On the paradox of high mesozooplankton biomass, throughout the year in the western Arabian Sea: Re-analysis of IIOE data and comparison with newer data

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The mesozooplankton data from the northwestern Indian Ocean collected during 1962-1965 by the International Indian Ocean Expedition (IIOE; displacement volumes from vertical net catches, 330 μm mesh, upper 200 m) showed highest biomass in the summer upwelling areas off Oman and Somalia but also suggested that zooplankton stocks were relatively large outside the SW monsoon. Catches by 200 μm nets off Oman (1963/64), Yemen (1984/85) and Somalia (1992/93) confirmed that mean biomass during winter is considerably above the level that is found in waters with the typical tropical structure. In the Gulf of Aden the NE monsoon is even the richest zooplankton season. This is due to winter cooling, with entrainment of nutrients into the upper layer, producing phytoplankton blooms. The relatively high zooplankton biomass outside the upwelling season seems less paradoxical since seasonal differences in phytoplankton production and stock are less extreme than previously thought. On the one hand the early 14C data underestimated primary production outside the SW monsoon, and on the other hand the CZCS images exaggerated the chlorophyll concentration during the SW monsoon. The productivity in the strong Somali Current upwelling is below potential due to large advection and mixing, and zooplankton stocks in July are probably much smaller than off Oman. Results from an Arabian Sea model [McCreary et al., Prog. Oceanog. 37 (1996) 193], including zooplankton biomass and grazing, support the observation that zooplankton development differs between subregions and that entrainment blooms produce zooplankton peaks during the NE monsoon as well. The IIOE data set seems still useful for comparison with existing and recently collected data from smaller-meshed nets, and for validation of JGOFS Arabian Sea modeling. Displacements from 330 and 230 μm catches were strikingly similar (RV Discovery 1963/64). In catches from hauls with a 50 μm net, the 50-300 μm fraction only added about 25% to the biomass > 300 μm (samples without contamination by phytoplankton, RV Baldridge 1995).

Early studies on zooplankton biomass and copepod numbers from standard hauls (0-200 m, mesh 330 μm) from the International Indian Ocean Expedition 1959-1965 (IIOE) present maps for the year divided into only two periods, the 'SW monsoon' (April 16 - October 15) and the 'NE monsoon' (October 16 - April 15). In the western Arabian Sea, with intense upwelling during the SW monsoon, there is a marked difference in primary production between these two periods ( > 1 versus < 0.3 gC.m⁻².d⁻¹), but mean zooplankton biomass and copepod number are large in both periods. It was recognized that seasonal coverage by IIOE of the NW Indian Ocean is incomplete, but later cruises (INDEX 1979, NIOP 1992/1993) confirmed that at least off Somalia there is no significant difference in zooplankton biomass (from catches in the upper 200 m by nets with mesh of about 330 μm) between the SW and the NE monsoon. The phenomenon of high zooplankton biomass during the NE monsoon was called the 'Arabian Sea Paradox'. Recently, more data from both IIOE and later expeditions became available to the author, making it worthwhile to extend a previous analysis of this apparent paradox with data sets regarding catches by nets of 200 μm, the mesh recommended by JGOFS.

Data sources

Similar to an earlier study, the original IIOE data on displacement volume were supplemented with the data on the number of copepods as determined by workers at the Indian Ocean Biological Centre (IOBC) in Cochin - a data set available at the World Data Center-A (WDC-A) - to summarize annual patterns of zooplankton abundance. On basis of the seasonal hydrography, from shipborne data in atlases and from SST and Coastal Zone Color Scanner (CZCS) satellite images, 6 provinces in the western NW Indian Ocean were recognized, including the upwelling areas off Oman and Somalia.
the Gulf of Aden and the equatorial region not treated before\textsuperscript{12,13} (see Fig. 1).

During the IIOE, the biologists onboard RRS ‘Discovery’ did, besides 200 m hauls with the Indian Ocean Standard Net (IOSN, 330 μm), series of hauls in strata down to 1000 m with a closing net equipped with 230 μm mesh. Regarding these catches on Discovery cruises 1 and 3, very little has been reported\textsuperscript{15,16}, except for an internal report on displacement volumes\textsuperscript{17}, and samples were not analyzed except for some stations off Somalia\textsuperscript{18}. Here a comparison of the displacement volumes of both the standard net and the 0-200 m catches by the 230 μm net is presented. The 230 μm samples from a section off Oman, sampled three times in spring and summer 1963/64, were selected for further analysis. Biomass data from a 200 μm net used on the UK JGOFS ARABESQUE cruises at stations off Oman\textsuperscript{19} in autumn 1994 will be cited for comparison.

The Marine Science and Marine Resources Research Center (MSRC, Aden) had cruises off Yemen during Feb.1984 - June 1985 with zooplankton sampling by a 200 μm net\textsuperscript{20,21}. This data set is rather unknown, but represents probably the best record of seasonal pattern of zooplankton abundance in the whole western part of the NW Indian Ocean. The original data were obtained and reprocessed.

After IIOE, the Somali Current east of the Horn of Africa was sampled for zooplankton by the American RV ‘Columbus Iselin’ during the Indian Ocean Experiment (INDEX) in March and July 1979. Taxonomic composition of 223 μm catches of both cruises and biomass results from 333 μm catches for July were published extensively\textsuperscript{18,22}, but the unexpectedly large 333 μm biomasses in March, though listed in a data report\textsuperscript{23}, were reported much later\textsuperscript{3,8}. In July 1992 and January 1993, the zooplankton off Somalia was sampled again by the Dutch RV ‘Tyro’ in the framework of the Netherlands Indian Ocean Programme (NIOP), using both 200 and 320 μm nets\textsuperscript{8,11}. During the US GLOBEC Arabian Sea cruises, the NOAA RV ‘Malcolm Baldridge’ sampled the upwelling areas off both Oman and Somalia in May and August 1995. Some preliminary results on hauls by a 50 μm net will be given, to indicate the contribution by plankton < 300 μm.

Depth layers sampled and zooplankton biomass determinations varied between the studies above. In most cases displacement volume was measured, so this variable was chosen for comparisons. In studies where dry weight or carbon content of the catch was measured, conversion factors as determined in Indo-Pacific waters with seasonal upwelling\textsuperscript{24} were used: with dry weight 12% of wet weight (displacement volume) and carbon 40% of dry weight. In the two studies of which results have not been published before (Oman 1963/64) or are rather unknown (Aden 1984/85), the hydrographic data will be presented in some detail.

**Results**

**Western Indian Ocean, IIOE data 1962-1965**

During IIOE, the net IOSN\textsuperscript{25}, with mouth diameter 113 cm and mesh size 330 μm, was used on most ships for vertical hauls from about 200 m to the surface. In the western NW-Indian Ocean, 14 cruises in total sampled zooplankton between summer 1962 and the beginning of 1965. From the WDC-A data set two variables were selected: the displacement of the catch as measured directly onboard and the number of copepods in the catch as determined later at IOBC from subsamples. For all data pooled, there was a good correlation between these variables \((n = 322, r^2 = 0.69, p < 0.0001)\).

The data were split according to months and subareas. Seasonal and spatial coverage was not optimal and there were only 8 data subsets with more than 10 hauls (Table 1), together comprising more than half of the total number of hauls. Ranges of displacement volume and copepod abundance were large, and in most cases the minimum and maximum values differing by a factor of about 10, and without clear differences between hauls by day or at night (Table 1). During the cruises off Oman and in the Somali Current during summer, this large patchiness of zooplankton was obviously related to upwelling plumes. Equatorial upwelling played a similar role in the data sets from the cruises that crossed the equator. However, also the December 1964 cruise in the Gulf of Aden and Somali Current showed both small and relatively big catches, indicating that winter conditions locally stimulate secondary production. Only at the May 1964 stations in the oligotrophic waters above the Carlsberg Ridge, patchiness was much less since large copepod catches were lacking (Table 1).

From the above results it is clear that the complete data set on monthly means (Fig. 1) should be interpreted with caution, due to the low number or
BAARS. Mesozooplankton Biomass Re-analysis of IIOE Data

Table I—Means and ranges of displacement volume and copepod abundance for subareas and months with more than 10 hauls with the Indian Ocean Standard Net. (D = hauls by day, N = hauls at night)

<table>
<thead>
<tr>
<th>Area, month</th>
<th>Number of hauls</th>
<th>Displ. vol. (ml.m⁻²)</th>
<th>Copepod abundance (n.m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ship</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>Off Oman, July 1963</td>
<td>20</td>
<td>57</td>
<td>D: 16 - 25</td>
</tr>
<tr>
<td>Equator, Jan. 1965</td>
<td>36</td>
<td>16</td>
<td>D: 3 - 35</td>
</tr>
</tbody>
</table>

lack of hauls in most months. Nevertheless, Fig. 1 suggests some regional differences in seasonal levels of zooplankton stocks. The Gulf of Aden seemed to be relatively rich in zooplankton during the NE monsoon (Feb.-Mar., n=4, 44 ml.m⁻²). Off Oman and in the Somali Current peaks of 50 or more ml.m⁻² occurred during the summer upwelling season. Mean displacement off Somalia during winter was only 14 ml. m⁻² (Dec.-Feb., n=36). Winter data were lacking off Oman but those for the adjacent central Arabian Sea waters suggested also a smaller zooplankton stock compared to summer (Jan.-Mar., n=9, 21 ml. m⁻², and July, n=8, 38 ml.m⁻², respectively). The waters over the Carlsberg Ridge were poorest in zooplankton throughout the year, with a mean displacement of 10 ml. m⁻² (n=40 in total). The equatorial region showed more variable zooplankton levels but no firm conclusion about seasonality can be drawn.

Comparison of 330 and 230 μm catches, Discovery 1963/1964

On RRS 'Discovery' cruises 1 and 3 a closable net (diameter net opening 70 cm) of 230 μm mesh was used for vertical tows, metered for flow and depth, in different strata at over 200 stations in total. Square metre displacement volumes for the strata 0-50, 50-100 and 100-200 m were calculated for those stations where also a 200 m haul with the IOSN had been made. A plot of the displacement volumes from these nets gave considerable scatter (Fig. 2) but correlation was high (n = 123, r² = 0.72, p < 0.0001). Surprisingly, displacement volumes (DV) from the 330 μm net were not significantly lower, regression giving DV 330 μm = 0.98 (DV 230 μm) + 1.73. One probable reason for this rather unexpected result is that for the IOSN catches the wet displacement volume comprised the entire sample, including gelatinous organisms¹⁴, whereas in the 230 μm catches incidentally caught large organisms were removed before displacement was measured²⁶. Neither in the IOSN nor 'Discovery' 230 μm data bases records on the frequency and size of these large organisms were found, so it is not feasible to estimate the potential contribution by this group in the
Fig. 1—HOE monthly zooplankton data, from vertical hauls with the Indian Ocean Standard Net from 200 m to the surface during cruises 1962-1965, arranged for different areas in the western NW Indian Ocean.

Fig. 2—Correlation diagram of displacement volumes from catches in the upper 200 m by IOSN 330 μm and 70 cm Ø vertical net 230 μm; 'Discovery' cruises 1 and 3, 1963/64

During 10-12 March 1964, at the end of the NE monsoon, the middle and outer parts of the section showed the typical structure of tropical waters, with a Deep Chlorophyll Maximum (DCM) at the bottom of the mixed layer at about 50-60 m. The mixed layer was not very oligotrophic though, as nitrate and chlorophyll concentrations were both 0.1-0.2 μM and mg m⁻³, respectively. At the shelf stations (bottom depths 56-71 m) there was doming, with the 1 μM nitrate contour at 10-30 m, and nitrate and chlorophyll in the upper layer increased by a factor of 2-4. Zooplankton biomass was evenly distributed, with both displacement volume and copepod number in the upper 50 m about similar in the different parts of the section (Fig. 3). Half or more of the 0-200 m displacement volumes. Another explanation could be that the fraction 230 - 330 μm is adding very little to the biomass > 330 μm.

Off Oman, spring-summer 1963/64, autumn 1994

During ‘Discovery’ cruise 3, a large area in the NW and equatorial Indian Ocean was covered. A section off Oman was sampled during March and May 1964. Stations were from the shelf west of the Halaaniyaat Islands (formerly the Kuria Muria IsI.) to about 15°N, 58°E (Fig. 3). On these sections no IOSN hauls were made, but the 230 μm net was used at all stations, so it seemed worthwhile to study these data sets, to compare the spring 1964 with the summer 1963 situation. In July 1963, ‘Discovery’ cruise 1 used the same net at many sections off Oman, and section 3, just east of the Halaaniyaat Islands, was selected for comparison. The hydrographic data of the selected sections, obtained from the British Oceanographic Data Center (Bidston), will be treated in some detail - only those for July 1993 were published37,28 - including chlorophyll concentrations. The original data on displacement17 were recalculated as square metre displacement volumes for standardized depth layers. The original samples were analyzed for copepod numbers. Again, there was a good correlation between displacement volume and copepod abundance (n = 73, r² = 0.80, p < 0.0001). Zooplankton data were pooled into shelf, middle and outer stations (Fig. 3), with most parts containing hauls both by day and at night. A more extensive report on these hitherto unpublished data is planned, however only summaries for the upper 200 m will be presented, here.
zooplankton biomass for the middle and outer stations stemmed from the 50-200 m layer.

During 25-27 May 1964, when the SW monsoon had already started, the hydrography clearly reflected the beginning of coastal upwelling. At the outer stations, the typical tropical structure was still present, with a DCM at 60-80 m and nitrate values above 20 µM well below 100 m (like in March). Towards the coast, isotherms and nitrate contours sloped upwards. In the middle part of the section the DCM was at ca. 40 m and 20 µM nitrate at ca. 80 m. At the innermost shelf station (bottom 36 m) the 1 and 10 µM nitrate concentrations had reached the subsurface (< 10 m). Upper layer chlorophyll a was 0.5 mg.m⁻³, against < 0.1 mg.m⁻³ at stations in the middle and outer parts. Zooplankton distribution was very similar to March, showing no clear response yet to the increased primary productivity above the shelf. It should be noted however, that the mean zooplankton biomass of 30-40 ml.m⁻², encountered in the upper 200 m of the sections of both March and May 1964, was considerably larger than the IOE data for a more offshore area like the Carlsberg Ridge, with about 10 ml.m⁻² (Fig. 1). In view of the previous chapter, it is doubtful whether mesh size accounts for this difference.

During July 1963, coastal upwelling was observed along the entire Arabian Sea coast off Oman. Strongest upwelling (SST < 20°C) was encountered in the Kuria Muria Bay and just north of Ras Madrakah. Surface temperature at the shelf stations of the third section (5 to 9 July, bottom 37-53 m) in between these upwelling centres was about 20°C, and surface nitrate was 15-25 µM. In the middle part, isotherms sharply sloped upwards to the coast, and surface nitrate was already about 10 µM. Upwelling was also noticed on the outer stations: the DCM had vanished, the 20 µM nitrate contour was now at ca 80 m, the
10 μM at 50 m and at the surface 2-3 μM was found. Zooplankton catches in the upper 50 m were very high at the shelf (Fig. 3). They were lower in 0-50 m for the other parts of the section but, especially at the middle stations, considerable amounts of zooplankton also occurred in the 50-100 and 100-200 m layers. Chlorophyll a concentrations were high along the entire section but well below 1 mg.m⁻², suggesting a high grazing pressure.

During the JGOFS ARABESQUE ‘Discovery’ cruises 210 and 212 (September and November 1994), some vertical hauls 100-0 m were made with a 200 μm net at three stations parallel to the 1963/64 sections (Fig. 3), but at larger distance from the coast. The position of A1 (19°N, 59°E) corresponded to ‘middle’, but A3 (16°N, 62°E) was a bit farther offshore than ‘outer’ (Fig. 3), and A7 (8°N, 67°E) was even east of ‘Carlsberg Ridge’ (Fig. 1) respectively. Catches were analysed for carbon content and are here converted to displacement. In September, at the end of the SW monsoon, coastal upwelling was still going on, and upper layer nitrate concentrations were over 5 μM at A1 and A3, but below 0.02 μM at A7. During November, in the intermonsoon, surface waters were nitrate depleted, and primary productivity at A1 had dropped from >3 in September to <1 gC.m⁻².d⁻¹. (NB—More extensive descriptions of hydrography and plankton dynamics are being reported elsewhere). Zooplankton biomass decreased markedly with distance from the coast, and from September to November: from 29 to 15 ml.m⁻² at A1, 14 to 7 ml.m⁻² at A3, and 5 to 2 ml.m⁻² at A7, respectively.

These autumn declines support the general patterns in the IIOE data (Fig. 1), though the 1994 values are relatively low. In the IIOE data for the region ‘Off Oman’ (Fig. 1), all from the year 1963, the mean stock in 0-200 m also declined by a factor of 2 from July (+Aug.) to October/November. But mean displacement volume in this and the adjacent area ‘AS’ (Fig. 1) was with ca 25 ml.m⁻² (range 8-40, 12 hauls in total) in November 1963 much higher than the November 1994 figures for A1/A3. Interannual variation but also patchiness and the fact that the 1994 hauls were limited to the upper 100 m could have played a role. Also the September 1994 A1 value, closest to the upwelling, was not very high either, as very similar mean displacements of 29 and 25 ml.m⁻² for the upper 100 m at the middle stations in March and May 1964, respectively, were found (Fig. 3). Eddies along the Omani coast produce filaments that extend far into the Arabian Sea, giving increased zooplankton biomass at sites downstream of the local enrichment in dynamical models (J.C. Kindle, Stennis Space Center, USA, pers.comm.). These phenomena might explain the discrepancies in the data sets above, as the single sections sailed in 1963/64 or the few stations sampled in 1994 gave self-evidently no insight into these time lags and spatial patterns. Summarizing all available data, the annual pattern of zooplankton biomass off Oman can be characterized as moderate to high levels in late winter and spring, followed by very high peaks during the summer upwelling season, and declining to moderate levels in autumn and probably winter, as suggested by the limited IIOE data (Fig. 1, ‘AS’, mean 21 ml.m⁻² for Jan.-March).

Gulf of Aden, seasonal pattern of 200 μm catches 1984/1985

MSRC cruises by RV ‘Ibin Magid’ sailed a section near Aden 11 times during Feb. 1984 - June 1985. In addition, five cruises (by RV ‘Dr. F. Nansen’ in Aug.1984) did sections along the entire south coast of Yemen, including the seasonal upwelling areas off Mukalla and off Ras Fartak (Fig. 4). Zooplankton sampling was by vertical hauls from 30 m and from 100 m to surface by a WP-2 net (mouth 0.25 m²) of mesh size 200 μm. Catches of the 0-30 m layer were used for estimating biomass by drying to constant weight at 60-70°C, and a limited set of 0-30 and all the 0-100 m catches were analyzed on major taxonomic groups. Hauls were made regardless of the time of the day, but most sections comprised stations both by day and at night, so data were averaged per section to show seasonal trends.

The Aden section showed low dry weight of plankton catches in spring, both in April and May 1984 and in May and June 1985 (Fig. 5). Spring was also the period with lowest nitrate concentrations and phytoplankton abundance. During other months that the Aden section was sampled, mean biomass was always much higher, with peaks during March and November 1984. The dry weight data from the other sections off Yemen (Table 2), generally confirm the annual pattern off Aden. Mean biomass at the start (Nov.) and during the NE monsoon (Feb.) was relatively large, though patchy distributed (Table 2), and out of a total of 72 hauls during these autumn/winter cruises only 7 gave dry weight
<1.2 g m⁻² (corresponding to a displacement of ca. 10 ml.m⁻², 0-30 m). May 1985 showed small catches everywhere, with one notable exception: for shelf station 23 off Ras Fartak (Fig. 4) on 21 May, where coastal upwelling had already started, a very high dry weight was measured (separately denoted in Table 2). At the same station an even higher value was recorded during August 1984, when upwelling with SST <21°C occurred along almost the entire Yemen coast east of 47°E and dense diatom blooms were observed off Mukalla and off Ras Fartak20. Surface nitrate concentrations during summer were 3 - 6 μM for the more inshore stations in the Gulf and well above 20 μM in the upwelling centres. At most stations along the 4 sections of August, biomass was comparable to displacements > 25 ml.m⁻² (0-30 m).

For the set of 0-30 m samples that was taxonomically examined, there was a rather poor correlation (n=55, r² = 0.35, p < 0.01) between dry weight of the total sample and copepod density (upper part Table 3). The copepod densities at the Ras Fartak shelf station (separately denoted in Table 3) were lower than expected on the base of the very high dry weights recorded here. Presumably, diatoms in these large catches substantially contributed to dry weight. Copepod densities calculated from the 0-100 m catches (lower part Table 3) varied less extreme both spatially and seasonally than total dry weight in the 0-30 m layer. Comparison of the copepod densities between 0-30 and 0-100 m reveals that at upwelling stations nearly all copepods were caught in the upper layer, whereas outside the upwelling season the vertical distribution seemed somewhat more homogeneous throughout the 100 m layer. Hence outside
the upwelling season, the 0-30 m dry weight data (Fig. 5, Table 2) were considerably underestimating total epizooplankton biomass and should probably at least be doubled for comparison with biomass from deeper 200 μm catches elsewhere in the NW Indian Ocean. On the basis of the 0-100 m copepod data (Table 3) it is clear that the waters off Yemen are very rich in zooplankton not only during upwelling but also from late autumn through winter.

What could be the cause for these large stocks in winter? Abrupt cooling and deepening of the mixed layer occurred\(^{(20)}\) from October to November 1984, probably associated with the increase of wind velocity at the onset of the NE monsoon. Surface cooling and convection continued till February 1985, when mixed layer depth was at a maximum of about 120 m. Apparently, entrainment of nutrients from the thermocline by winter cooling stimulated phytoplankton and zooplankton production, resulting in large stocks at the beginning and during the NE monsoon. Average nitrate concentrations in the upper part of the euphotic zone of the Gulf\(^{(20)}\) were generally 0.6 - 3 μM, indicating that primary production was presumably much higher than usual for tropical waters.

The Somali Current area, several data sets

Data on seasonal differences of primary productivity and zooplankton stock of the Somali Current area during II0E, INDEX and NI0P are summarized in Fig. 6. NI0P data for the Gulf of Aden and Snellius-II data for the eastern Banda Sea - by the same workers and methods - are added for comparison. Details can be found in the original sources (see legend Fig. 6). Mean primary production in the northern Somali Basin during the peak of the SW monsoon (July/Aug.) was very similar for II0E, INDEX and NI0P but primary production was relatively low compared with the Banda Sea during summer, with relatively weak upwelling, or the Gulf of Aden during winter. Given the very strong coastal upwelling off Somalia, this is at first sight rather unexpected. From the observations during the NI0P cruise in July 1992, it has been concluded that the conditions in a large part of the Somali Basin are not optimal for phytoplankton development in the upwelled water: the advection by the fast Somali Current is very large, whereas mixing depths in downstream areas around Socotra and in the Great Whirl exceed the photic zone, preventing phytoplankton stocks to build up and leaving a considerable part of the upwelled nutrients unused\(^{(31)}\). Only locally, in eddies north of Ras Hafun outside the main current, the residence time of the water is long enough to produce large diatom blooms. In this view, the productivity in the Somali Current upwelling is, on average, far below its potential\(^{(10,11)}\). On the other hand, during January 1993 primary productivity was considerably higher than previous estimates of 0.3 gC.m\(^{-2}.d^{-1}\) during the NE monsoon (Fig. 6). Surface waters were not depleted due to nutrient entrainment caused by deepening of the mixed layer during windy periods. This phenomenon was even more pronounced in the Gulf of Aden. The low winter primary production values during II0E\(^{(9)}\) and INDEX\(^{(32)}\) were presumably measured in more oligotrophic waters. However, these measurements were made prior to the introduction of ultraclean incubation techniques in the early eighties, and might have underestimated actual productivity.

Monsoonal differences in primary production were generally reflected in the zooplankton stocks, represented by displacement volumes of catches by nets of ca 330 and 200 μm mesh (Fig. 6). The Gulf of Aden was comparatively rich in zooplankton compared to the Banda Sea. The zooplankton data for the Somali Basin were diverse, ranging from a large seasonal difference during 1964 (II0E, see Table 1) and a puzzling lack of difference during 1979 (INDEX). During INDEX, sampling was not beyond 200 miles from the coast, so larger zooplankton stocks more downstream of the Somali Current could have been missed in July 1979. However, when sampling was extended to over 350 miles from the Somali coast during July 1992, mean sizes of the more offshore catches were not larger than those in the Somali Current. Climatological means of wind and current velocity are very similar for July and August, but there is considerable variation within the season, and between years, in upwelling intensity and the positions and northward migration of the upwelling wedges\(^{(8,35,36)}\). It is difficult to conclude whether the differences in summer stocks in the Somali Basin point to seasonal or interannual differences. It can only be stated that in July 1979 and 1992 zooplankton stocks in the strong upwelling system of the Somali Current remained below potential, like primary production, whereas in August 1964 a high stock size comparable to that in the Oman upwelling was found (Figs 1, 3). Zooplankton
biomasses during March 1979 and January 1993 were, with 23 and 20 ml.m⁻² respectively, higher than in December 1964 and well above those of oligotrophic waters, reflecting the enrichment by winter cooling during the NE monsoon. The Gulf of Aden catches during winter were very large (Fig. 6).

Displacement volumes during NIOP were somewhat higher for the 200 μm catches than for the 320 μm catches (Fig. 6), the more since the 200 μm data concerned 0-150 or 0-200 m catches, and the latter 0-300 m. Large organisms were removed before measurement in both cases. Some of the 200 μm displacements were discarded for calculation due to large amounts of phytoplankton in the catch 8,11. Mean cubic metre densities of copepods in the Somali Current samples (Table 4) were lowest in the 330-330 μm samples of IIOE and NIOP, and much higher in the 200-223 μm samples of INDEX and NIOP. Density trends from the coarser nets corresponded with the differences in displacement volume between the cruises in two different monsoons. For the INDEX 223 μm samples, there was no significant difference in the total number of organisms 22 or in the number of copepods (Table 4), in line with the about equal biomass from the 333 μm catches from March and July 1979 (Fig. 6). Contrarily, NIOP 200 μm samples had 5 times higher copepod density during July 1992 than during Jan.1993. This was not caused by a very large number of juveniles (small copepodids) in July, since conversion of copepod length to dry weight still gave a factor 5 difference. Probably the number of NIOP hauls taxonomically examined was too low to warrant any firm conclusion. Moreover, time and place of 320 and 200 μm net sampling was not the same, indicating that part of the discrepancies in the NIOP results might be due to patchiness.

During the GLOBEC Arabian Sea legs in May and August 1995, a better impression of the influence of mesh size on displacement volume was obtained. Catches from 50 μm vertical net hauls from 75 m to the surface were sieved over 300 μm, and displacement volumes measured for both fractions 11. In the areas with low upper layer chlorophyll concentrations, the fraction 50-300 μm added only 25% to the biomass > 300 μm (Table 5). For the upwelling areas, this was generally about 50%, but many of the 50-300 μm fractions contained phytoplankton. Currently, these samples are studied taxonomically, to determine the amount of zooplankton in these fractions. The GLOBEC displacement data (Table 5) indicate at least that differences in zooplankton biomass between 320 and 200 μm nets should probably be smaller than suggested by the NIOP data (Fig. 6).

Table 4—Mean number of copepods (n.m⁻³) in the Somali Current area (n = number of hauls)

<table>
<thead>
<tr>
<th>Cruise</th>
<th>NE monsoon</th>
<th>SW monsoon</th>
</tr>
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<tbody>
<tr>
<td>IIOE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>330 μm</td>
<td>79 (n=24)</td>
<td>275 (n=32)</td>
</tr>
<tr>
<td>0-200 m</td>
<td></td>
<td></td>
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<tr>
<td>NIOP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>320 μm</td>
<td>94 (n=4)</td>
<td>145 (n=4)</td>
</tr>
<tr>
<td>0-300 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>INDEX</td>
<td></td>
<td></td>
</tr>
<tr>
<td>223 μm</td>
<td>377 (n=14)</td>
<td>332 (n=25)</td>
</tr>
<tr>
<td>0-200 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>NIOP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>200 μm</td>
<td>306 (n=4)</td>
<td>1535 (n=4)</td>
</tr>
<tr>
<td>0-150 m</td>
<td></td>
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</tr>
</tbody>
</table>

Fig. 6—Seasonal differences in primary production and zooplankton standing stock for different areas. Number of observations (and sources): primary production Gulf of Aden 5+315; IIOE 7+22; INDEX 23+1212; NIOP 10+1411; Banda Sea 16+1012; zooplankton Gulf of Aden 4+512 and 8+412; IIOE 24+32 (Table 1); INDEX 14+2512; NIOP 8+812 and 13+1011; Banda Sea 16+1612 and 47+4421.
The GLOBEC data showed a rapid response of zooplankton biomass at the start of the coastal upwelling off Somalia 10°N and Oman 17-22°N in May 1995 (Table 5). Remarkably, zooplankton biomass in the centre of the western Arabian Sea was considerable too, though temperature and chlorophyll profiles were rather similar to the very oligotrophic waters more to the south during transit over the Carlsberg Ridge to Somalia 5°N (where upwelling had not started yet). For August 1995, the low mean displacement > 300 µm in the Somalia 10°N upwelling in comparison to those of the more northern areas is noteworthy, indicating again that zooplankton development off Somalia is sometimes below its potential compared to the Oman upwelling.

Discussion

The NW Indian Ocean is one of the key areas selected by JGOFS to understand the role of the oceans in the greenhouse effect. Mesozooplankton biomass and grazing are among the JGOFS Core Measurements. Zooplankton plays an important role in the consumption and sedimentation of new production, and therewith in the modelling of the carbon dioxide dynamics of the ocean. For variables such as zooplankton biomass that are not detectable from space, modellers are in need of sufficient field data for comparison with simulation results. During the JGOFS Arabian Sea process Study 1992-1997, zooplanktologists used gear with mesh size 200 µm as recommended by JGOFS, or with even smaller mesh (the US ships applied 150 µm nets), to ensure that all stages of mesozooplankton were retained. The number of cruises with zooplankton sampling is, however, rather limited, and coverage in time and space certainly does not meet the degree that modellers like. This paper shows that 200 µm mesh size has been used before in the area, and that data sets off Oman (Discovery 1963/64) and off Yemen (Ibn Magid 1984/85) add to our knowledge of seasonal patterns. Remarkably, displacement volumes from 230 µm nets and from the 330 µm Indian Ocean Standard Net for hauls done at the very same stations by 'Discovery' in the whole western Indian Ocean during 1963/64 showed no significant difference, implying that the large IIIOE data base can still be very useful for comparison with newly collected data and modelling results.

Since biomass from the IIIOE data sets is in displacement units, whereas recent JGOFS cruises used dry weight or carbon measurements, the question of comparability arises. Note, however, that generally very good correlations between these variables exist - here conversion factors found for Banda Sea samples were used - whereas all variables suffer the same disadvantage if applied on the total sample: no discrimination between zooplankton and phytoplankton. Catches by finer-

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<th>Table 5—Displacement volumes (nl.m⁻²) of the &gt; 300 µm and the 50-300 µm fraction in the upper 75 m and chl a concentration (5 m depth) during 30 April - 23 May 1995 and 1 - 19 August 1995 (US GLOBEC Arabian Sea)</th>
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<tr>
<td><strong>Chl a</strong></td>
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<td>(mg.m⁻³)</td>
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<td><strong>Upwelling Oman</strong> (17-22° N)</td>
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<td><strong>Central Arabian Sea</strong></td>
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<td><strong>Upwelling Somalia</strong> (10°N)</td>
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<td><strong>Oligotrophic stations</strong></td>
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* Part of samples with phytoplankton; ** all samples with phytoplankton, X = no stations
considerable amounts of phytoplankton, and probably for this reason the correlation coefficient between copepod density and dry weight of the total sample (200 μm, Yemen 1984/85) was rather poor. Tedium taxonomic analysis is in such cases unavoidable. The good correlation between the number of copepods, dominant both in numbers and in biomass, and the displacement volume in the IIOE data, indicate that displacement is potentially a fair index for zooplankton biomass in cases without sincere contamination. Note that copepod densities were higher for 200 μm than 330 μm samples (Table 4) but the copepod(ite)s passing 330 μm probably contribute relatively little to biomass. In samples without ‘contamination’ by phytoplankton, the fraction 50-300 μm added only ca. 25% to the >300 μm displacement (Table 5). In conclusion, the comparability of data sets is probably less hampered by mesh size than by limited number of samples (as patchiness is large, Table 1) or restricted depth of tows (Table 2, 3).

According to the zooplankton maps of the whole Indian Ocean, mean displacement volumes in the offshore regions of the central Indian Ocean (between 10°S and 15°N), are around 10 ml.m⁻² throughout the year. In the NW Indian Ocean, the Carlsberg Ridge area belongs to this category. For the other areas treated in this paper (Fig. 1), the IIOE data indicated that zooplankton stocks are on average considerably larger, with highest peaks in the coastal upwellings during summer. The new data sets supported and extended the rather fragmented IIOE picture, but also indicated that there were regional differences. Main suggestions were that stock sizes in the Somali upwelling are often below potential compared to the Omanii upwelling, and that the Gulf of Aden is often richer in winter than in summer (apart from the Ras Fartak summer upwelling more to the east). In the satellite chlorophyll patterns through the year (the CZCS images, 1978-1986), it can already be noted that the very high concentrations during the summer SW monsoon extend over a much larger area off Oman than off Somalia. Winter phytoplankton blooms are conspicuous in the northern Arabian Sea but were also noticed in the Gulf of Aden. This is triggered at the beginning of the NE monsoon, with nutrient entrainment by mixed layer deepening, facilitated by decreasing air and sea surface temperatures. The low primary productions recorded in winter before 1980, are now subject of debate, also because new measurements off Oman during 1994 did show less difference with the upwelling season (Jan.-March/April ca 1.0 gC.m⁻².d⁻¹ versus July/August 1.4 gC.m⁻³.d⁻¹; compare NIOP data in Fig. 6) than the factor of more than 3 found previously. The large seasonal chlorophyll signal in the CZCS pictures is currently being debated as well, as remote sensing US airplane flights during summer 1994 were severely biased by aeolian dust, a phenomenon that was not accounted for in the original algorithms. Thus in the present CZCS data the summer chl concentrations might have been largely exaggerated (R.T. Barber, Duke University, USA, pers.comm.).

The only period that a large part of the western Arabian Sea seems really oligotrophic is during spring, when the typical tropical structure with a DCM occurs (Discovery March and May 1964, Baldridge May 1995). May is the month with the lowest chl levels in offshore regions according to the CZCS composites. But in May, coastal upwelling has already started, so locally zooplankton stocks are developing as well. Puzzling is that stocks are relatively large at more offshore stations off Oman too (Fig. 3, Table 5). Speculatively, this is caused by entrainment blooms triggered by the increased wind velocity at the start of the SW monsoon.

There is at present theoretical support for many of the above suppositions. A recent physical-biological model, including the simple chain nutrients-algae-zooplankton-detritus, of the Arabian Sea is able to simulate the major features of phytoplankton dynamics as observed by the CZCS. The model does not only produce upwelling blooms off Somalia and Oman but also entrainment blooms (including the central Arabian Sea in spring and the whole northern Arabian Sea in Feb.-March) and detrainment blooms (central Arabian Sea in autumn). The model also includes zooplankton biomass and grazing, and shows marked differences between Oman and Somalia. In the latter area, biomass in July-August is relatively small, since zooplankton is advected by the Somali Current out of the upwelling wedges before stocks are able to develop. Larger biomasses are reached in September-October, and persist till March. Seasonality is much stronger off Oman, with very large biomasses during July-September, and a short but equally high winter peak in March.
Undoubtedly, the spatial resolution of the model is not very large, and, since the coasts are represented by simple straight lines, it does not produce upwellings at the Yemen/Oman capes already in May (but in July) or the cape-associated eddies and filaments into the Arabian Sea as in the field or in finer-scale models (J.C. Kindle, Stennis Space Center, pers. comm.). However, the model nicely illustrates that significant differences may occur in zooplankton biomass patterns between different regions of the Arabian Sea. The results also support the regular, or at least occasional, occurrence of large zooplankton biomass in winter, due to entrainment blooms.

The statement of the ‘Arabian Sea Paradox’ was based on the assumption that the seasonal variation in phytoplankton productivity and stock was much larger than in zooplankton. However, it was argued above that seasonal variation in primary productivity and chl concentrations in the western Arabian Sea is less extreme than previously thought. Recent work in the eastern Arabian Sea\(^a\)^\(^b\)\(^c\) also showed that fairly high production (>0.6 gC.m\(^{-2}\).d\(^{-1}\)) and surface chl (0.3 mg.m\(^{-3}\)) occurred during the NE monsoon due to winter cooling and that mean mesozooplankton biomass did not vary significantly between seasons, with, on average, around 20 ml.m\(^{-2}\) (mixed layer). Biomass did not even drop in the oligotrophic spring intermonsoon (April/May, with primary production <0.3 gC.m\(^{-2}\).d\(^{-1}\) and surface chl <0.05 mg.m\(^{-3}\)). Bacterial and microzooplankton biomass was highest in that period, presumably sustained by the dissolved organic carbon pool built up during the winter phytoplankton blooms, and zooplankton probably switched to feeding on the microbial loop.\(^d\) So this could be another mechanism why zooplankton biomass remains high in many areas of the Arabian Sea for relatively long time after the wane of phytoplankton blooms, and explain the relatively high zooplankton biomass offshore near Oman during spring. During the JGOFS Arabian Process Study 1992-1997 many new (and hitherto lacking) data on all different compartments of the pelagic food chain have been collected, and it would be a major challenge to incorporate these into more detailed physical-biological models to simulate the seasonal cycles in different areas of this intriguing sea.

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Linda Stathoplos and Ronald Moffatt

References

\(^a\)\(^b\)\(^c\)\(^d\)\(^e\)\(^f\)\(^g\)\(^h\)\(^i\)\(^j\)\(^k\)\(^l\)\(^m\)\(^n\)\(^o\)\(^p\)\(^q\)\(^r\)\(^s\)\(^t\)\(^u\)\(^v\)\(^w\)\(^x\)\(^y\)\(^z\)


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