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# Mesozooplankton production and grazing in the Arabian Sea

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## Abstract

Growth rates, grazing and fecal pellet production by mesozooplankton size classes in the surface 200 m are compared over two inshore/offshore transects in the Northern Arabian Sea during different monsoon seasons. We derived these rate parameters from measured biomass and several empirical models that estimate copepod production from temperature, body weight and food availability. The multivariate regression published by Hirst and Shearer (1997, *Marine Ecology Progress Series*, 154, 155–165) gave the most reasonable rate estimates when compared to direct grazing measurements as well as published data on copepod ingestion and growth rates. In general, zooplankton rate estimates were highest at the inshore stations where phytoplankton production and zooplankton biomass were maximum. Overall cruise means of zooplankton biomass and rate estimates during the early and late NE Monsoon, Spring Inter-monsoon and SW Monsoon were not significantly different. The estimated zooplankton community (all size fractions) growth rate averaged  $0.12 \text{ d}^{-1}$  over all stations during the different monsoon seasons. Although smaller zooplankton size fractions grew faster, slower growing  $> 2 \text{ mm}$  zooplankton dominated the zooplankton biomass of the Arabian Sea and this resulted in a lower overall community growth rate. Estimated total carbon (phytoplankton, protozoa and detritus) ingestion averaged  $44 \text{ mM C m}^{-2} \text{ d}^{-1}$ , which was approximately 40% of primary production. Expressed as a percentage of biomass, we found that zooplankton ingested approximately 40% of their body carbon  $\text{d}^{-1}$ . Zooplankton fecal pellet production averaged  $13 \text{ mM C m}^{-2} \text{ d}^{-1}$  or roughly 12% of primary production. This estimated fecal pellet

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production was greater than measurements of the export flux during the NE Monsoon and Spring Intermonsoon. However, estimated fecal pellet production was less than measured export flux during the SW Monsoon when sinking phytoplankton likely contributed directly to the export flux. Our data suggest that relative to other ocean basins, the grazing impact of mesozooplankton is significant in the Arabian Sea as a consequence of the high zooplankton biomass, abundance of diatoms, and warm temperatures, which result in high zooplankton metabolic demands and growth rates. The observation that the average zooplankton biomass ( $110 \text{ mM C m}^{-2}$ ) did not change significantly over the monsoon seasons suggests that zooplankton production ( $13 \text{ mM C m}^{-2} \text{ d}^{-1}$ ) and zooplankton mortality were similar over the study interval. © 2000 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

The Arabian Sea experiences extremes in atmospheric forcing that result in the greatest seasonal variability observed in any ocean basin. Monsoonal winds cause oscillations in rates of nutrient supply and primary production (Krey and Babenerd, 1976; Banse and English, 1994). The seasonal monsoon cycles also can be reflected in changes in zooplankton abundance (Smith, 1982; Banse, 1991; Smith et al., 1998; Wishner et al., 1998) and in the gravitational flux of carbon both from the euphotic zone and to the sediments (Nair et al., 1989; Ittekkot, 1991; Lee et al., 1998). The US Joint Global Ocean Flux Study (JGOFS) Arabian Sea Process Study was designed to produce a seasonally and spatially resolved carbon budget of the Arabian Sea basin.

Developing predictive models of carbon flux and their relation to primary production requires a mechanistic understanding of the pelagic ecosystem. The amount of biogenic material leaving surface waters is dependent on how it is partitioned by the plankton community (Frost, 1984; Michaels and Silver, 1988; Roman et al., 1995; Verity and Smetacek, 1996). The species composition of the autotrophs and heterotrophs determines the amount of carbon that is either recycled in the euphotic zone or is exported to depth. Mesozooplankton ( $> 200 \mu\text{m}$ ), through their processes of ingestion, metabolism and egestion, can be important in determining the size and composition of sinking particulate matter. Mesozooplankton produce rapidly sinking ( $> 200 \text{ m d}^{-1}$ ) fecal pellets that can dominate the gravitational flux of biogenic material (Fowler and Knauer, 1986; Small et al., 1989; Altabet and Small, 1990). In addition, mesozooplankton can contribute to the flux of biogenic material through their daily vertical excursions in the water column. Recent calculations (Longhurst et al., 1990; Dam et al., 1995a; Zhang and Dam, 1997) suggest that respiratory carbon and excreted dissolved nitrogen from mesozooplankton that migrate below the euphotic zone during the day can represent significant downward fluxes of carbon and nitrogen relative to gravitational fluxes.

Models (e.g., Frost, 1984; Frost and Franzen, 1992) and direct measurements (e.g., Roman et al., 1993; Dam et al., 1993, 1995b; Roman and Gauzens, 1997) suggest that mesozooplankton usually have a minor role in grazing primary production ( $< 25\% \text{ d}^{-1}$ ) in oceanic waters. It is interesting to note, however (Roman and

Gauzens, 1997), that the fraction of primary production that mesozooplankton consume is often similar to the amount of “new” production (see Dugdale and Goering, 1967). A major component of mesozooplankton diets is often protozoa (e.g., Kleppel, 1992; Dam et al., 1995a; Verity and Paffenhöffer, 1996; Roman and Gauzens, 1997). Thus, the role of mesozooplankton in the carbon cycle of the euphotic zone and in the export of carbon from the euphotic zone will be underestimated if only phytoplankton ingestion by mesozooplankton is included.

Previous mesozooplankton grazing studies in the Arabian Sea have emphasized individual copepod species (e.g., Smith, 1982; Petipa, 1985; Sazhina, 1985). Copepods dominate the zooplankton community of the Arabian Sea, where over 50 species of copepods occur in the surface waters of the Arabian Sea, with roughly 11 species co-dominant during any particular season (Timonin, 1971; Madhupratap et al., 1992). Thus, if the research goal is to estimate the total grazing impact of mesozooplankton community in the Arabian Sea, it is not practical to emphasize individual copepod species’ ingestion rates. Mesozooplankton biomass data from the US JGOFS Arabian Sea Process Study has been published recently by Smith et al. (1998) and Wishner et al. (1998). In this paper we report estimates of production, grazing and fecal pellet production by mesozooplankton (copepod) size-classes. These rate estimates are compared over two inshore/offshore transects in the Northern Arabian Sea during different monsoon seasons. We derive these rate parameters from measured biomass and several models that estimate copepod production from temperature, body weight and food availability. These ingestion estimates are compared to direct ingestion measurements derived from in situ incubations. Finally, our estimates of mesozooplankton production, grazing, and fecal pellet production are compared to estimates of primary production and the sinking flux of carbon from the euphotic zone to assess the role of mesozooplankton in the carbon cycle in the Arabian Sea.

## 2. Methods

### 2.1. Zooplankton biomass

Mesozooplankton collections were conducted in the northern Arabian Sea between Oman and India north of 10°N (Fig. 1) during January 1995 (late NE Monsoon; cruise TN043), March 1995 (Spring Intermonsoon; cruise TN045), August/September 1995 (late SW Monsoon; cruise TN050) and December 1995 (early NE Monsoon; cruise TN054). At long (roughly 48 h) station occupations, designated S2, S4, S7, S11, S15 and N7 (Fig. 1) we conducted day and night stratified tows with two multiple opening/closing net and environmental sampling systems (MOCNESS; Wiebe et al., 1985). One MOCNESS had a 1-m<sup>2</sup> mouth area and 153- $\mu$ m-mesh nets and the other MOCNESS had a 0.25-m<sup>2</sup> mouth area and 64- $\mu$ m-mesh nets. At shorter station occupations, we conducted a single oblique Bongo tow (333- and 153- $\mu$ m nets equipped with flowmeters and a time/depth recorder) in the surface 200 m at whatever time of day the station was occupied. Details of the towing procedures and biomass

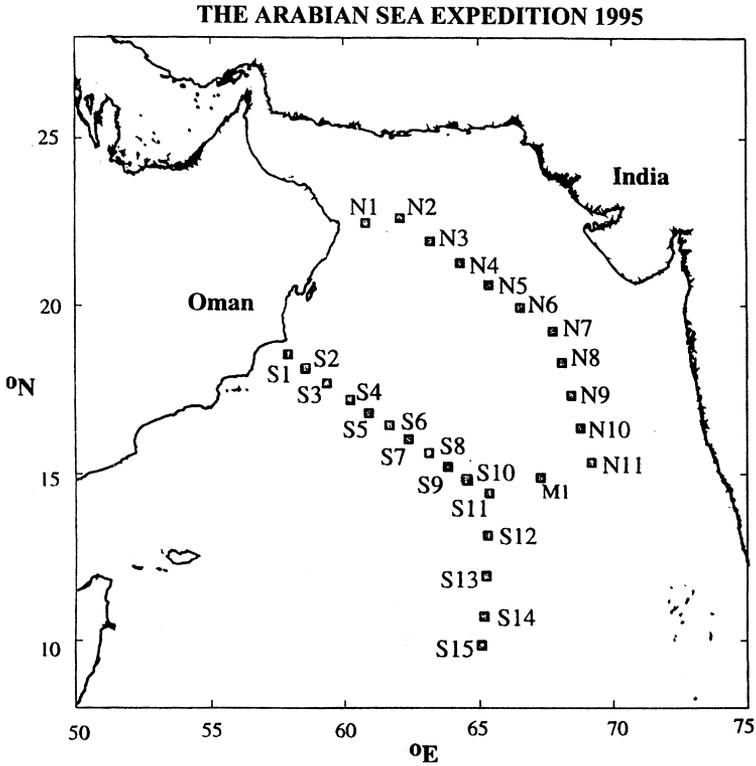


Fig. 1. Map of Arabian Sea with cruise track sampling stations. Stations labeled “S” are southern section; stations labeled “N” are northern section.

analysis are provided by Smith et al. (1998) and Wishner et al. (1998). The zooplankton biomass data are available on the US JGOFS website (<http://usjgofs.whoi.edu>). The zooplankton catch from the nighttime MOCNESS tows and the BONGO tows was size-fractionated shipboard through 2000- 1000- 500- 200- and 64- $\mu$ m-mesh sieves. Depending on the net system and cruise, we used three different methods to estimate zooplankton carbon biomass. Direct carbon analysis on aliquots from fresh zooplankton samples were run on a C–H–N analyzer. Carbon was determined from fresh displacement volumes using the regression of Wiebe et al. (1977). In other samples, dry weights were measured on aliquots of fresh samples. We used a carbon: dry weight conversion of 40% (Beers, 1966) to estimate the zooplankton carbon biomass from dry weight.

2.2. Direct estimates of zooplankton ingestion

Zooplankton ingestion was estimated directly from in situ incubations with radioisotopes. At the long stations on cruises TN043 and TN045 zooplankton grazing rates were estimated from the uptake of autotrophic ( $\text{NaH}^{14}\text{CO}_2$ -labeled) and

heterotrophic ( $[^3\text{H}\text{-methyl}]\text{thymidine}$ -labeled) particles in short-term in situ incubations (Roman and Rublee, 1981). Details of the method and potential sources of error are described in Roman and Gauzens (1997). Carbon consumption by the zooplankton was estimated by multiplying the grazing rate of the zooplankton ( $\text{d}^{-1}$ ) on autotrophs ( $^{14}\text{C}$  uptake) and heterotrophs ( $^3\text{H}$  uptake) by the concentration of phytoplankton and protozoa, respectively, determined from microscope counts and carbon conversions (Garrison et al., 1998; Dennett et al., 1999). The sum of these calculations represents an estimate of the total carbon ingested by the zooplankton.

### 2.3. Indirect estimates of zooplankton ingestion

Our direct estimates of zooplankton ingestion were made on two of the four Arabian Sea process cruises and only at the six long stations (Fig. 1). In order to estimate zooplankton ingestion at stations where we only had zooplankton biomass data, we examined three different models that can be used to estimate zooplankton ingestion.

The Huntley and Lopez (1992) method assumes that the instantaneous growth rate of copepods ( $g$ ) is: independent of body size, independent of species, not food limited, and is strongly dependent on habitat temperature. Using data on copepod adult and egg weights and generation times at temperatures that ranged from  $-1.7$  to  $30.7^\circ\text{C}$ , Huntley and Lopez (1992) estimated copepod instantaneous growth rate ( $g, \text{d}^{-1}$ ) =  $0.0445e^{0.111T}$ , where  $T$  is the habitat temperature in  $^\circ\text{C}$ . Copepod production ( $\text{mM C m}^{-3} \text{d}^{-1}$ ) =  $Bg$ , where  $B$  is biomass ( $\text{mM C m}^{-3}$ ). Our interpretation of the Huntley and Lopez (1992) model is that it represents a maximum potential growth rate (not food limited) and thus maximum potential ingestion and egestion rate. We can estimate copepod ingestion ( $\text{mM C m}^{-3} \text{d}^{-1}$ ) by assuming a gross growth efficiency (growth/ingestion) of 30%. It has been suggested that copepod gross growth efficiency can vary with food quality and temperature, ranging from approximately 14 to 50% with a mean of approximately 30% (Omori and Ikeda, 1984). A similar mean gross growth efficiency was recently determined by Straille (1997) for both protozoa and crustacean zooplankton. Copepod fecal pellet production is estimated from the derived ingestion estimates and an assumed 70% assimilation efficiency ( $n = 104$ ,  $\text{SD} = 0.16$ ; Conover, 1978). The actual efficiencies of mesozooplankton growth and assimilation likely varied over the stations and seasons of the Arabian Sea study. However, these efficiencies have been shown to vary 20–50% over a range of temperatures, food qualities and mesozooplankton sizes, whereas mesozooplankton biomass during our study varied by more than an order of magnitude.

Hirst and Sheader (1997) combined published data on copepod growth rates, body weights ( $0.002\text{--}43 \mu\text{M C}$ ) and habitat temperature ( $0\text{--}29.8^\circ\text{C}$ ) in a multivariate regression equation that relates intrinsic growth rate ( $g = \text{d}^{-1}$ ) to temperature ( $T = ^\circ\text{C}$ ) and copepod weight ( $W_c = \mu\text{g C individual}^{-1}$ ),  $g = 0.0732 \times 10^{0.0246T} / W_c^{0.2962}$ . Ingestion and fecal pellet production are estimated from the derived copepod production rates,  $P = gB$ , a 30% gross growth efficiency, and 70% assimilation efficiency. Note that the Hirst and Sheader (1997) estimate of copepod growth differs from the Huntley and Lopez (1992) model in that it predicts growth rate declines with increasing body size.

The 93 published growth rates used to generate the Hirst and Shearer (1997) equation covered a range of food conditions. Thus, the predicted growth rates may be less than a maximum intrinsic growth rate if the growth rates included in the regression analysis were food-limited.

The third equation used to predict rates of copepod growth, ingestion and egestion includes temperature, copepod body size, and a food limitation parameter (Huntley and Boyd, 1984). At food concentrations below the saturation concentration ( $C < C_c$ ), copepod growth ( $g$ ,  $d^{-1}$ ) is food limited:  $g = aCbW^n - kW^m$ , where  $a$ , assimilation efficiency, is assumed to be 0.7 (Conover, 1978),  $C$  is the food concentration ( $mM C m^{-3}$ ),  $b$  is the clearance rate coefficient,  $W$  is copepod body weight,  $n$  is an assimilation coefficient and  $k$  and  $m$  are respiratory coefficients. The coefficients  $b$ ,  $n$ ,  $k$  and  $m$  are all influenced by the habitat temperature,  $T$ :  $b = 1.777e^{(0.234T)}$ ,  $n = 0.681e^{(0.0199T)}$ ,  $m = 0.858e^{(-0.008T)}$ ,  $k = 0.375e^{(0.0546T)}$ . Thus, growth is controlled by habitat temperature,  $T$ , food concentration  $C$ , and copepod body weight,  $W$ . When food is in excess of the critical concentration, copepods attain a maximum growth rate that is determined solely by habitat temperature:  $g \max = 0.0543e^{(0.110T)}$ . Zooplankton must have a minimum food concentration ( $C_m$ ) in order to balance respiratory losses with assimilated energy. When assimilation balances respiration  $aC_m bW^n = kW^m$ ; thus,  $C_m = kW^{m-n}/ab$ ,  $C_m$  has units of  $mM C m^{-3}$ . When food concentration exceeds the critical concentration,  $C_c$ , then copepod growth rate is  $g \max = aC_c bW^n - kW^m$ . The critical food concentration can thus be estimated from:  $C_c = C_m + g \max/abW^{(n-1)}$ . Huntley and Boyd (1984) derived the above equations using copepods weighing 0.3–3.3  $\mu M C$ . The majority of copepods in our biomass collections were within this size range.

We used two different estimates of “available” food for the copepods. We calculated the average particulate organic carbon (POC) in the 25-m depth intervals where we had stratified MOCNESS tows at the six long stations (Fig. 1). The POC data were obtained from the US JGOFS database (Azam and Ducklow in <http://usjgofs.whoi.edu>). The POC values represent the “upper limit” of available food because POC measurements include free-living bacteria, small ( $< 2 \mu m$ ) algae and protozoa and detritus, much of which cannot be captured by copepods (Nival and Nival, 1976; Berggreen et al., 1988). The other, more conservative, estimate of available food we used in the Huntley and Boyd (1984) equation was microplankton carbon. These estimates were derived from microscope counts, size estimates, and the use of  $C/volume$  conversions to estimate the  $C$  biomass of diatoms, dinoflagellates, tintinnid ciliates, non-loricate ciliates, and foraminifera/actinopods available on the US JGOFS database (Caron and Garrison in <http://usjgofs.whoi.edu>). It is likely that there are algae, protozoa, and detritus that copepods ingest that are not included in these microplankton biomass measurements; thus, we feel that this estimate of available copepod food represents a “minimum” value.

Copepod production ( $mM C m^{-3} d^{-1}$ ) is the product of the estimated growth rate ( $g$ ) and the biomass ( $B$ ). At the longer time-series stations on the southern transect (Fig. 1), we use night measurements of zooplankton biomass in 25-m intervals for the surface 200 m. The 64–200  $\mu m$  zooplankton fraction is from the 0.25- $m^2$  MOCNESS and the larger zooplankton size fractions are from the 1.0- $m^2$  MOCNESS. At the

shorter stations we use zooplankton biomass data from the Bongo tows. Whereas the size-fractionated MOCNESS data are from night tows, the Bongo tows were taken at whatever time we occupied the station. While there were some diel shifts in the vertical distribution of zooplankton within in the upper water column, day/night differences in the integrated (0–100 m or 0–200 m) zooplankton biomass at the Arabian Sea stations was usually not significantly different (Smith et al., 1998; Wishner et al., 1998).

All three equations use habitat temperature to estimate copepod growth. Temperature data were obtained by taking the average of all CTD casts from a particular station listed in the US JGOFS database (Morrison in <http://usjgofs.whoi.edu>). We used the average temperature of the 25-m bins for the MOCNESS zooplankton collections. We assumed that most of the zooplankton collected in the Bongo tows were caught in the surface mixed layer and therefore used the average temperature of the mixed layer with the integrated zooplankton biomass in the production equations. Our stratified MOCNESS tows (Smith et al., 1998; Wishner et al., 1998) support this assumption.

We assumed that copepods comprised all of the measured zooplankton biomass. Based on previous studies in the Arabian Sea (Timonin, 1971; Madhupratap et al., 1992) as well as selected counts from our MOCNESS collections (Smith et al., 1998), this is a reasonable assumption. We derived an average copepod weight in a particular size fraction by assuming that upper size limit of the fraction, determined by the sieve (64, 200, 500, 1000, 2000  $\mu\text{m}$ ) represented the average length of copepods retained in the fraction. We used a combination of direct measurements and published length-weight regressions for copepods to estimate the “average” copepod body carbon weight of the fraction: 64–200  $\mu\text{m}$  = 0.02  $\mu\text{M}$ , 200–500  $\mu\text{m}$  = 0.17  $\mu\text{M}$ , 500–1000  $\mu\text{m}$  = 0.42  $\mu\text{M}$ , 1000–2000  $\mu\text{m}$  = 1.67  $\mu\text{M}$ , > 2000  $\mu\text{m}$  = 16.67  $\mu\text{M}$ . If we assume that the size of copepods caught on sieves was determined by their width and used a length:width ratio of 3 : 1, we would calculate approximately the same individual weights. The actual mean weight of the mesozooplankton caught in each size fraction likely varied with station and season, but we expect that this variation is less than the order of magnitude variation in the total weight biomass of the various mesozooplankton size fractions.

### 3. Results

#### 3.1. Zooplankton biomass

The general differences among estimates of zooplankton biomass caught with the different net systems is illustrated in the samples collected along the southern transect (Fig. 2). In general, the estimates of > 200- $\mu\text{m}$  zooplankton biomass in the surface 200 m caught with the three sampling systems were similar. At the inshore stations, the 1- $\text{m}^2$  MOCNESS with the 153- $\mu\text{m}$  mesh nets caught more > 200- $\mu\text{m}$  zooplankton than the 0.25- $\text{m}^2$  MOCNESS equipped with 64- $\mu\text{m}$  mesh nets during cruises TN050 and TN054 when the large copepods *Calanoides carinatus* and *Pleuromamma indica* were abundant. There were no significant differences (Mann Whitney U-test;

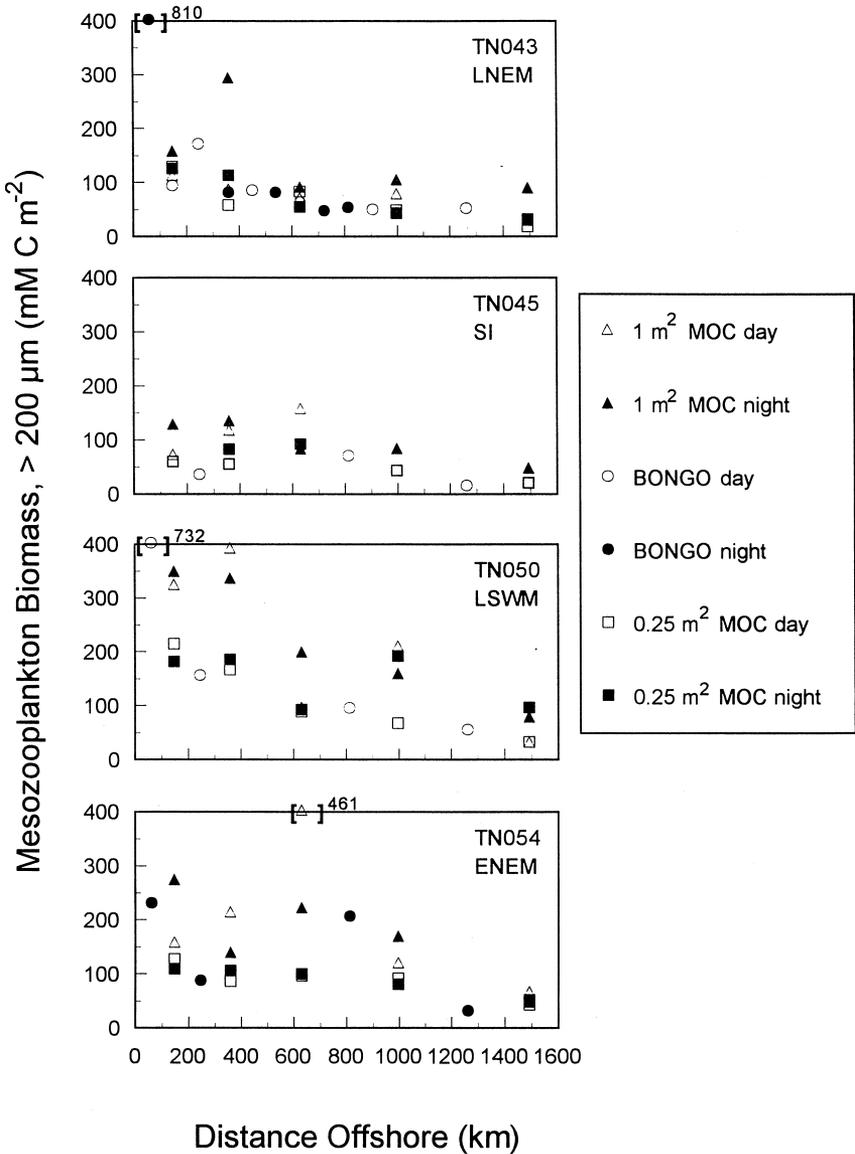


Fig. 2. Biomass of > 200 μm zooplankton (mM C m<sup>-2</sup>) in the surface 200 m on the southern transect during the late NE Monsoon (LNEM, cruise TN043), Spring Intermonsoon (SI, cruise TN045), late SW Monsoon (LSWM, cruise TN050) and early NE Monsoon (ENEM, cruise TN054), collected with the 2 MOCNESS systems and Bongo nets during day and night tows.

$P > 0.05$ ) between the amount of zooplankton caught with the Bongo (153-μm mesh) net and MOCNESS systems. In this paper we will use zooplankton data collected with the Bongo net and 1-m<sup>2</sup> MOCNESS for > 200-μm zooplankton. At the long

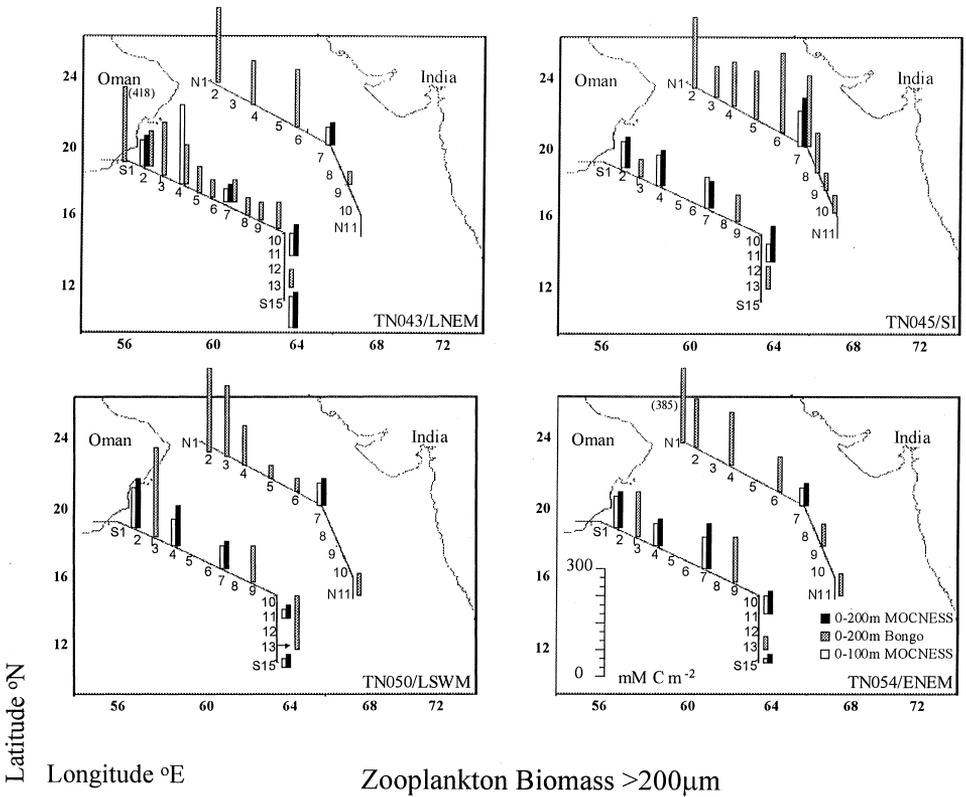


Fig. 3. Biomass of > 200 µm zooplankton ( $\text{mM C m}^{-2}$ ) in the surface 200 m (MOCNESS and Bongo tows) and surface 100 m (MOCNESS tows) at the Arabian Sea stations during the late NE Monsoon (LNEM, cruise TN043), Spring Intermonsoon (SI, cruise TN045), late SW Monsoon (LSWM, cruise TN050) and early NE Monsoon (ENEM, cruise TN054).

stations when both MOCNESS systems were employed, we will also use the 64–200-µm zooplankton fraction collected with the 0.25- $\text{m}^2$  MOCNESS.

Over the whole study, the integrated zooplankton biomass ranged from approximately 30 at station S15 during the early NE Monsoon (TN054) to 418  $\text{mM C m}^{-2}$  at station S1 during the late NE Monsoon (TN043). The average > 200-µm integrated biomass in the surface 200 m at all stations sampled in the Arabian Sea basin over all four cruises was 110  $\text{mM C m}^{-2}$ . Note that MOCNESS estimates of zooplankton biomass integrated to 100 m and integrated to 200 m were similar, indicating that most of the zooplankton occupied the surface 100 m (Fig. 3).

### 3.2. Comparison of estimated zooplankton rates

Grazing rates for the 200–2000-µm fractions determined from the in situ isotope incubations and for the three models are compared because larger zooplankton

Table 1  
Grazing ( $\text{mM C m}^{-2} \text{d}^{-1}$ ) comparisons, 200–2000  $\mu\text{m}$  zooplankton

Cruise/period	In Situ	Hirst–Sheader	Huntley–Lopez	Huntley–Boyd <sup>MC</sup>	Huntley–Boyd <sup>POC</sup>
TN043/LNEM					
Mean	9.23	12.16	53.21	3.38	23.45
SD	11.46	10.79	44.20	2.61	15.81
TN045/SI					
Mean	6.09	20.01	103.47	6.06	54.15
SD	4.22	6.18	33.33	2.04	19.60

(> 2000  $\mu\text{m}$ ) avoid the in situ grazing chambers (Table 1). The comparisons of the integrated grazing estimates from the six long stations show that the Hirst and Sheader (1997) equation and Huntley and Boyd (1984) equation, which uses microplankton carbon as “available” food give ingestion estimates that are closest to the direct ingestion measurement. The isotope incubation technique is subject to several sources of error, most of which result in underestimates of zooplankton grazing rates (Roman and Gauzens, 1997). The highest estimates of ingestion were derived from the Huntley and Lopez (1992) equation, which assumes that food is not limiting to copepod growth and that the instantaneous growth rate is independent of body size. Estimates of the critical food concentration ( $C_c$ ; Huntley and Boyd, 1984), which is the concentration of food necessary for maximum growth rate, show that both POC and microplankton concentrations are often below particulate carbon estimates necessary for maximum copepod growth rates (Table 2). However, these estimates of particle abundance are from discrete bottle collections that may miss layers of enhanced particle concentration (Cowles et al., 1993). Thus, our comparisons of particle abundance and estimated critical food concentrations do not prove food limitation of copepod growth, but rather suggest the possibility of food limitation.

A more complete comparison of the indirect ingestion estimates for > 64- $\mu\text{m}$  zooplankton (Table 3) shows significant differences ( $P < 0.05$ , Kruskal–Wallis rank test; least significant difference post-comparison test) between ingestion estimates derived from Huntley–Lopez > Huntley–Boyd (carbon as POC) > Hirst–Sheader and Huntley–Boyd (carbon as microplankton). There were no significant differences between ingestion rates estimated with the Hirst–Sheader and Huntley–Boyd (carbon as microplankton) equations ( $P > 0.05$ , Mann Whitney U-test). Ingestion estimates based on the Huntley and Boyd (1984) equation using POC as “available” food may overestimate ingestion because > 50% of the measured POC is < 3  $\mu\text{m}$  (POC measurements on GFF versus 3.0- $\mu\text{m}$  silver filters) and cannot be readily captured and ingested by the zooplankton (Nival and Nival, 1976; Berggreen et al., 1988). Lower ingestion estimates were derived from the Huntley and Boyd (1984) equation using microplankton carbon as available food (Table 3). This calculation may underestimate grazing if the zooplankton graze in layers of microplankton that are more abundant than the discrete bottle estimates as well as if zooplankton consume food

Table 2  
Average estimated critical food concentration ( $C_c$ ) for zooplankton size classes in surface 25 m, POC and microzooplankton carbon (MC) ( $\text{mM C m}^{-3}$ )

Station	Cruise TN043		Cruise TN043		Cruise TN043		Cruise TN043		Cruise TN045		Cruise TN045		Cruise TN050		Cruise TN050		Cruise TN054		Cruise TN054	
	Cc	POC	MC	Cc	POC	MC	Cc	POC	Cc	POC	MC	Cc	POC	Cc	POC	MC	Cc	POC	MC	MC
S2	7.24	11.02	1.44	7.06	6.54	0.36	7.48	nd	0.96	7.08	7.53	nd	0.96	7.08	7.53	nd	7.08	7.53	nd	nd
S4	7.17	5.42	0.88	7.06	7.84	0.23	7.17	nd	0.59	7.10	4.56	nd	0.59	7.10	4.56	nd	7.10	4.56	nd	nd
S7	7.18	6.22	0.47	7.05	6.62	0.27	7.07	nd	0.57	7.06	5.21	nd	0.57	7.06	5.21	nd	7.06	5.21	nd	nd
S11	7.11	4.87	0.84	7.04	2.70	0.32	7.05	nd	0.82	7.04	6.25	nd	0.82	7.04	6.25	nd	7.04	6.25	nd	nd
S15	7.04	3.27	0.34	nd	nd	nd	7.04	nd	0.38	7.04	4.84	nd	0.38	7.04	4.84	nd	7.04	4.84	nd	nd
N7	7.20	3.29	0.42	7.15	9.03	0.75	7.04	nd	0.64	7.05	6.31	nd	0.64	7.05	6.31	nd	7.05	6.31	nd	nd

Table 3  
Estimated ingestion ( $\text{mM C m}^{-2} \text{d}^{-1}$ )

Cruise/Station	Huntley–Lopez	Hirst–Sheader	Huntley–Boyd <sup>MC</sup>	Huntley–Boyd <sup>POC</sup>
TN043/S2	188.65	32.53	38.33	110.40
TN043/S4	552.07	88.58	45.26	268.35
TN043/S7	81.84	11.56	3.95	42.44
TN043/S11	154.19	24.09	10.57	82.02
TN043/S15	245.53	24.19	4.68	131.65
TN043/N7	152.74	38.14	7.85	61.97
TN045/S2	214.31	37.99	23.27	115.10
TN045/S4	206.99	29.82	10.78	129.76
TN045/S7	262.18	58.51	11.37	136.26
TN045/S11	152.97	23.26	9.50	70.85
TN045/S15	nd	nd	nd	nd
TN045/N7	253.52	46.67	20.64	140.22
TN050/S2	204.23	43.94	19.62	nd
TN050/S4	167.19	34.67	9.58	nd
TN050/S7	187.89	29.10	16.88	nd
TN050/S11	111.25	27.72	9.76	nd
TN050/S15	106.83	17.02	6.24	nd
TN050/N7	190.76	27.56	14.77	nd
TN054/S2	265.15	58.98	nd	159.13
TN054/S4	211.23	57.09	nd	112.53
TN054/S7	281.23	50.52	nd	159.59
TN054/S11	209.79	38.43	nd	108.79
TN054/S15	77.07	23.84	nd	34.86
TN054/N7	177.58	43.53	nd	84.31

(detritus, fecal pellets and smaller protozoa and phytoplankton) that are not included in these microplankton counts. In addition, microplankton counts are only available for a limited number of stations, and thus we could not estimate zooplankton grazing for all the stations where we have measurements of zooplankton biomass.

The Huntley and Lopez (1992) zooplankton rate estimates appear high when compared to literature values. The correlation of zooplankton biomass and the Huntley–Lopez ingestion rates for all four cruises was:  $\text{Ingestion} = 2.51 \times \text{Biomass} + 0.015$ . This means that the Huntley and Lopez (1992) equation predicts that the copepods are ingesting  $2.51 \times$  their body carbon per day. While it is possible that copepod nauplii and early copepodites ingest over 100% of their body weight per day at high food concentrations (Fernandez, 1979; Berggreen et al., 1988), a daily ration of 251% for a mixed zooplankton community in oceanic waters appears unrealistic. The larger zooplankton fractions ( $> 1000 \mu\text{m}$ ) comprise over 50% of total zooplankton biomass in the euphotic zone of Arabian Sea waters (Smith et al., 1998; Wishner et al., 1998). Thus, it is highly unlikely that a zooplankton community comprised of these larger-sized copepods would have such a high weight-specific ingestion rate. Ingestion

versus biomass for all the zooplankton size-fractions using the Hirst and Sheader (1997) equation (Fig. 4) suggests that the Arabian Sea zooplankton consumed approximately 40% of their body weight per day. The weight-specific ingestion rates were an inverse function of body size, ranging from an average of 22%  $\text{d}^{-1}$  for  $> 2000\text{-}\mu\text{m}$  zooplankton to 167%  $\text{d}^{-1}$  for the  $64\text{--}200\text{-}\mu\text{m}$  zooplankton fraction.

Ingestion rates are estimated from growth rates ( $g$ ) in the models of Huntley and Lopez (1992), Hirst and Sheader (1997), and Huntley and Boyd (1984); when food concentration is above the critical food concentration). We can compare these estimates of instantaneous growth rate at three temperatures that represent the

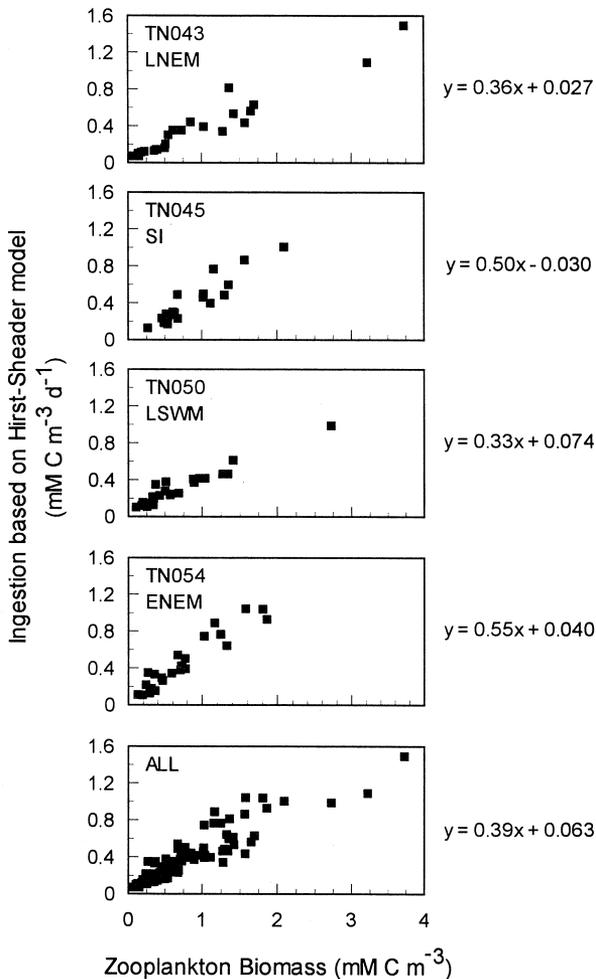


Fig. 4. Zooplankton ( $> 200\ \mu\text{m}$ ) ingestion ( $\text{mM C m}^{-3} \text{d}^{-1}$ ) estimated with the Hirst-Sheader model as a function of zooplankton biomass ( $\text{mM C m}^{-3}$ ) during the late NE Monsoon (LNEM, cruise TN043), Spring Intermonsoon (SI, cruise TN045), late SW Monsoon (LSWM, cruise TN050) and early NE Monsoon (ENEM, cruise TN054).

Table 4  
Estimated growth rate ( $\text{d}^{-1}$ )

	Temperature 20°	Temperature 25°	Temperature 30°
Hirst–Sheader 64–200 $\mu\text{m}$	0.37	0.49	0.64
Hirst–Sheader 200–500 $\mu\text{m}$	0.19	0.25	0.33
Hirst–Sheader 500–1000 $\mu\text{m}$	0.14	0.19	0.25
Hirst–Sheader 1000–2000 $\mu\text{m}$	0.09	0.12	0.16
Hirst–Sheader > 2000 $\mu\text{m}$	0.05	0.06	0.08
Huntley–Lopez	0.41	0.71	1.24
Huntley–Boyd	0.49	0.85	1.47

temperature range in the euphotic zone of the Arabian Sea (Table 4). The Huntley–Lopez and Huntley–Boyd estimates of  $g$  represent maximum rates with no food limitation and no dependence on body size. Growth rates estimated from the Hirst and Sheader (1997) equation are inversely proportional to body size and the data used in the regression equation likely include some food-limited growth. The range of estimated growth rates for the different zooplankton size-fractions using the Hirst and Sheader (1997) equation are reasonable when compared to published growth rates for similar-sized copepods at these temperatures (Kimmerer and McKinnon, 1987; McKinnon, 1996). Given the possibility of food limitation, published evidence of slower growth rates for larger zooplankton (Kleppel et al., 1996), and the uncertainty of what measurement to use for “available food” in the Huntley and Boyd (1984) equation, in subsequent analysis we will use the Hirst and Sheader (1997) equation to estimate zooplankton production, grazing and fecal pellet production. For our purposes, the Hirst and Sheader (1997) model yields reasonable estimates of zooplankton rates that can be used to assess the temporal and spatial patterns of zooplankton grazing and growth in the Arabian Sea.

### 3.3. Spatial and temporal pattern in zooplankton grazing, production and egestion

Estimated grazing by > 200- $\mu\text{m}$  zooplankton on the two transects over the different monsoon seasons (Fig. 5) shows a range from approximately  $10 \text{ mM C m}^{-2} \text{ d}^{-1}$  at the southern most station (S15) during the early NE Monsoon (TN054) to  $152 \text{ mM C m}^{-2} \text{ d}^{-1}$  at the inshore station (N1) on the northern transect during the late NE Monsoon cruise (TN043). In general, zooplankton grazing decreased going from inshore to offshore and was higher on the northern transect compared to the southern transect. It was somewhat surprising that zooplankton grazing in the Arabian Sea did not show more variation over the different monsoon seasons. The average integrated ingestion rate by > 200- $\mu\text{m}$  zooplankton in the surface 200 m at all stations sampled in the Arabian Sea over all four cruises was  $44 \text{ mM C m}^{-2} \text{ d}^{-1}$ ,  $\text{SD} = 31 \text{ mM C m}^{-2} \text{ d}^{-1}$ . We have 64–200- $\mu\text{m}$  size-fraction data only for the southern transect where this zooplankton fraction ingests 6–10  $\text{mM C m}^{-2} \text{ d}^{-1}$ . The total (> 64- $\mu\text{m}$ ) zooplankton ingestion on the southern transect would thus be approximately  $50 \text{ mM C m}^{-2} \text{ d}^{-1}$ .

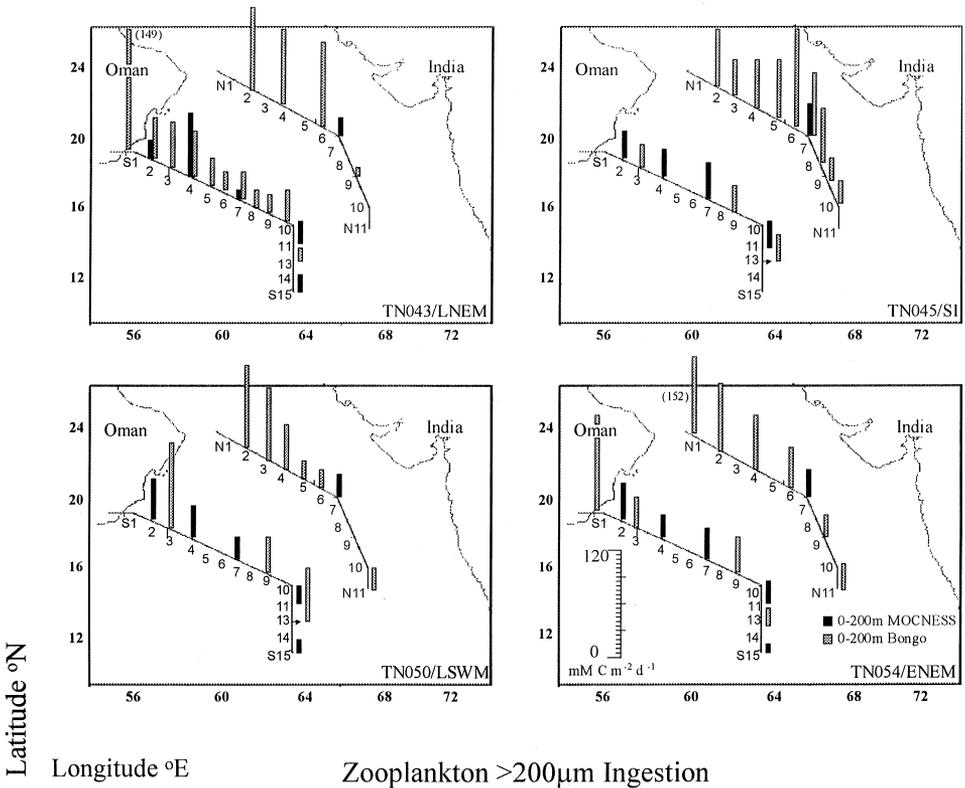


Fig. 5. Zooplankton (> 200 µm) ingestion ( $\text{mM C m}^{-2} \text{d}^{-1}$ ) estimated with the Hirst–Sheader model and zooplankton biomass data collected in the surface 200 m with MOCNESS and Bongo tows at the Arabian Sea stations during the late NE Monsoon (LNEM, cruise TN043), Spring Intermonsoon (SI, cruise TN045), late SW Monsoon (LSWM, cruise TN050) and early NE Monsoon (ENEM, cruise TN054).

A comparison of the contributions of the different zooplankton size-fractions shows that, in general, zooplankton > 1000 µm comprised > 50% of the total zooplankton biomass and ingestion in the surface 200 m (Fig. 6). The smaller zooplankton size fractions have a greater contribution to total ingestion than to total biomass because of their higher weight-specific ingestion rates. For example, on average 64–200 µm zooplankton contributed 10% of the total zooplankton biomass but over 25% of the total estimated zooplankton ingestion (Fig. 6). There were no clear seasonal or inshore/offshore changes in the contributions of the different zooplankton size-fractions to biomass or ingestion. Vertical changes in the zooplankton grazing are compared for station S4 which is in the area of upwelling during the SW Monsoon (Fig. 7). Zooplankton ingestion rates at station S4 were highest in the upper water column. The highest ingestion rate of the 64–200-µm zooplankton was found in the surface 50 m at S4 during the early NE Monsoon cruise (TN054), whereas the highest ingestion rate of the > 2000-µm zooplankton fraction occurred at the same station

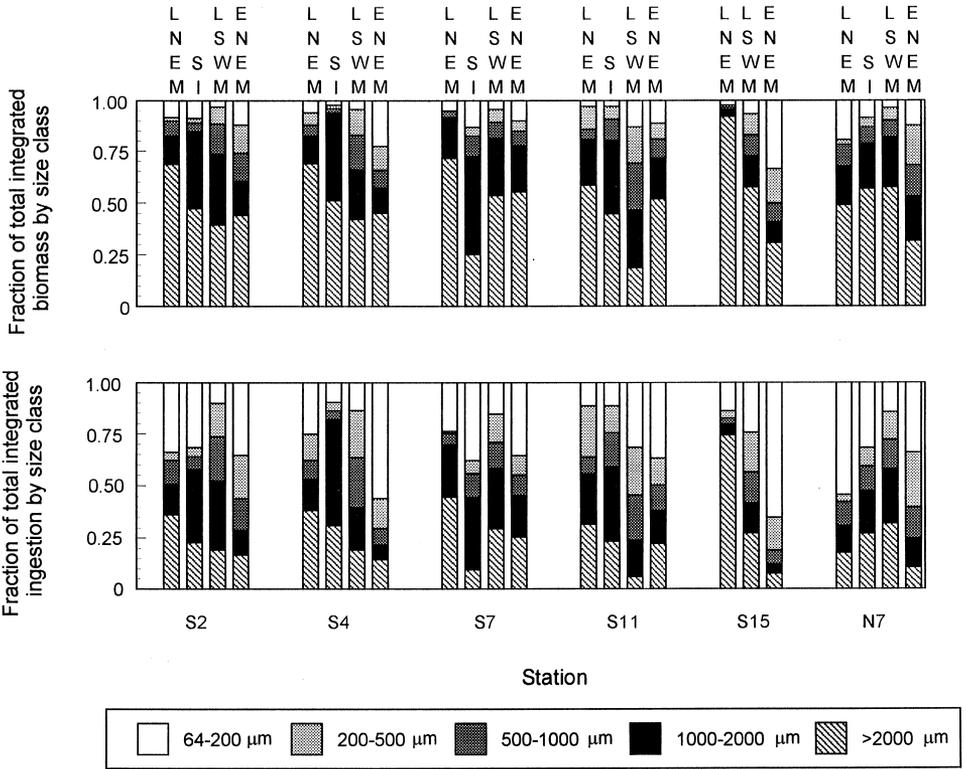


Fig. 6. Contribution of the different zooplankton size-fractions to total zooplankton biomass and estimated ingestion in the surface 200 m. Station designations at the bottom of figure with monsoon season indicated at the top of the histograms.

during the late NE Monsoon. This shift in zooplankton size-structure suggests a copepod developmental response to the enhanced phytoplankton production during the NE Monsoon.

Our calculations of zooplankton production and egestion (fecal pellet production) give the same values because we assume a 30% gross growth efficiency and a 70% assimilation efficiency ( $\text{Ingestion} = \text{Production}/0.3$ ;  $\text{Egestion} = \text{Ingestion} \times 0.3$ ). The estimates of zooplankton production and egestion for the Arabian Sea basin show a minimum value of  $2 \text{ mM C m}^{-2} \text{ d}^{-1}$  during the early NE Monsoon (TN054) at station S15 and a maximum value of  $48 \text{ mM C m}^{-2} \text{ d}^{-1}$  at station S1 during the late NE Monsoon (TN043; Fig. 8). Zooplankton production shows the same general pattern as primary production (Barber/ Marra in <http://usjgofs.whoi.edu>), with the highest production values usually at the nearshore stations. The average  $> 200\text{-}\mu\text{m}$  zooplankton integrated production/egestion rate in the surface 200 m at all stations sampled in the Arabian Sea basin over all four cruises was  $13 \text{ mM C m}^{-2} \text{ d}^{-1}$ . If we

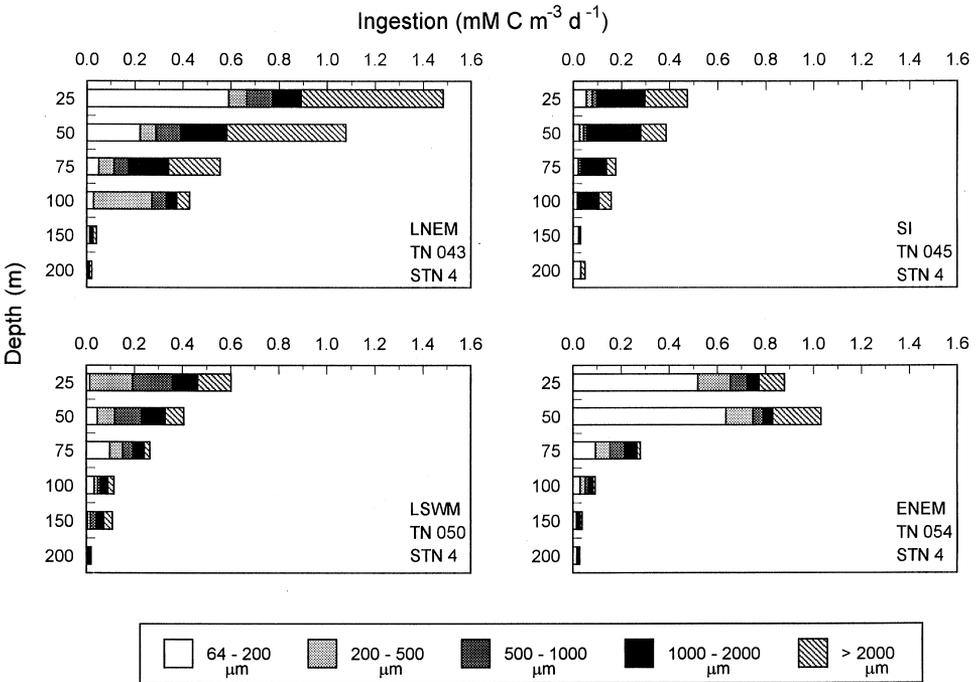


Fig. 7. Ingestion ( $\text{mM C m}^{-3} \text{d}^{-1}$ ) by the different zooplankton size fractions in the surface 200 m at station S4 during the late NE Monsoon (LNEM, cruise TN043), Spring Intermonsoon (SI, cruise TN045), late SW Monsoon (LSWM, cruise TN050) and early NE Monsoon (ENEM, cruise TN054).

include the 64–200- $\mu\text{m}$  zooplankton fraction (only data for southern transect) total zooplankton production/egestion would be approximately 20% higher.

We found significant ( $P < 0.05$ ) relationships between estimates of primary production (Barber/Marra in <http://usjgofs.whoi.edu>), with zooplankton ingestion ( $y = 9.23 + 0.29x$ ;  $r = 0.49$ ), and for primary production with zooplankton production ( $y = 2.67 + 0.09x$ ;  $r = 0.49$ ) for the four cruises (Fig. 9). The grazing ratio (zooplankton ingestion/primary production) was highest during the SW Monsoon cruise (TN050) and lowest during the late NE Monsoon (Fig. 10). Note, however, that the variability of the grazing ratio as well as our estimates of zooplankton biomass, production, ingestion and egestion over the Arabian Sea stations during a particular cruise is as great as seasonal changes we observed (Fig. 11). The average grazing ratio for all stations on the four cruises was 0.40. The overall average of the production ratio (zooplankton production/primary production) for all stations on the four cruises was 0.12.

A comparison of our estimates of fecal pellet production to measured POC flux from the surface 100 m (Buesseler et al., 1998) does not show a predictive relationship (Fig. 12). The highest POC flux estimates are from the SW Monsoon cruise (TN050)

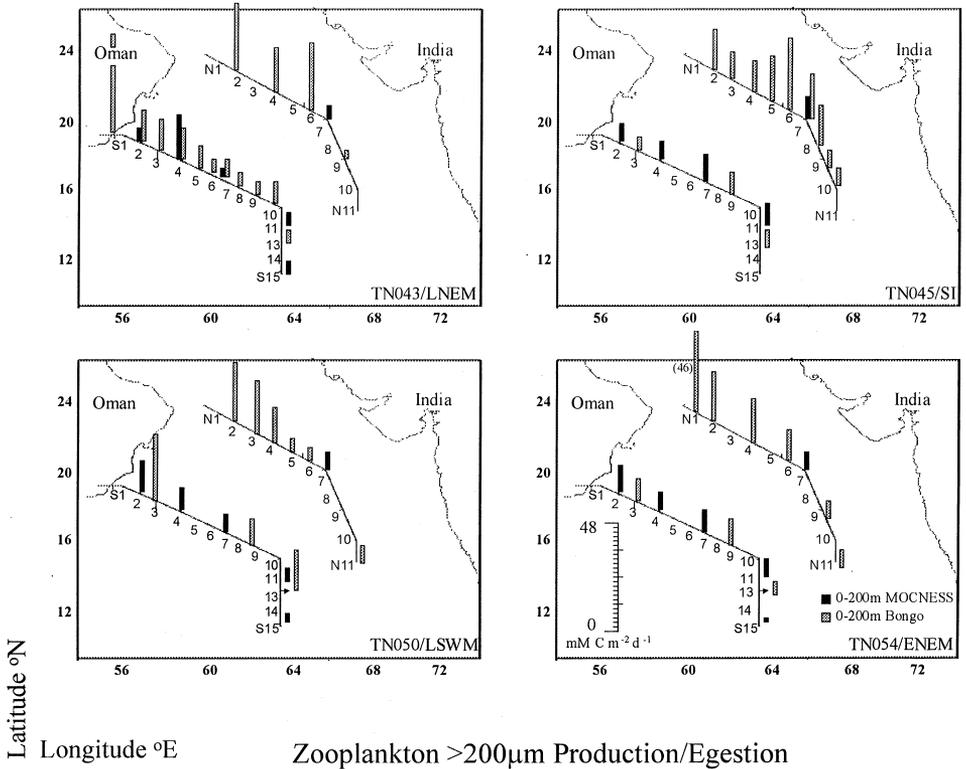


Fig. 8. Zooplankton (> 200 µm) production and egestion ( $\text{mM C m}^{-2} \text{d}^{-1}$ ) estimated with the Hirst–Sheader model and zooplankton biomass data collected in the surface 200 m with MOCNESS and Bongo tows at the Arabian Sea stations during the late NE Monsoon (LNEM, cruise TN043), Spring Intermonsoon (SI, cruise TN045), late SW Monsoon (LSWM, cruise TN050) and early NE Monsoon (ENEM, cruise TN054).

when upwelling resulted in high primary productivity (Barber/Marra in <http://usjgofs.whoi.edu>) at the nearshore stations inside the region of positive wind stress of the Findlater Jet. It is likely that this high primary production was not all grazed by microzooplankton and mesozooplankton and sank, directly contributing to the estimated gravitational POC flux.

**4. Discussion**

The growth rate ( $\text{d}^{-1}$ ) for the Arabian Sea zooplankton community (weighted mean of all size-fractions) estimated with the Hirst and Sheader (1997) model ranged from approximately 0.08 to 0.18  $\text{d}^{-1}$ , with a mean of 0.12  $\text{d}^{-1}$  for all stations on the four cruises. Although the smaller zooplankton size-fractions grew at rates  $> 0.25 \text{d}^{-1}$

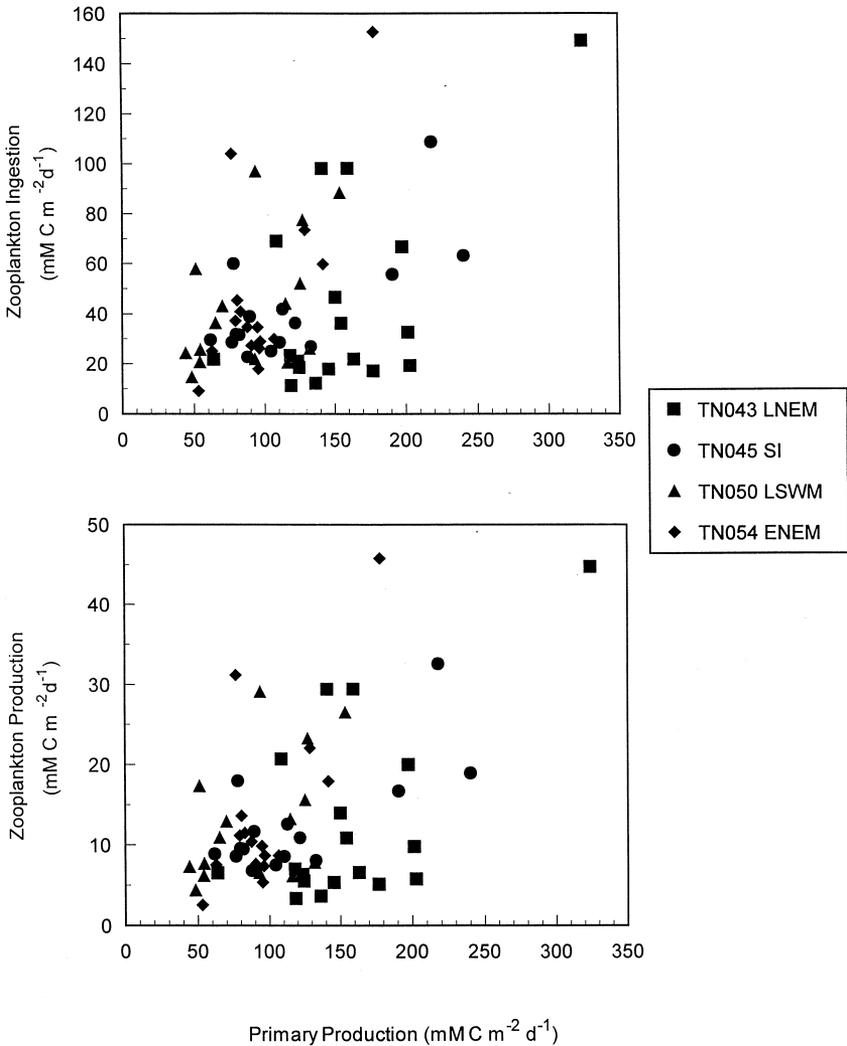


Fig. 9. Zooplankton ( $> 200 \mu\text{m}$ ) ingestion and production in the surface 200 m as a function of primary production during the late NE Monsoon (LNEM, cruise TN043), Spring Intermonsoon (SI, cruise TN045), late SW Monsoon (LSWM, cruise TN050) and early NE Monsoon (ENEM, cruise TN054). Primary production data from Barber and Marra.

(Table 4),  $> 2000\text{-}\mu\text{m}$  zooplankton were usually the largest fraction of  $> 200\text{-}\mu\text{m}$  zooplankton biomass, and their slower weight – specific growth rates (Table 4) resulted in a lower overall zooplankton community growth rate. Using changes in the size of *Calanoides carinatus* and published development rates, Smith (1992) estimated that this dominant Arabian Sea copepod grew at approximately  $0.14 \text{ d}^{-1}$ . Sazhina (1985) reported higher growth rates  $0.33\text{--}0.45 \text{ d}^{-1}$  for smaller copepod species in the

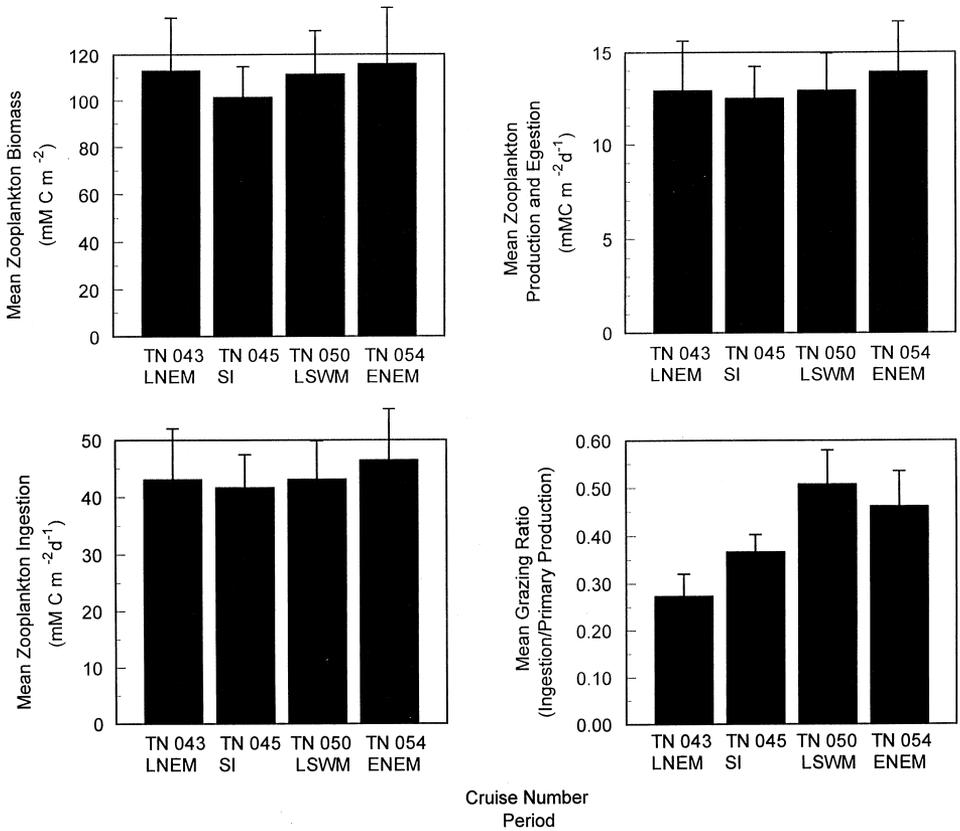


Fig. 10. Mean and standard error of > 200 μm zooplankton biomass, ingestion, production, egestion and grazing ratio (zooplankton ingestion/primary production) at all the Arabian Sea stations (northern and southern sections) during the late NE Monsoon (LNEM, cruise TN043), Spring Intermonsoon (SI, cruise TN045), late SW Monsoon (LSWM, cruise TN050) and early NE Monsoon (ENEM, cruise TN054).

equatorial countercurrent of the Indian Ocean, rates that also would be predicted from the Hirst and Sheader (1997) model, given the higher weight-specific growth rates of these smaller copepods. Thus, the Hirst and Sheader (1997) model appears to give reasonable estimates of zooplankton growth rates in the Arabian Sea.

Given the different types of food that copepods ingest (e.g., Kleppel, 1992), the effects of water motion and turbulence on zooplankton feeding behavior (e.g., Saiz and Kiørboe, 1995) as well as the multiple effects of containment and incubation on phytoplankton, protozoa and copepods (Venrick et al., 1977; Roman and Rublee, 1980), it is difficult to measure zooplankton ingestion rates, especially for oceanic copepods. The Hirst and Sheader (1997) model used to estimate zooplankton growth rate and the assumption of a 30% gross growth efficiency gave reasonable estimates of zooplankton ingestion when compared to the in situ incubations with isotopically-labeled prey. Daily ingestion rates expressed as a function of biomass were

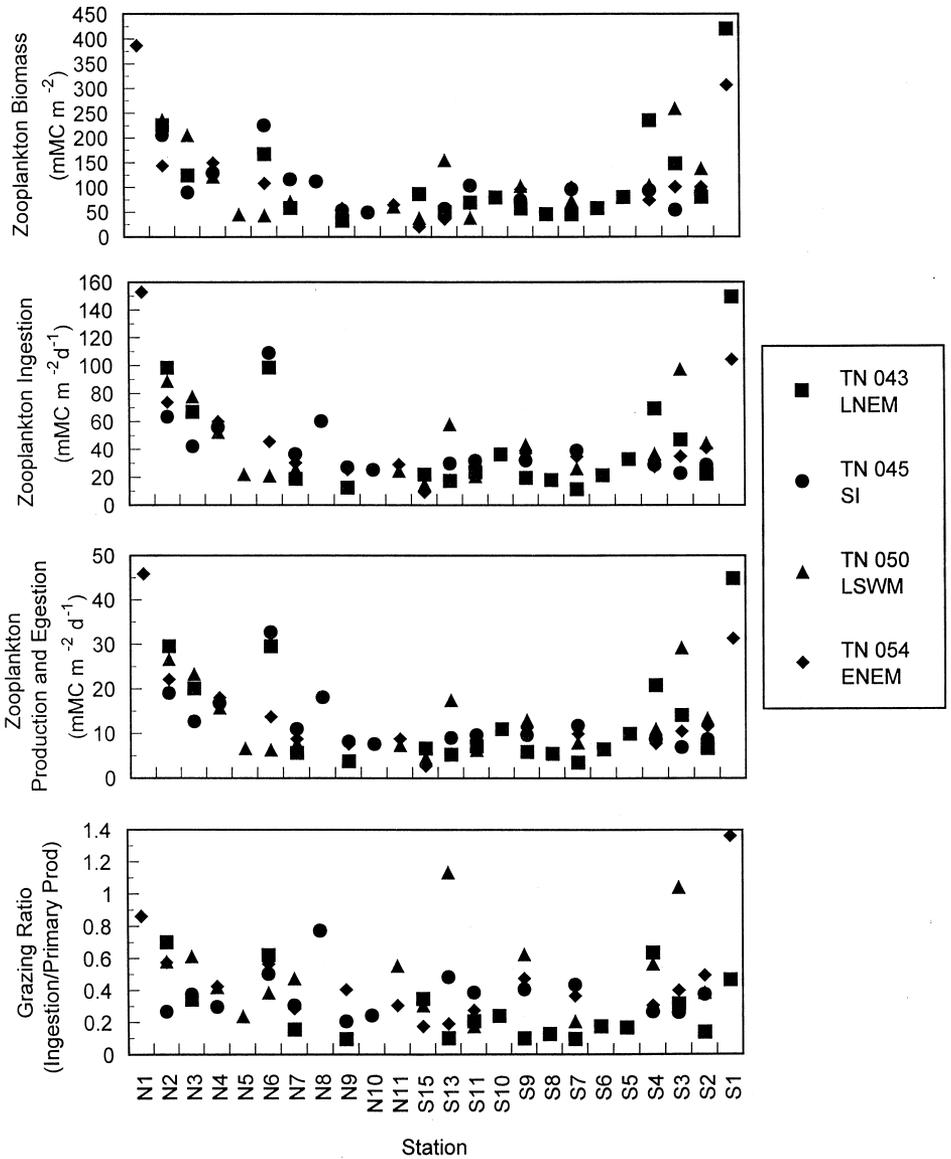


Fig. 11. Zooplankton (> 200 μm) biomass, ingestion, production, egestion and grazing ratio (zooplankton ingestion/primary production) at all the Arabian Sea stations (northern and southern sections) during the late NE Monsoon (LNEM, cruise TN043), Spring Intermonsoon (SI, cruise TN045), late SW Monsoon (LSWM, cruise TN050) and early NE Monsoon (ENEM, cruise TN054).

comparable to published values for the given zooplankton size-fractions and ambient temperatures. *Calanoides carinatus*, a dominant copepod in the upwelling area off Somalia in the Arabian Sea, was found to have a weight-specific carbon ingestion rate of 0.13 to 0.62 d<sup>-1</sup> (Smith, 1982) based on cell counts of phytoplankton in shipboard

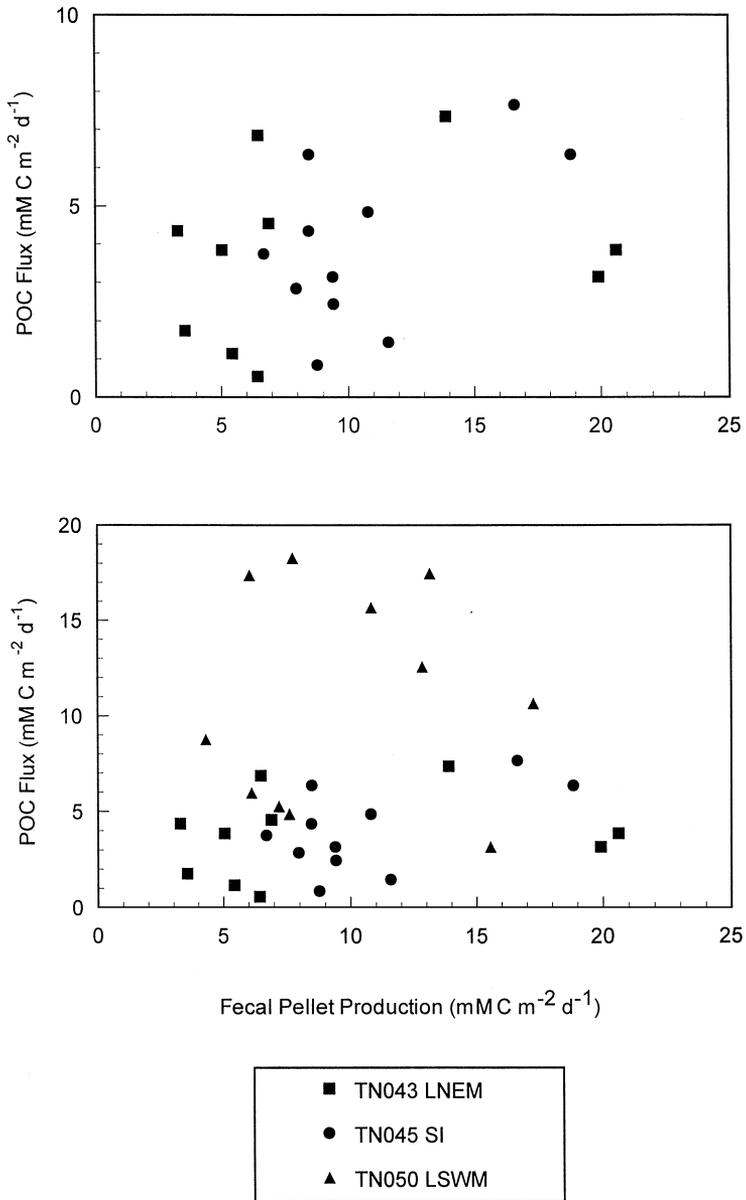


Fig. 12. Particulate organic carbon (POC) flux as a function of estimated zooplankton (> 200 μm) fecal pellet production in the surface 200 m during the late NE Monsoon (LNEM, cruise TN043), Spring Intermonsoon (SI, cruise TN045) and late SW Monsoon (LSWM, cruise TN050) upper graph and only TN043 and TN045 lower graph.

incubations. We found an average weight-specific carbon ingestion rate for all size fractions of zooplankton at all stations on the four cruises of  $0.40 \text{ d}^{-1}$  (Fig. 4). Smith (1982) estimated that the grazing impact of this dominant copepod averaged  $14 \text{ mM C m}^{-2} \text{ d}^{-1}$  compared to our broader seasonal and spatial average grazing rate of  $44 \text{ mM C m}^{-2} \text{ d}^{-1}$ .

Relative to other ocean basins, the grazing impact of mesozooplankton is significant in the Arabian Sea as a consequence of the high zooplankton biomass, abundance of diatoms during upwelling and warm temperatures, which result in high zooplankton metabolic demands and growth rates. For example, in the equatorial Pacific Ocean ( $0^\circ$ ,  $140^\circ\text{W}$ ) grazing rates of  $> 200\text{-}\mu\text{m}$  zooplankton on phytoplankton ( $^{14}\text{C}$ -labeled particles) averaged  $2 \text{ mM C m}^{-2} \text{ d}^{-1}$  (zooplankton biomass =  $23 \text{ mM C m}^{-2}$ ) during El Niño conditions in March/April and  $15 \text{ mM C m}^{-2} \text{ d}^{-1}$  (zooplankton biomass =  $31 \text{ mM C m}^{-2}$ ) during “normal” equatorial upwelling conditions in October (Roman and Gauzens, 1997). The average  $> 200\text{-}\mu\text{m}$  zooplankton grazing rate in the Arabian Sea was  $44 \text{ mM C m}^{-2} \text{ d}^{-1}$  (zooplankton biomass  $110 \text{ mM C m}^{-2}$ ). In the Sargasso Sea off Bermuda,  $> 200\text{-}\mu\text{m}$  zooplankton grazing rates on phytoplankton ( $^{14}\text{C}$ -labeled particles) were  $< 1 \text{ mM C m}^{-2} \text{ d}^{-1}$  (zooplankton biomass =  $8 \text{ mM C m}^{-2}$ ) in August and  $5 \text{ mM C m}^{-2} \text{ d}^{-1}$  (zooplankton biomass =  $22 \text{ mM C m}^{-2}$ ) in March/April (Roman et al., 1993). Although the water temperature of these three areas was similar, estimates of the weight-specific zooplankton ingestion rates (ingestion/biomass) were lower in the Sargasso Sea (0.12, 0.23) and the March/April equatorial Pacific Ocean station (0.11) as compared to our Arabian Sea estimates (0.40) and the October equatorial Pacific Ocean results (0.47). The low weight-specific ingestion rates in the Sargasso Sea and March/April equatorial Pacific Ocean station based only on phytoplankton ingestion are not realistic and suggest that the zooplankton were also ingesting heterotrophic prey. Calculations of equatorial Pacific Ocean zooplankton metabolic demands (Dam et al., 1995b) and food-web models for that region (Frost and Franzen, 1992) also suggest that the copepods consume considerable quantities of microzooplankton.

Zooplankton ingestion rates are estimated from growth rates and published growth efficiencies and thus represent total carbon ingested. We know that a major portion of a copepod diet is from protozoa, thus we do not mean to imply that our estimates of zooplankton ingestion equate to phytoplankton carbon ingestion. However several lines of evidence suggest that phytoplankton comprise the major portion of the carbon ingested by copepods in the Arabian Sea. Both pigment composition (Latasa and Bidagare, 1998) and cell counts (Garrison et al., 1998; Dennett et al., 1999) suggest that diatoms can be a significant component of the Arabian Sea phytoplankton community, especially at stations influenced by the Findlater Jet. In many ocean waters  $> 90\%$  of total chlorophyll is  $< 2 \mu\text{m}$  and therefore too small to be efficiently grazed by copepods. At our Arabian Sea stations, the chlorophyll  $> 2 \mu\text{m}$  averaged 30, 25 and 63% of total chlorophyll during the late NE Monsoon, Spring Intermonsoon and SW Monsoon, respectively (Roman, unpublished). We used the in situ bottle incubations with dual isotopes (thymidine and bicarbonate) to estimate zooplankton ingestion of autotrophic and heterotrophic carbon (Roman and Rublee, 1981; Roman and Gauzens, 1997). In the Sargasso Sea (Roman et al., 1993) and equatorial Pacific

Ocean (Roman and Gauzens, 1997), this technique suggested that over 50% of the particulate matter ingested by copepods was heterotrophic protozoa. Our in situ zooplankton grazing estimates on the southern transect of the Arabian Sea during the late NE Monsoon (TN043) and Spring Intermonsoon (TN045) showed that approximately 80% of the carbon ingested by copepods was phytoplankton. This observation is consistent with both the size and biomass of phytoplankton.

If we assume that phytoplankton production and grazing are in balance, then the sum of microzooplankton and mesozooplankton grazing should equal primary production. The average mesozooplankton grazing ratio (estimated total carbon consumed by zooplankton/primary production) for all stations during the four cruises was 0.40. The grazing ratio ( $m/\mu_0$ ) for microzooplankton estimated from dilution experiments (Landry et al., 1998; Caron and Dennett, 1999) for all stations during the four cruises was approximately 0.74. It is not surprising that the sum of both grazing components is  $> 1$  because, as mentioned previously, the rate estimates for mesozooplankton are total (phytoplankton, microzooplankton, detritus) carbon ingested. The estimated ingestion rates do suggest that, when averaged over the spatial and temporal domain of the study, phytoplankton production and removal by grazing were approximately equal in the Arabian Sea.

The potential fecal pellet production derived from the estimated ingestion rates and a 70% assimilation efficiency are in the same range as the gravitational flux of organic carbon at 100 m estimated from  $^{234}\text{Th}$  inventories (Buesseler et al., 1998). Estimates of fecal pellet production were generally higher than measured export rates for the late NE Monsoon (TN043), the Spring Intermonsoon (TN045), and for the offshore stations of the SW Monsoon (TN050), but lower than export rates for the inshore stations during the SW Monsoon (Figs. 9 and 12). When estimated fecal pellet production rates are higher than measured export rates, it suggests that fecal pellets are recycled in the upper water column. Higher export rates compared to fecal pellet production rates (Fig. 12) suggest that sinking phytoplankton must have contributed directly to the gravitational export. Chlorophyll in trap material as well as biochemical markers (Lee et al., 1998) also suggest that significant amounts of phytoplankton were sinking in the area west of the Findlater Jet during the SW Monsoon. The ratio of export production/primary production ranged from 0.02 to 0.08 during the early NE Monsoon and the Spring Intermonsoon, but from 0.05 to 0.25 during the SW Monsoon (Buesseler et al., 1998). The ratio of fecal pellet production/primary production was approximately 0.12 for all four cruises with the SW Monsoon ratio below this average (Fig. 9).

Except for some of the inshore stations, zooplankton biomass in the Arabian Sea basin did not change appreciably over the four seasons sampled (average  $110 \text{ mM C m}^{-2}$ ; Figs. 2 and 3). This means that zooplankton production, approximately  $13 \text{ mM C m}^{-2} \text{ d}^{-1}$ , did not accumulate over the study period, instead being removed by mortality and advection. Smith et al. (1998) used estimates of myctophid biomass in the area off Oman between the Findlater Jet and the coast and an average fish daily ration of 4% to estimate the amount of zooplankton consumed by myctophids. These estimates of 17, 7 and  $16 \text{ mM C m}^{-2} \text{ d}^{-1}$  are surprisingly close to our overall zooplankton production average of  $13 \text{ mM C m}^{-2} \text{ d}^{-1}$ . Our indirect

estimates show that zooplankton production is approximately 12% of primary production. The suggestion that this secondary production is consumed by fish planktivores is consistent with our past notions of the transfer efficiency of aquatic food webs (Slobodkin, 1961; Ryther, 1969).

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