabolic rates of epipelagic zooplankton as a function of body mass and temperature. Mar Biol. 85: 1–11

Khmeleva, N. N. (1967). Role of radiolarians in the estimation of primary production in the Red Sea and the Gulf of Aden. Dokl. Akad. Nauk SSSR 172: 1430–1433 (in Russian)

Khmeleva, N. N. (1970). On the primary production in the Red Sea and the Gulf of Aden. Biol. Morya, Kiev 21: 107–133 (in Russian)

King, F. D., Devol, A. H., Packard, T T. (1978). Plankton metabolic activity in the eastern tropical North Pacific. Deep Sea Res. 25: 689–704

Krey, J. (1973). Primary productivity in the Indian Ocean I. In: Zeitzschel, B. (ed.) The biology of the Indian Ocean. Springer, Berlin, p. 115–128

Lafond. E. C., Lafond, K. G. (1971). Oceanography and its relation to marine organic production. In: Costlow, J. D. Jr (ed.) Fertility of the sea, Vol. 1. Gordon & Breach, New York, p. 241–265

Lenz, J., Schneider, G., El Hag, A. G. D., Gradinger, R., Fritsche, P., Moigis, A., Pillen, T., Rolke, M., Weisse, T (1988). Planktological data from the central Red Sea and the Gulf of Aden – RV 'Meteor', cruise No. 5/2, January–March 1987. Ber. Inst. Meereskde Kiel 180

Menzel, D. W., Ryther, J. H. (1960). Zooplankton in the Sargasso Sea off Bermuda and its relation to organic production. J. Cons. perm. int. Explor. Mer 26: 250–258

Omori, M., Ikeda, T. (1984). Methods in marine zooplankton ecology. Wiley & Sons, New York

Peters, R. H. (1983). The ecological implications of body size. Cambridge University Press, Cambridge

Petzold, M. (1986). Untersuchungen zur Horizontal- und Vertikalverteilung des Phytoplanktons im Roten Meer. Diploma thesis, University of Hamburg

Pillen, T (1989). Zur Phytoplanktonverteilung im Roten Meer und im Golf von Aden während der 'Meteor'-Expedition (Mindik 5/2) im Frühjahr 1987 Diploma thesis, Kiel University

Ryther, J. H., Hall, J. R., Pease, A. K., Bakun, A., Jones, M. M. (1966). Primary organic production in relation to chemistry and hydrography of the western Indian Ocean. Limnol. Oceanogr 11 371–380

Schneider, G. (1989). Carbon and nitrogen content of marine zooplankton dry material: a short review. Plankton Newsletter 11: 4–7

Schneider, G., Lenz, J. (1987). Die Bedeutung der Größenstruktur des Zooplanktons für den Energietransfer im pelagischen Ökosystem der Auftriebsregion vor NW-Afrika. Ber. Inst. Meereskde Kiel 174

Schneider, G., Lenz, J., Rolke, M. (1991). Zum Bestand und Stoffumsatz des Ultra-, Mikro- und Mesoplanktons im Roten Meer und im Golf von Aden. Ber. Inst. Meereskde Kiel 205

Shaikh, E. A., Roff, J. C., Dowidar, N. M. (1986). Phytoplankton ecology and production in the Red Sea off Jiddah, Saudi Arabia. Mar. Biol. 92: 405–416

Sherr, E., Sherr, B. (1988). Role of microbes in pelagic food webs: a revised concept. Limnol. Oceanogr. 33: 1225–1227

Shushkina, E. A., Pavlova, Ye. P. (1973). Metabolism rate and production of zooplankton in the equatorial Pacific. Oceanology, Wash. 13: 278–284

Verch, N., Petzold, M., Mahnke, P., Quadfasel, D. (1989). Hydrographic bottle data obtained in the Red Sea and Gulf of Aden during RV 'Meteor' cruise 5 – Mindik 1987. Institute of Oceanography, University of Hamburg, Tech. Rep. 2-89

Weikert, H. (1982). The vertical distribution of zooplankton in relation to habitat zones in the area of the Atlantis II Deep, central Red Sea. Mar. Ecol. Prog. Ser 8: 129–143

Weikert, H. (1987). Plankton and the pelagic evironment. In: Edwards, A., Head, S. M. (eds.) Red Sea. Key Environmental Series. Pergamon Press, Oxford, p. 90–111

Weikert, H. (1988) New information on the productivity of the deep Eastern Mediterranean and Red Seas. Rapp. Comm. int. Mer Médit. 31: 305

Weisse, T. (1989). The microbial loop of the Red Sea: dynamics of pelagic bacteria and heterotrophic nanoflagellates. Mar Ecol. Prog. Ser. 55: 241–250

This article was submitted to the editor

Manuscript first received: May 21, 1991
Revised version accepted: September 25, 1991