# Distribution, abundance, and feeding ecology of decapods in the Arabian Sea, with implications for vertical flux

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## Abstract

Macrozooplankton and micronekton samples were collected on two cruises in the Arabian Sea conducted during the Spring Intermonsoon period (May) and the SW Monsoon period (August) of 1995. Discrete depth samples were collected down to depths of 1000–1500 m. Quantitative gut content analyses were performed on four species of decapod shrimps, *Gennadas sordidus*, *Sergia filictum, Sergia creber,* and *Eupasiphae gilesii*, as well as on the pelagic crab *Charybdis smithii*. Of the shrimps, only *S. filictum* and *S. creber* increased significantly in abundance between the Spring Intermonsoon and SW Monsoon seasons. These four species were found at all depths sampled, and most did not appear to be strong vertical migrators. *G. sordidus* and *S. filictum* did appear to spread upward at night, especially during the SW Monsoon, but this movement did not include the entire population. *S. creber* showed signs of diel vertical migration only in some areas. All four shrimp species except, to some degree, *S. creber* lived almost exclusively within the oxygen minimum zone (150–1000 m), and are likely to have respiratory adaptations that allow them to persist under such conditions. Feeding occurred at all depths throughout these species' ranges, but only modest feeding occurred in the surface layer (0–150 m). *G. sordidus* appeared to feed continuously throughout the day and night. Estimated contribution of fecal material to vertical flux ranged from < 0.01–2.1% of particulate flux at 1000 m for the shrimps and 1.8–3.0% for *C. smithii*. © 2000 Published by Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

In the Arabian Sea, the SW Monsoon in the summer (June–September) leads to the formation of unique and intense western boundary upwelling zones off the SE coast of Oman and off Somalia (Currie et al., 1973). In addition, Bauer et al. (1991) reported strong downwelling in the central Arabian Sea during the SW Monsoon, and a peak in pigment concentration coincident with the shoaling of the thermocline in coastal upwelling regions. With the SW Monsoon fully established, high primary productivity (Krey, 1973) and zooplankton biomass (Rao, 1973,1979) are commonly found in the fertile upwelling regions off Oman and Somalia.

The massive amounts of organic material produced by these seasonal cycles in productivity, coupled with certain circulation features of the Arabian Sea, contribute to the formation of a large suboxic zone (Olson et al., 1993). It is the thickest low-oxygen layer in the ocean today, covering most of the northern Arabian Sea. According to Olson et al. (1993), the layer is nearly 1 km thick, extending from 100 to 1000 m depth. Oxygen concentrations in this zone are as low as $< 4.0$ μmol/kg, compared to $\sim 200$ μmol/kg at the surface. Studies in other low-oxygen environments, such as the eastern tropical Pacific Ocean, have shown that many zooplankton and micronekton species avoid waters with oxygen concentrations below 3.0–4.0 μmol/kg (Judkins, 1980; Sameoto, 1986). Low oxygen levels have also been found to influence biomass distributions and alter species compositions of zooplankton and fish in the Arabian Sea (Vinogradov and Voronina, 1961; Kinzer et al., 1993).

Consumers, such as macrozooplankton and pelagic fishes, can facilitate the vertical flux of organic material in two ways (Angel, 1984). The packaging of material into rapidly sinking fecal pellets, is considered "passive" transport since organisms do not participate directly in the vertical movement. Alternatively, "active" transport occurs when vertically migrating organisms accelerate the transfer of organic material to depth as gut contents to be either defecated, or assimilated into biomass, and then respired or consumed by predators at depth (Longhurst and Harrison, 1988; Longhurst et al., 1990).

Decapod crustaceans are a diverse and abundant taxon, yet this group has been little studied in the Arabian Sea. The work presented here focuses mainly on decapod shrimps, but also includes gut contents and defecation rates for the pelagic crab *Charybdis smithii*, which is endemic to this region. In addition to their widespread distribution, decapods are an omnivorous group, and many species are known to perform diel vertical migrations (Omori, 1974; but see Angel et al., 1982). Thus, they could have a significant grazing and predatory impact on the seasonal phytoplankton and zooplankton blooms characteristic of this region, as well as on mesopelagic fishes, at a wide range of depths in the water column.

The objectives of this study were twofold: (1) to describe the horizontal and vertical distribution of some particularly abundant decapod shrimps in the Arabian Sea (*Gennadas sordidus, Sergia filictum, S. creber*, and *Eupasiphae gilesii*), including possible explanations for these distribution patterns, and (2) to estimate the potential contribution of the shrimps, as well as *Charybdis smithii*, to vertical flux of organic material.

## 2. Materials and methods

### 2.1. Sampling design

Macrozooplankton and micronekton samples were collected in the Arabian Sea during two cruises aboard the RV *Malcolm Baldrige*. In order to observe any effect of the strong seasonal variation in climate on zooplankton abundance and distribution, and vertical flux of organic material, the cruises were planned for two different seasons. The first cruise took place during the Spring Intermonsoon season, May 5–23, 1995. Stations off the coast of Somalia (between ∼ 5°N 49°E and 10°N 52°E) were sampled first, followed by collections in the central oligotrophic waters near the Woods Hole Oceanographic Institution (WHOI) mooring ( ∼ 15°20′N 61°30′E) and US Joint Global Ocean Flux Study (US JGOFS) mooring (16°N 62°E). The ship then headed northwest to occupy stations along the coast of Oman (between ∼ 19°N 58°E and 22°N 60°E). The second cruise was during the SW Monsoon season, July 31–August 19, 1995; two stations were occupied in the Gulf of Aden (14°N 51°E) before heading south to the Somali coast (ca. 11°N 51°E), and then east to the central moorings.

Approximately 30 oblique hauls were completed on each of the two cruises using a Multiple Opening-Closing Net/Environmental Sensing System (MOCNESS) (Wiebe et al., 1985) with five 3-mm knotless mesh nets attached to a 10-m$^2$ frame (MOC-10). The first net was fished as the trawl descended to the maximum sampling depth. Each of the other four nets was then fished over selected depth intervals as the trawl ascended; only data from these four nets will be discussed here. Depth intervals of 0–150, 150–500, 500–750, and 750–1000 m were sampled at most stations (Table 1). However, in the Somali coast region, depths sampled ranged from 0–1500 m during the May cruise to 0–900 m during the August cruise. Instruments were attached to the MOC-10 frame which provided continuous real-time measurements of temperature, salinity, oxygen concentration, frame angle, and flow rate. Volumes filtered ranged from ∼ 3000 to 45,000 m$^3$ for each net on the trawl. Day and night replicate hauls were taken in most areas in an attempt to detect any statistically significant differences in vertical distribution due to diel vertical migration.

### 2.2. Treatment of specimens

All biological specimens were stored in 5% formalin solution until they could be sorted taxonomically in the lab; most taxa were then identified to species. The decapod shrimps accounted for 10–15% of the total macrozooplankton and micronekton biomass in these samples (Madin et al., 2000), while adults of the pelagic crab *Charybdis smithii* composed upto 46% of the biomass during the SW Monsoon season. Four large and abundant species of decapod shrimps, as well as *C. smithii*, were chosen for gut content analyses, and these are the focus of the work presented here. Abundance and distributions of the rest of the catch, including juveniles of these five species, are described elsewhere (Madin et al., 2000; Van Couwelaar et al., 1997).

Table 1
Summary of number of hauls collected at each location and depths sampled. Day hauls are those in which the trawl was launched prior to sunset, and night hauls are those in which the trawl was launched after sunset

| Location | Day hauls | | Night hauls | | Depths sampled (m) | |
|---|---|---|---|---|---|---|
| | May | Aug | May | Aug | May | August |
| Central mooring | 5 | 4 | 4 | 3 | 0–150 | 0–150 |
| | | | | | 150–500 | 150–500 |
| | | | | | 500–750 | 500–750 |
| | | | | | 750–1000 | 750–1000 |
| Somali coast | 3 | 2 | 4 | 2 | 0–100 | 0–150 |
| | | | | | 100–500 | 150–300 |
| | | | | | 500–1000 | 300–500 |
| | | | | | 1000–1500 | 500–900 |
| Omani basin/coast | 6 | 3 | 5 | 4 | 0–150 | 0–150 |
| | | | | | 150–300 | 150–300 |
| | | | | | 300–500 | 300–500 |
| | | | | | 500–1000 | 500–1000 |

The shrimps were identified as the penaeid *Gennadas sordidus* (Kemp, 1910), two sergestids, *Sergia filictum* (Burkenroad, 1940; B. Kensley, personal communication) and *Sergia creber* (Kensley, 1971), and the caridean *Eupasiphae gilesii* (Crosnier, 1988). Total abundances and wet weights were recorded for all adult individuals of these five species, as well as wet weight and carapace length for each individual dissected. Some smaller sergestid and euphausiid species were found in larger numbers in our samples (Madin et al., 2000); yet the size of the four taxa considered here made them significant contributors to the total decapod biomass (14–34% at Somali and Omani coast stations, and 74–90% at the central mooring), as well as potentially significant contributors to flux given the ability of large organisms to produce large, rapidly sinking fecal pellets (Angel et al., 1982; Emerson and Roff, 1987).

### 2.3. Crab defecation and fecal pellet sinking rates

After several trawls during the August cruise, 3–6 live crabs were removed from the catch and placed individually in 20 l of seawater. These were then held in the dark in freshly collected surface seawater (22–24°C) for several hours. Tanks were checked intermittently, and feces removed, over an 8–12 h period. Forty–four portunid crabs were measured from 10 trawls in three geographic locations. Collected feces were immediately placed on pre-ashed glass fiber filters, folded, and dried at 60°C in glassine envelopes. After the cruise, the samples were stored frozen at $-20°C$ until analysis for carbon and nitrogen could be performed at the University of California, Santa Barbara Marine Science Institute Analytical Lab with a Control Equipment Corp. Model 240XA elemental analyzer. Empty filters, handled

and stored along with sample filters, were used to correct for background carbon and nitrogen.

Sinking rates of feces were measured in a 1-l graduated cylinder at laboratory temperatures, positioned on a gimbaled frame, so the cylinder remained vertical despite the ship's motion. Fecal pellet sinking rates were measured for 24 different specimens. Feces were placed gently near the surface, and the time was recorded as the feces sank. Duplicate measurements were made on nearly all the feces sampled, and several samples were measured three or more times.

## 2.4. Gut content analyses

As many as 20 intact individuals of *Gennadas sordidus* from each net in each haul were dissected; fewer of the other three shrimp species were dissected due to lower abundances. As many as ten individuals of *Charybdis smithii* from each net were dissected. The foregut was removed from each organism, and wet weight of the intact gut was recorded before the contents were separated from the gut tissue. Qualitative observations were made of relative gut fullness and type of contents. Contents were separated from the gut tissue and weighed wet. After drying for a minimum of 24 h in a drying oven at 60°C, they were weighed again. Dry weight was measured twice for each sample, and the mean of these two measurements was used in all calculations. Dry weights of individual animals were calculated as 23% of wet weight (Childress and Nygaard, 1974; Båmstedt, 1981), and these were used to calculate average weight-specific gut contents (mg dry weight gut content/g dry weight predator) for each sample as a measure of relative gut fullness. The highest values of average weight-specific gut content are taken to represent maxima in gut fullness. Total gut content per unit volume sampled (mg dry weight gut content/1000 m$^3$) was calculated in order to describe potential particulate flux in the form of gut content.

Locations at which the most extensive sampling occurred have been grouped into three general regions: the central mooring, the Somali coast, and the Omani Basin/Omani coast. These locations represent distinct oceanographic regimes, including central oligotrophic waters and coastal upwelling areas, and will be the areas of focus for this study. Data collected near the central mooring are of particular interest in this study because a time-series of collections was performed at this station during each of the two cruises. During each time-series, trawls were completed approximately every 4–5 h over a 48 h period. Time-series data were used to determine diel patterns in migration and feeding.

## 2.5. Data analysis

In order to examine regional and seasonal differences in overall abundance, average water column abundance of each species, summed over all depths sampled, was analyzed using the Statistical Package for the Social Sciences (SPSS) to perform a two-factor analysis of variance (ANOVA). Because four discrete depths were sampled in each haul, abundance (# of animals/1000 m$^3$), weight-specific gut content (mg/g), and average carapace length for each of the four dissected shrimp species were

then analyzed using a four-factor repeated measures ANOVA. In all tests, each haul was treated as a separate subject and depth served as the repeated measures factor (e.g., Brown et al., 1997). Region, season, and day/night were treated as between-subjects factors. Because adult *Charybdis smithii* was only collected during one season, a three-factor repeated measures ANOVA for weight-specific gut content was performed for this species with depth as the repeated measures factor, and region and day/night as between-subjects factors. A Huynh-Feldt epsilon (*e*) value of 1.00 was calculated for all within-subjects *F*-tests, indicating that the assumption of sphericity of the variance–covariance matrices was met. Thus, no adjustments to degrees of freedom were necessary (O'Brien and Kaiser, 1985).

## 3. Results

Horizontal and vertical distributions will be described only for adults of the four shrimp species. For a detailed description of the distribution of *Charybdis smithii* in the NW Indian Ocean, including data collected during these two cruises see Van Couwelaar et al. (1997).

### 3.1. Horizontal distributions

All four shrimp species were found in every region sampled. *Gennadas sordidus* was, overall, the most abundant of these four taxa, with the highest numbers occurring at the central mooring station (Fig. 1). Both *Sergia filictum* and *Eupasiphae gilesii* follow this same pattern. *Sergia creber*, in contrast, was most abundant off the Somali coast. A two-factor ANOVA for abundance supports these observations, showing statistically significant regional differences in mean abundance for all four species (*G. sordidus*: $F = 12.677, p < 0.001$; *S. filictum*: $F = 14.122, p < 0.001$; *S. creber*: $F = 4.349, p = 0.030$; *E. gilesii*: $F = 53.309, p < 0.001$).

Adults of each of the four species were more abundant during the SW Monsoon season than during the Spring Intermonsoon in every region sampled, with the exception of *Gennadas sordidus* off the Somali coast. However, the ANOVA showed significant seasonal effects on abundance only for *Sergia filictum* ($F = 12.282$, $p = 0.003$) and *S. creber* ($F = 7.674, p = 0.013$). Region × season interactions were significant only in *S. filictum* ($F = 7.980, p = 0.003$).

### 3.2. Vertical distributions

Some evidence of diel vertical migration was found for all four species, but patterns were not consistent for all regions and seasons sampled. The four-factor repeated measures ANOVA for abundance (Table 2) did not yield statistically significant depth × day/night interaction effects for any of the four species, indicating that for the data set as a whole, there were no consistent changes in depth distribution between day and night. However, when each region is looked at separately, patterns do begin to emerge (Fig. 2).
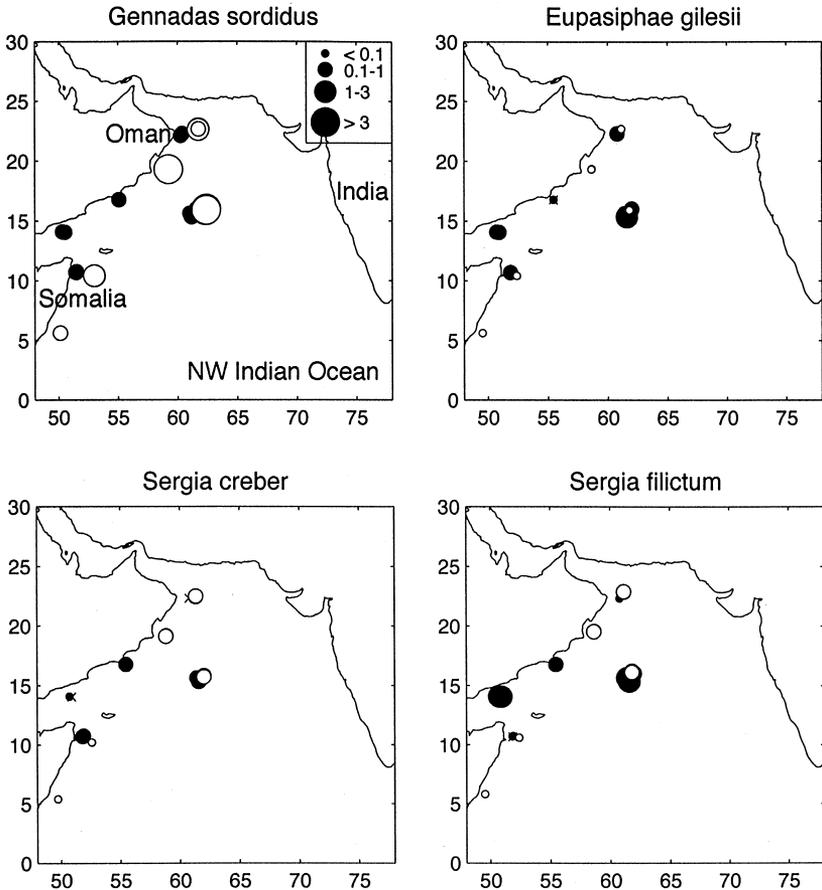
Fig. 1. Weighted mean abundance (number of animals per 1000 m³) summed over all depths sampled for both day and night hauls. ○ = Spring Intermonsoon season; ● = SW Monsoon season.

In all regions, *Gennadas sordidus* was found at all depths sampled (Fig. 2a). At the central mooring station, these animals were captured at night in shallower depths (0–500 m) only during the SW Monsoon season (Fig. 2a). In the Omani Basin/coast and Somali coast regions, a large portion of the population moved up by night from daytime depths of > 500 m (Fig. 2a), but all individuals did not migrate as a unit. Despite the apparent seasonal difference in vertical distribution patterns at the central mooring station, seasonal changes were not found to be statistically significant (Table 2). However, a significant depth × region effect was found. This effect is most likely due to the sizable differences in abundance between regions in the 500–750 m and 750–1000 m depth intervals.

*Sergia filictum* appeared to avoid the surface layer (0–150 m) in all regions sampled, both night and day (Fig. 2b). No clear diel migration patterns were seen at the central mooring station. At the Omani Basin/coast stations, there was some movement to

Table 2
Summary of results of four-factor repeated measures ANOVA for abundance (number of animals/1000m³), with depth as the repeated measures factor. (d.f. = degrees of freedom, $F$ = $F$-value, $P$ = significance)

| Abundance ($\#$/1000 m³) | d.f. | $F$ | $P$ |
|---|---|---|---|
| *Gennadas sordidus* | | | |
| Depth | 3.51 | 6.947 | 0.001[a] |
| Region | 2.17 | 7.960 | 0.004[b] |
| Season | 1.17 | 2.581 | 0.127 |
| Day/Night | 1.17 | 0.269 | 0.611 |
| Depth × Region | 6.51 | 2.668 | 0.025[c] |
| Depth × Season | 3.51 | 0.726 | 0.541 |
| Depth × Day/Night | 3.51 | 2.020 | 0.123 |
| *Sergia filictum* | | | |
| Depth | 3.54 | 2.739 | 0.052 |
| Region | 2.18 | 17.055 | < 0.001[a] |
| Season | 1.18 | 13.304 | 0.002[b] |
| Day/Night | 1.18 | 0.363 | 0.554 |
| Depth × Region | 6.54 | 1.051 | 0.403 |
| Depth × Season | 3.54 | 1.256 | 0.299 |
| Depth × Day/Night | 3.54 | 0.721 | 0.544 |
| *Sergia creber* | | | |
| Depth | 3.51 | 0.542 | 0.656 |
| Region | 2.17 | 2.410 | 0.120 |
| Season | 1.17 | 7.630 | 0.013[a] |
| Day/Night | 1.17 | 0.010 | 0.923 |
| Depth × Region | 6.51 | 1.414 | 0.227 |
| Depth × Season | 3.51 | 0.317 | 0.813 |
| Depth × Day/Night | 3.51 | 1.265 | 0.296 |
| *Eupasiphae gilesii* | | | |
| Depth | 3.4 | 17.117 | < 0.001[a] |
| Region | 2.8 | 50.419 | < 0.001[a] |
| Season | 1.8 | 9.546 | 0.006[b] |
| Day/Night | 1.18 | 3.512 | 0.077 |
| Depth × Region | 6.54 | 15.767 | < 0.001[a] |
| Depth × Season | 3.54 | 2.932 | 0.042[c] |
| Depth × Day/Night | 3.54 | 2.354 | 0.082 |

[a]Significant at $\alpha \leqslant 0.001$.
[b]Significant at $\alpha \leqslant 0.01$.
[c]Significant at $\alpha \leqslant 0.05$.

shallower depths by night, and again, not all individuals were involved. It is difficult to discern any patterns in vertical distribution for *S. filictum* in the Somali coast region due to low sample sizes. The ANOVA for abundance yielded no significant (depth × region) or (depth × season) interaction effects (Table 2), indicating no consistent trends in vertical distribution across all regions and seasons sampled.
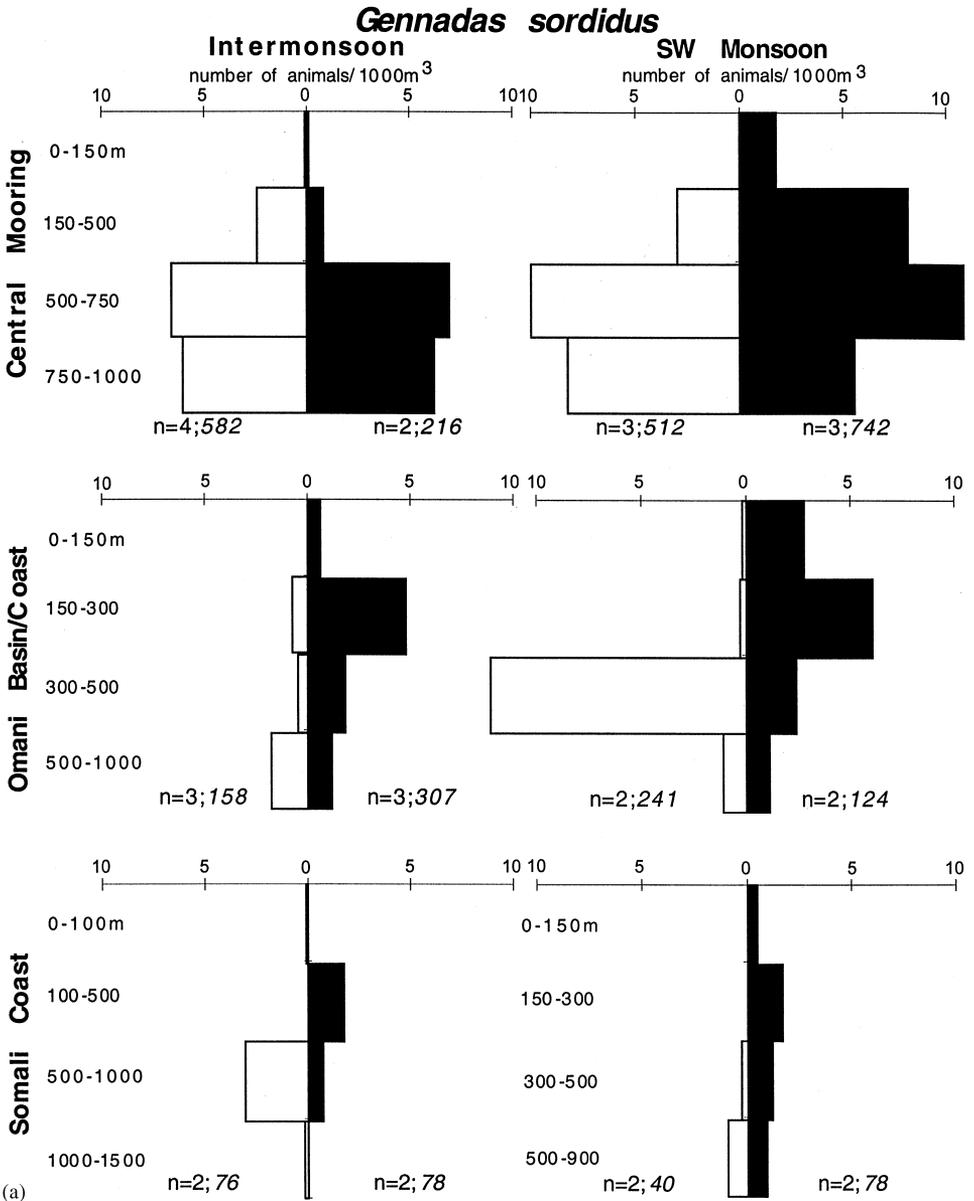
Fig. 2. Average abundance (number of animals per 1000 m$^3$) of (a) *Gennadas sordidus*, (b) *Sergia filictum*, (c) *Sergia creber*, and (d) *Eupasiphae gilesii* in each region, at each depth sampled. *n* = number of tows; *total number of animals collected*. Note the difference in depths sampled in the Somali Coast region between the Spring Intermonsoon and SW Monsoon seasons. (□ = day hauls, ■ = night hauls)

*Sergia creber* was virtually absent at the central mooring station during the spring intermonsoon season (Fig. 2c), but abundances were higher during the SW Monsoon and the population was sampled at night in the top 150 m. This species was
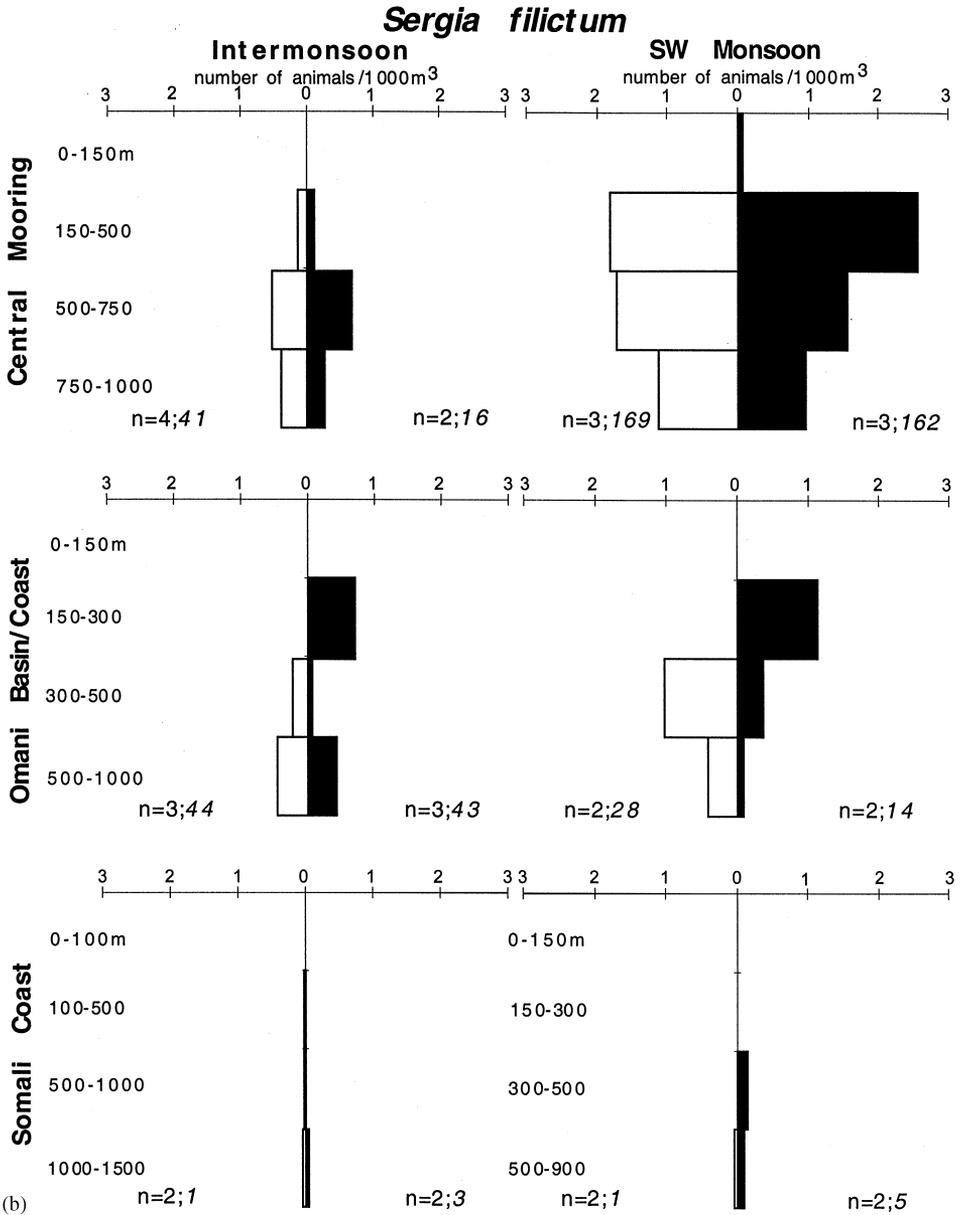
Fig. 2 (*continued*)

completely absent from the Omani Basin/coast region during the Spring Intermonsoon season, and was found only at night during the SW Monsoon, when it occurred in small numbers in the surface layer (Fig. 2c). Abundances were low in the Somali coast region, but *S. creber* was sampled at shallower depths by night than by day during the
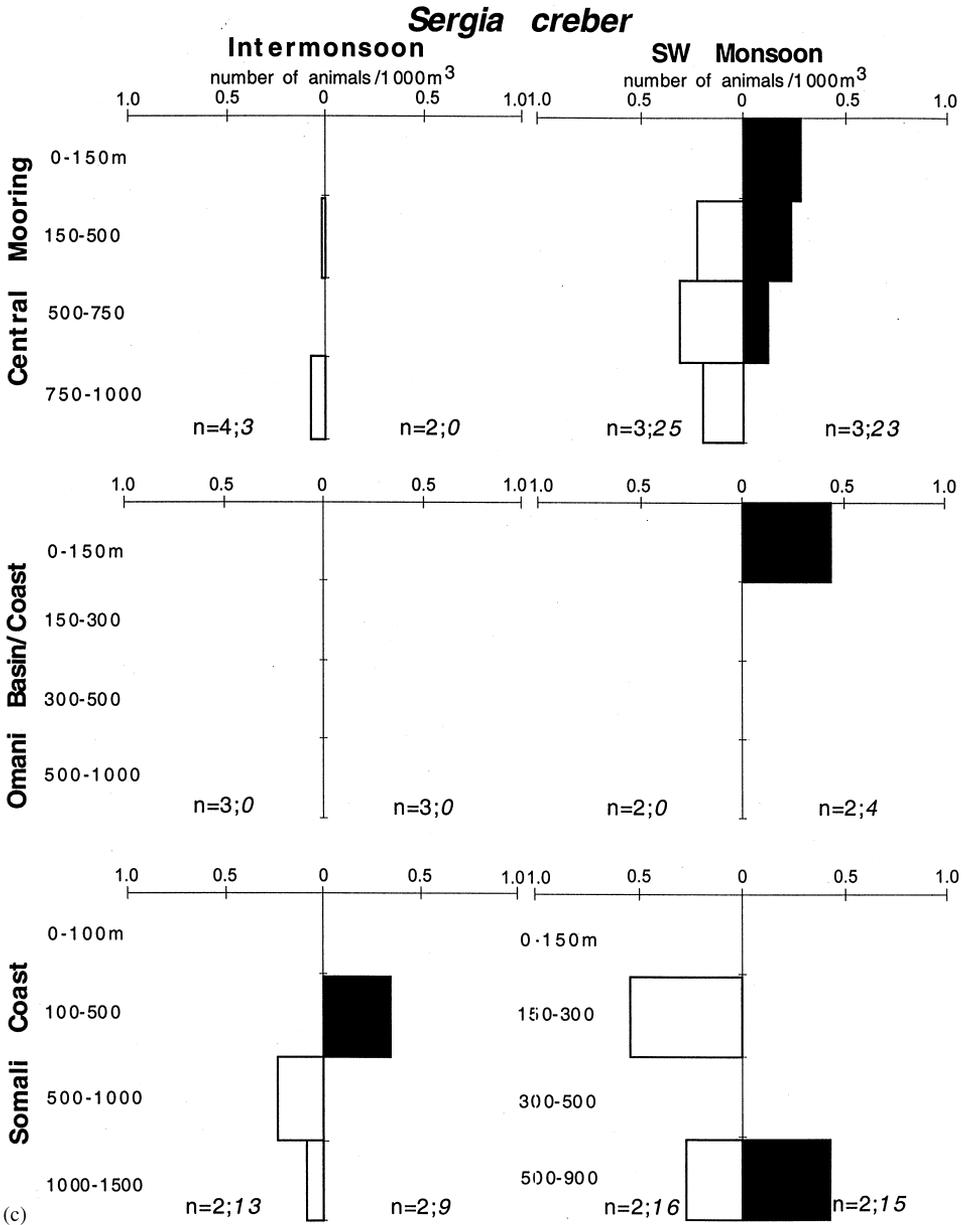
Fig. 2 (*continued*)

Spring Intermonsoon season (Fig. 2c). In the SW Monsoon season, the reverse was true. *S. creber* completely avoided the surface layer (0–150 m) in both seasons. The repeated measures ANOVA for abundance did not show a significant change in vertical distribution with region or season (Table 2). However, sample sizes were small.
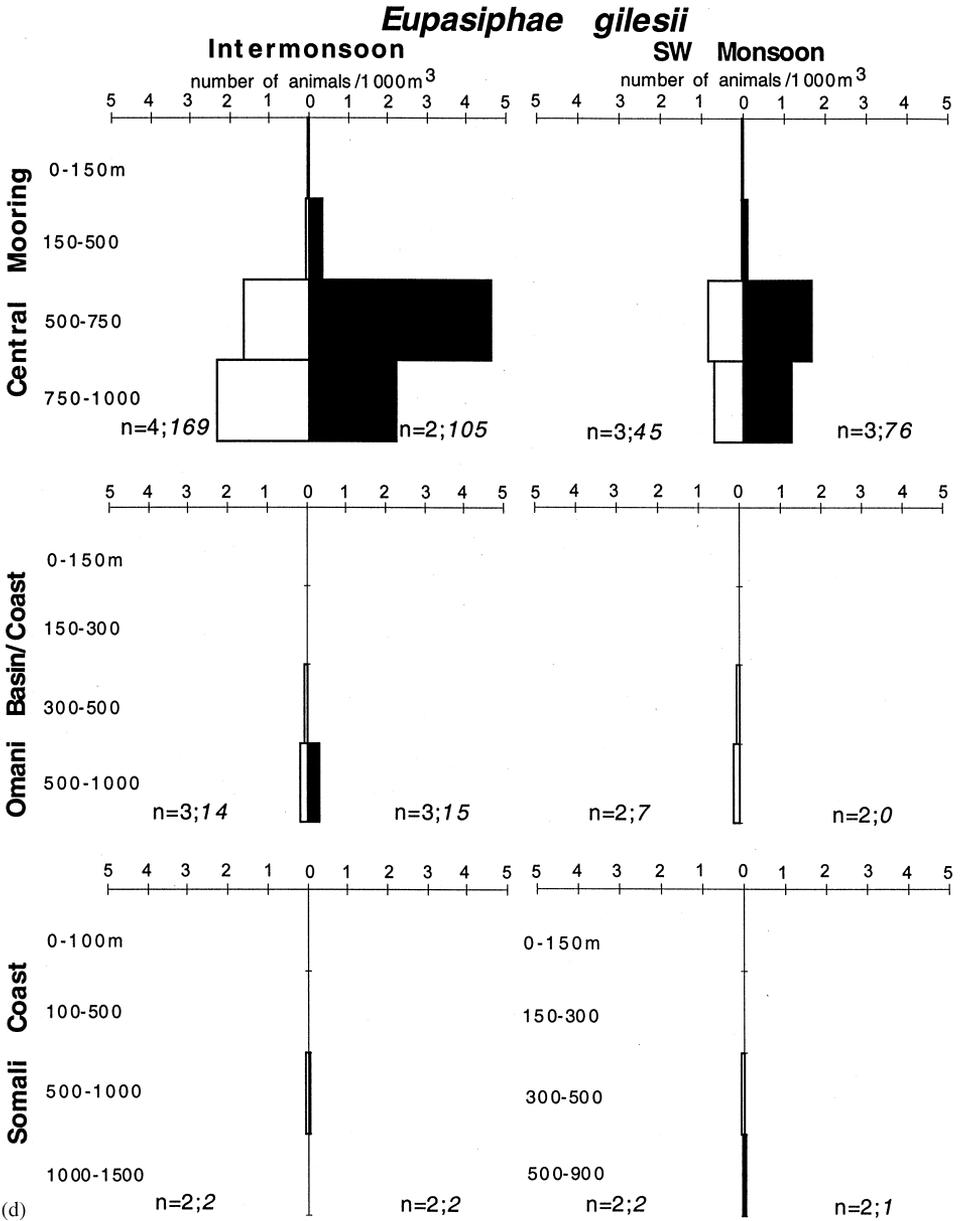
Fig. 2 (*continued*)

Maximum abundances of *Eupasiphae gilesii* at the central mooring station were shallower at night than during the day, yet nearly all individuals were still found below 500 m (Fig. 2d). During the SW Monsoon, more animals were captured at night

than during the day, but the proportion at each depth was similar to daytime samples, with the exception of a very small number of individuals found in the upper 500 m. Given the low abundance of *E. gilesii* in both the Omani Basin/coast and Somali coast regions, we simply note that this species completely avoided the upper 300–500 m of the water column, both day and night (Fig. 2d). These observations are supported by the results of the repeated measures ANOVA for abundance (Table 2). The significant (depth × region) and (depth × season) effects probably resulted from high abundances in the two deepest depth intervals at the central mooring station relative to other regions, and during the Spring Intermonsoon relative to the SW Monsoon.

The two 48-h time–series provided more highly resolved temporal data on vertical distribution. Here we present representative 24-h cycles. *Gennadas sordidus* remained deep in the water column throughout the day and night during the Spring Intermonsoon season, with relatively few individuals entering the upper 500 m at night (Fig. 3a). During the SW Monsoon, vertical migration was more apparent. Some individuals began to ascend in the late afternoon, and relatively large numbers were found in the upper 500 m after sunset. However, even at night most of the population still remained at depth ( > 500 m).

*Sergia filictum* also remained deep throughout the day during the Spring Intermonsoon period (Fig. 3b). During the SW Monsoon, there was movement into the upper layers ( < 500 m) in the late afternoon, where some individuals remained into the night. By late morning, all animals were down below 750 m.

Few individuals of *Sergia creber* were collected during time-series sampling at the central mooring station during the Spring Intermonsoon period (Fig. 3c). During the SW Monsoon, individuals appeared to move from intermediate daytime depths (500–750 m) into the surface layers (0–500 m) after sunset, where they remained into the late night hours.

*Eupasiphae gilesii* mostly remained below 500 m throughout the day and night during both seasons (Fig. 3d). Although a small number of animals were found in the upper 500 m during the SW Monsoon, there did not appear to be a diel pattern to vertical movement.

Any observed migration patterns in these four species did not involve the whole population, so a repeated measures ANOVA was performed for average carapace length, in order to determine whether migration was size-related. Average carapace length was found to vary significantly with depth in *Gennadas sordidus* ($F = 9.991$, $p < 0.001$), *Sergia filictum* ($F = 21.299$, $p < 0.001$), and *Eupasiphae gilesii* ($F = 8.965$, $p < 0.001$), with larger organisms occurring at greater depths in all three species. A significant day/night difference was also detected for *G. sordidus* ($F = 7.656$, $p = 0.013$), with individuals captured during the day generally smaller than those captured at night. The day/night effect was nearly significant for *E. gilesii* as well ($F = 3.913$, $p = 0.063$), but individuals captured during the day were larger than those captured at night. The only significant effect found for *Sergia creber* was a depth × day/night interaction ($F = 3.619$, $p = 0.019$), suggesting that the size of animals at each depth differed between day and night samples. Larger individuals were found at depth during the day, and nearer the surface at night.
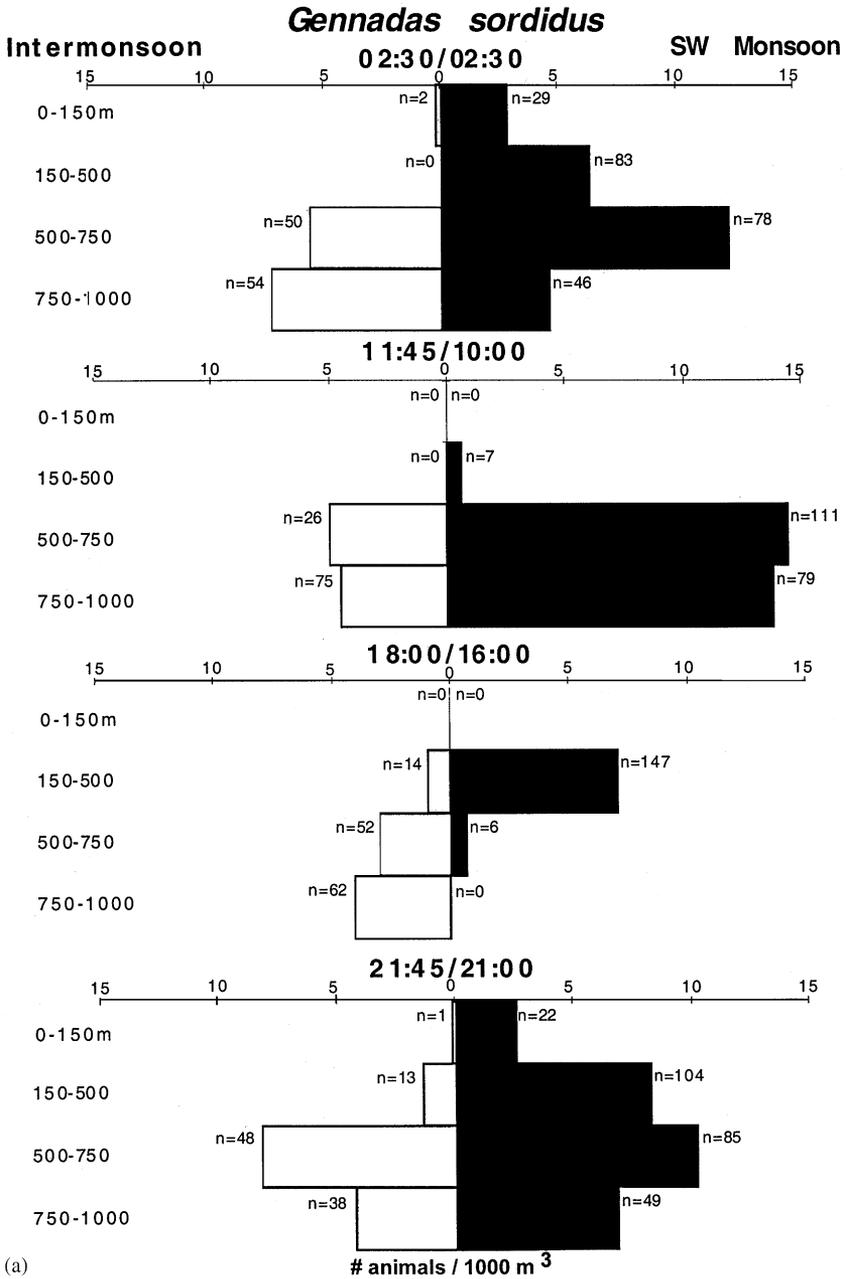
Fig. 3. Abundance (number of animals/1000m$^3$) of (a) *Gennadas sordidus*, (b) *Sergia filictum*, (c) *Sergia creber*, and (d) *Eupasiphae gilesii* at each depth interval over a 24 h. period at the central mooring station. The left axes each show data from one haul during a 48 h. time series conducted during the Spring Intermonsoon season. The right axes show data from one haul at a comparable time of day or night during the SW Monsoon time series. Local time shown is equivalent to GMT + 4 h. $n$ = total number of individuals collected in each depth interval.

**Sergia filictum**
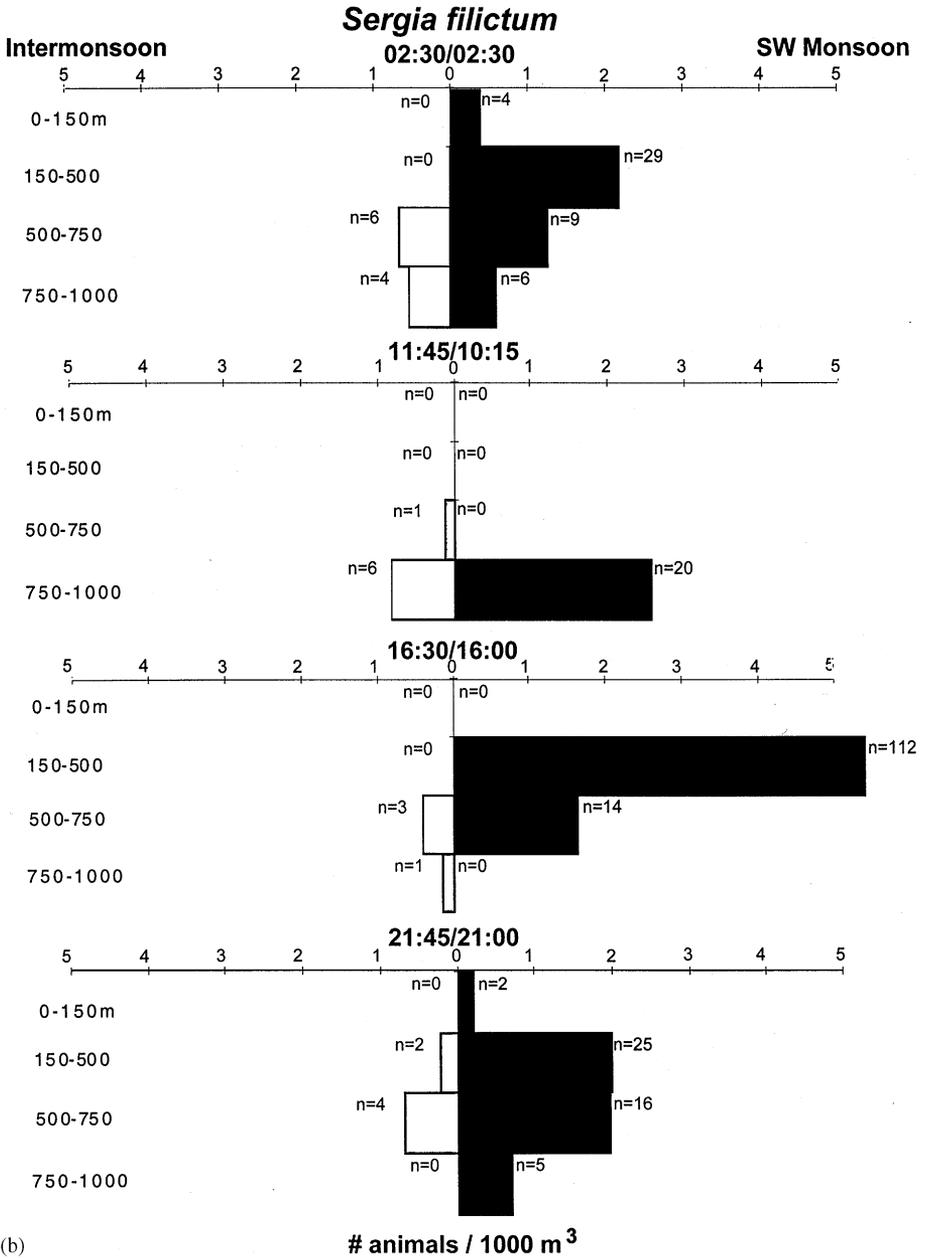
Fig. 3 (*continued*)

## 3.3. Oxygen

Surface oxygen concentrations during both seasons were about 200 μmol/kg throughout the sampled regions. However, oxygen was extremely low ( $\leqslant$ 1.0 μmol/kg)
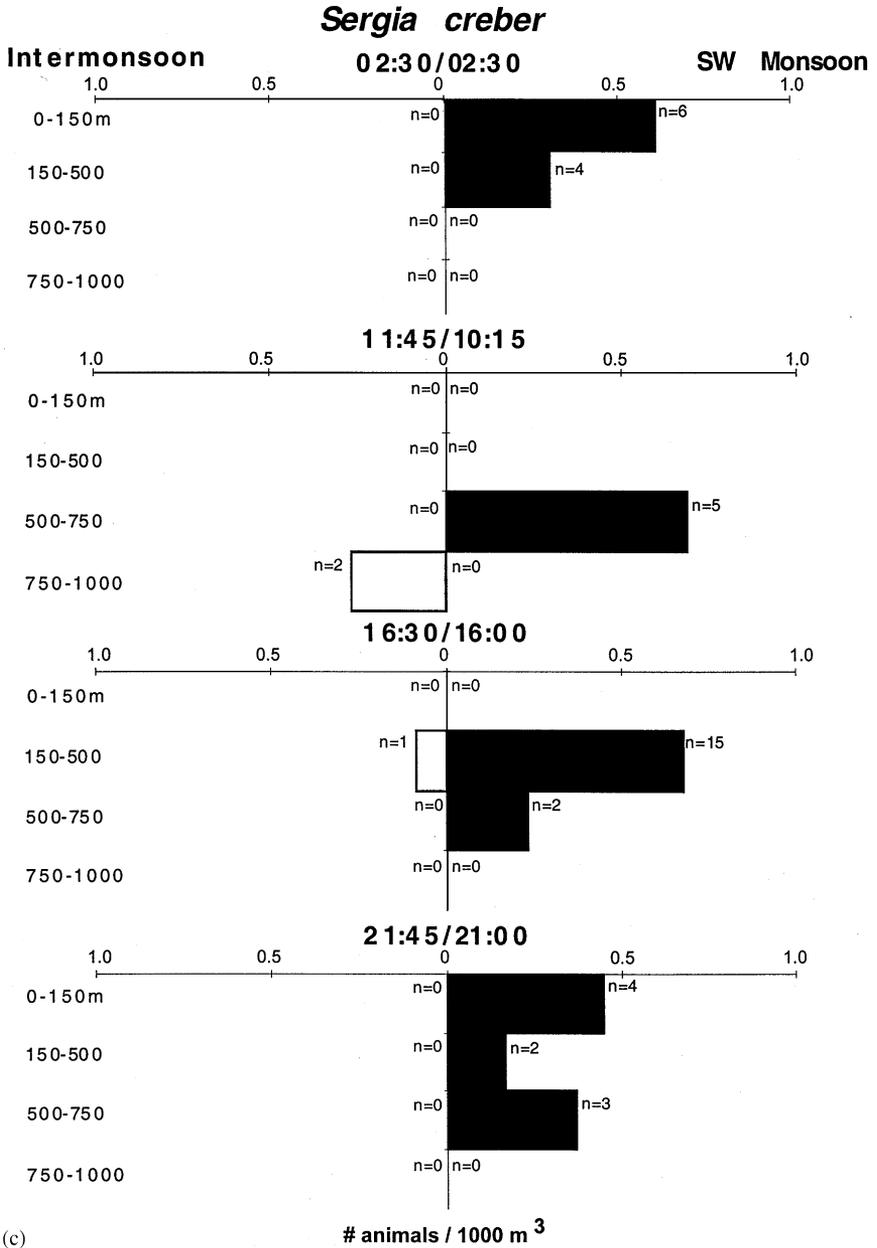
Fig. 3 (*continued*)

below about 200 m depth in the Omani Basin/coast region and at the central mooring station (Fig. 4). A sharp oxycline was detected at $\sim$ 150 m at the central mooring station, below which suboxic conditions extended to the maximum sampling depth. Similar conditions existed in the Omani Basin/coast region. At the Somali

## Eupasiphae gilesii

**Intermonsoon**                    **02:30/02:30**                    **SW Monsoon**



(d)

# animals / 1000 m$^3$

Fig. 3 (*continued*)

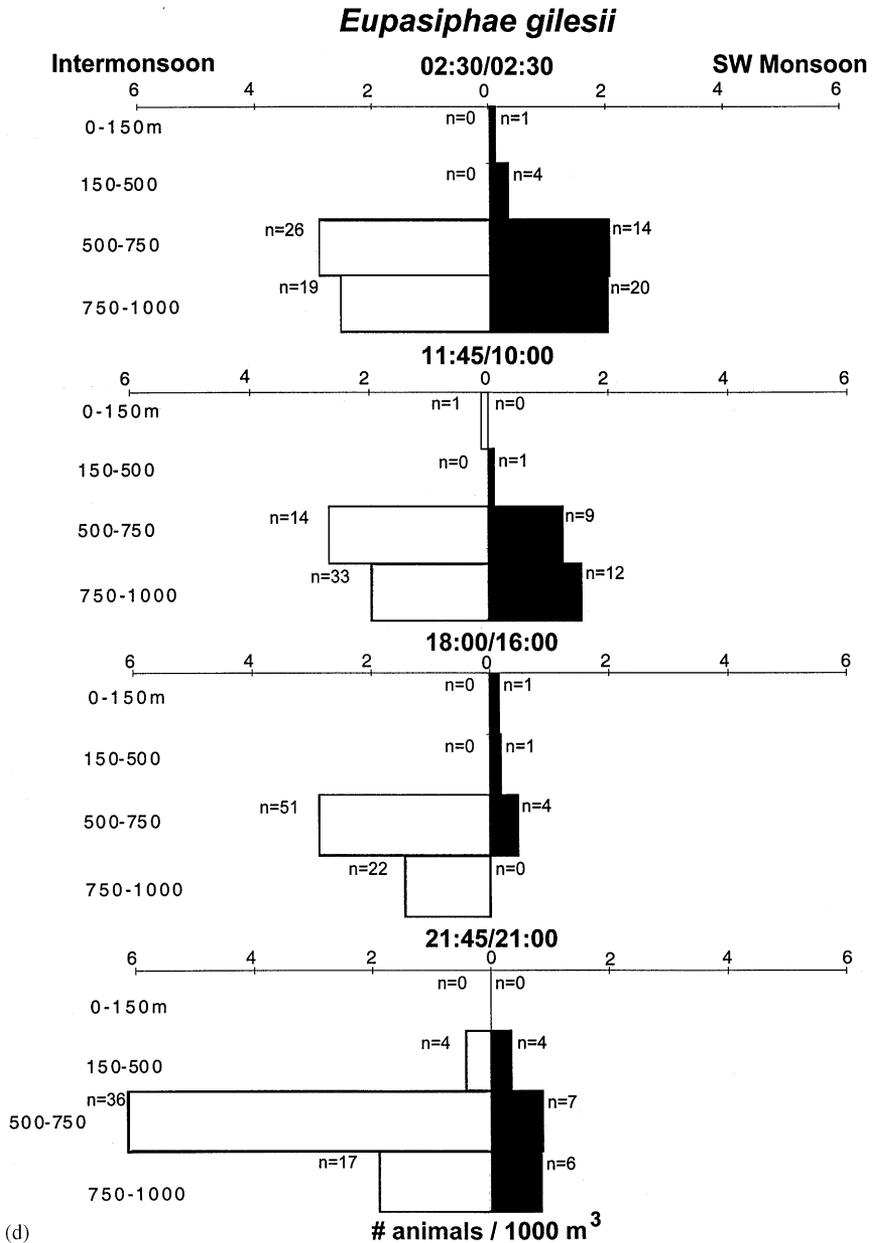coast stations, the oxycline was also found at about 150 m, but concentrations only decreased to about 30 μmol/kg below this depth. During the Spring Intermonsoon, oxygen increased below 1000 m, and was > 50 μmol/kg at 1500 m depth.
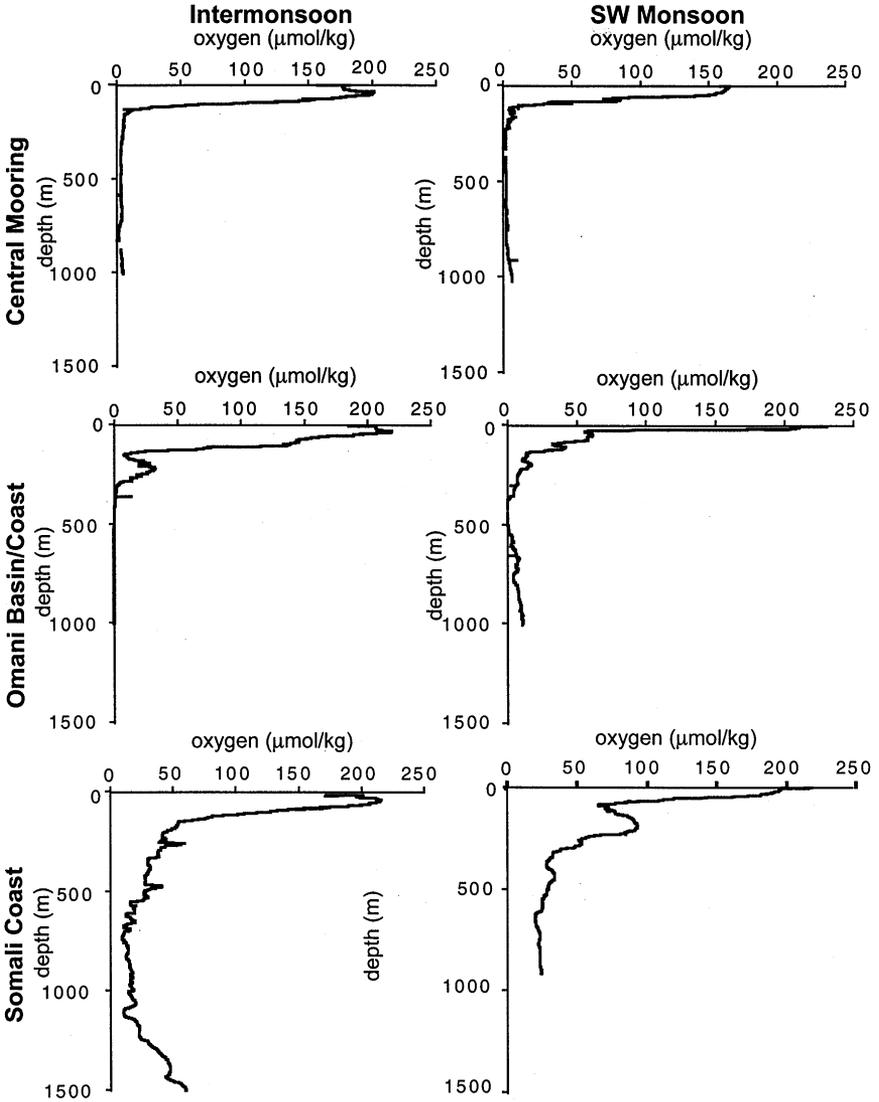
Fig. 4. Representative oxygen profiles (μmol/kg) from each region in each season. Data were collected by instrumentation attached to the MOCNESS trawl during ascent.

## 3.4. Crab defecation and fecal pellet sinking rates

Table 3 summarizes the carbon and nitrogen content of crab fecal pellets produced over a 12-h period, and shows less than a two-fold variation between regions. Coupling the measured average defecation rate (418 mg C and 84 mg N crab$^{-1}$) with the average crab biomass, average fecal C and N release rates were calculated at 0.4%

Table 3
Summary of fecal pellet carbon and nitrogen (mg) produced by adult *Charybdis smithii* (carapace width 30-50mm) from each region sampled during 12 h. ship-board incubations immediately after collection. (*n* = number of crabs measured)

|  | *n* | Fecal carbon (mg) mean (range) | Fecal nitrogen (mg) mean (range) |
|---|---|---|---|
| Central Mooring | 21 | 0.8 (0–2.4) | 0.08 (0–0.26) |
| Somali Coast | 14 | 0.7 (0–1.8) | 0.08 (0–0.22) |
| Omani Basin | 9 | 1.2 (0.4–1.8) | 0.19 (0.05–0.28) |

of body C and 0.2% of body N per day. Multiplying the overall crab abundance by the same defecation rate, we obtained estimates for average fluxes of about 0.7 mg $C\,m^{-2}\,d^{-1}$ and 0.08 mg $N\,m^{-2}\,d^{-1}$. Crab feces were elongate, with a width of 1 mm and a variable length of 6–20 mm. The average sinking rate for all measured pellets (*n* = 24) was $11.8 \pm 2.9$ mm $s^{-1}$, which is equivalent to about 1000 m $d^{-1}$. As water viscosity increases with lowered temperatures, one would expect the sinking speed to decrease. For these fast-sinking pellets, however, the temperature effect would increase travel time to the bottom no more than a few days, even in the deepest waters.

### 3.5. Gut contents

Although the focus of this work is on quantitative measurements of gut contents, qualitative observations of diet also were made during dissections. The diet of each species was generally consistent among regions and seasons. *Gennadas sordidus* guts contained mostly a greenish material likely to be detritus or marine snow (Heffernan and Hopkins, 1981; Hopkins et al., 1994) and crustacean remains, mainly from copepods. Fish eggs, scales, and bones, and occasional radiolarians also were found. *Sergia filictum* and *Sergia creber* also appeared to feed heavily on crustaceans, although euphausiids and other shrimp were more prevalent in the gut than copepods. Fish remains also were found fairly regularly. *Eupasiphae gilesii* guts contained copepod and shrimp remains, as well as fish remains, mostly from myctophids, with approximately equal frequency. On average, ~ 30% of the gut contents of *Charybdis smithii* were comprised of fish remains, and ~ 70% were euphausiid and decapod shrimp remains.

The remainder of this section will deal exclusively with the quantitative aspects of the gut content analyses. As with species abundance, no clear and consistent patterns emerged in vertical distribution of weight-specific gut content for these five species (Fig. 5). However, some trends specific to particular regions and seasons are noteworthy.

No significant diel patterns in vertical distribution of gut content were detected for *Gennadas sordidus* (Fig. 5a). In general, food was found in guts from nearly all depths sampled, both day and night. Despite a marked day/night difference in vertical distribution of *G. sordidus* in the Omani Basin/coast region during the SW Monsoon
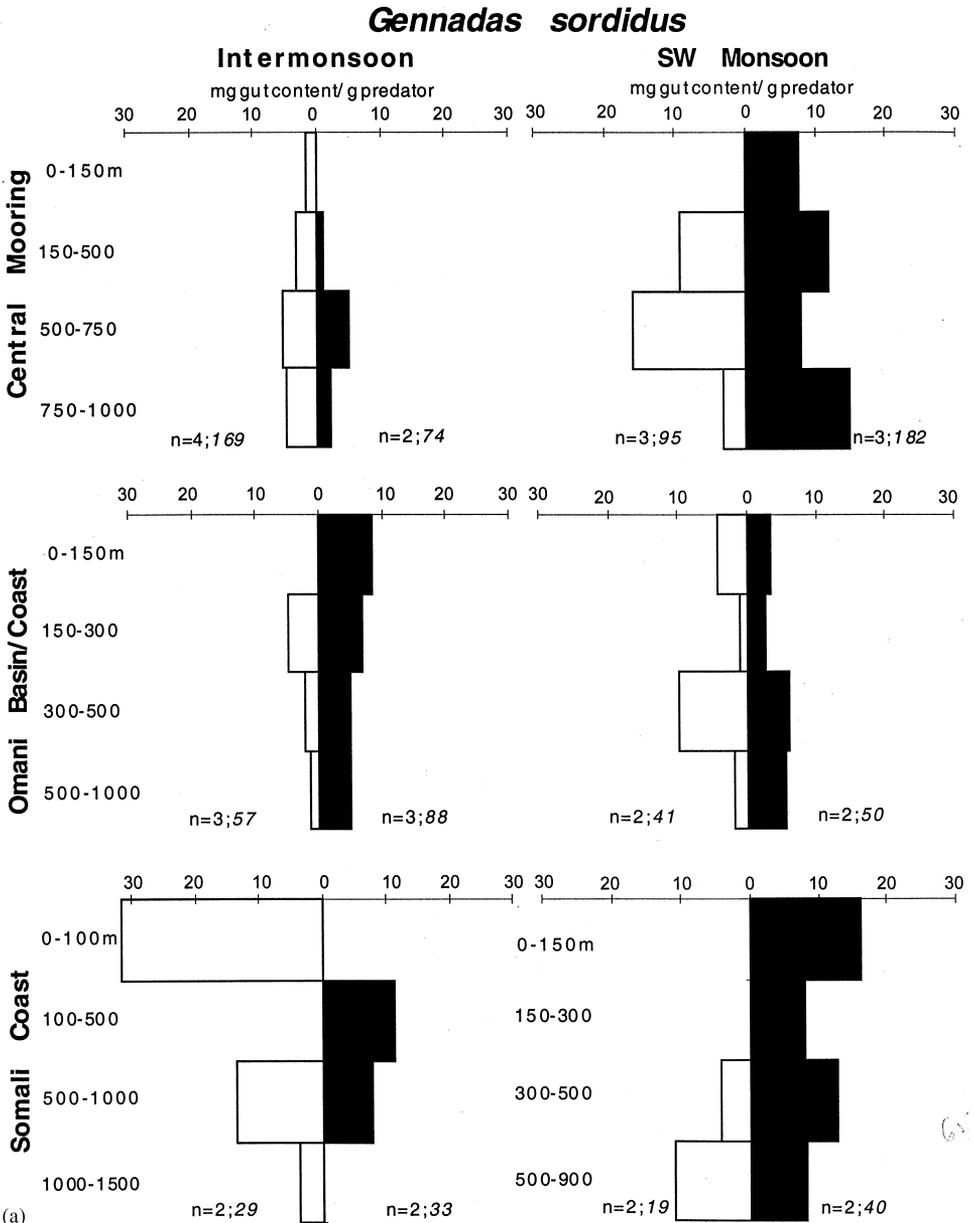
Fig. 5. Average weight-specific gut content (mg gut content/ g predator) for (a) *Gennadas sordidus*, (b) *Sergia filictum*, (c) *Sergia creber*, and (d) *Eupasiphae gilesii* at each depth interval sampled. *n* = number of tows; number of animals dissected. (□ = day hauls, ■ = night hauls)

season (Fig. 2a), weight-specific gut content did not show the same trend, with the highest values found > 300 m both day and night (Fig. 5a). During the SW Monsoon along the Somali coast, the distinct day/night difference in vertical distribution of gut
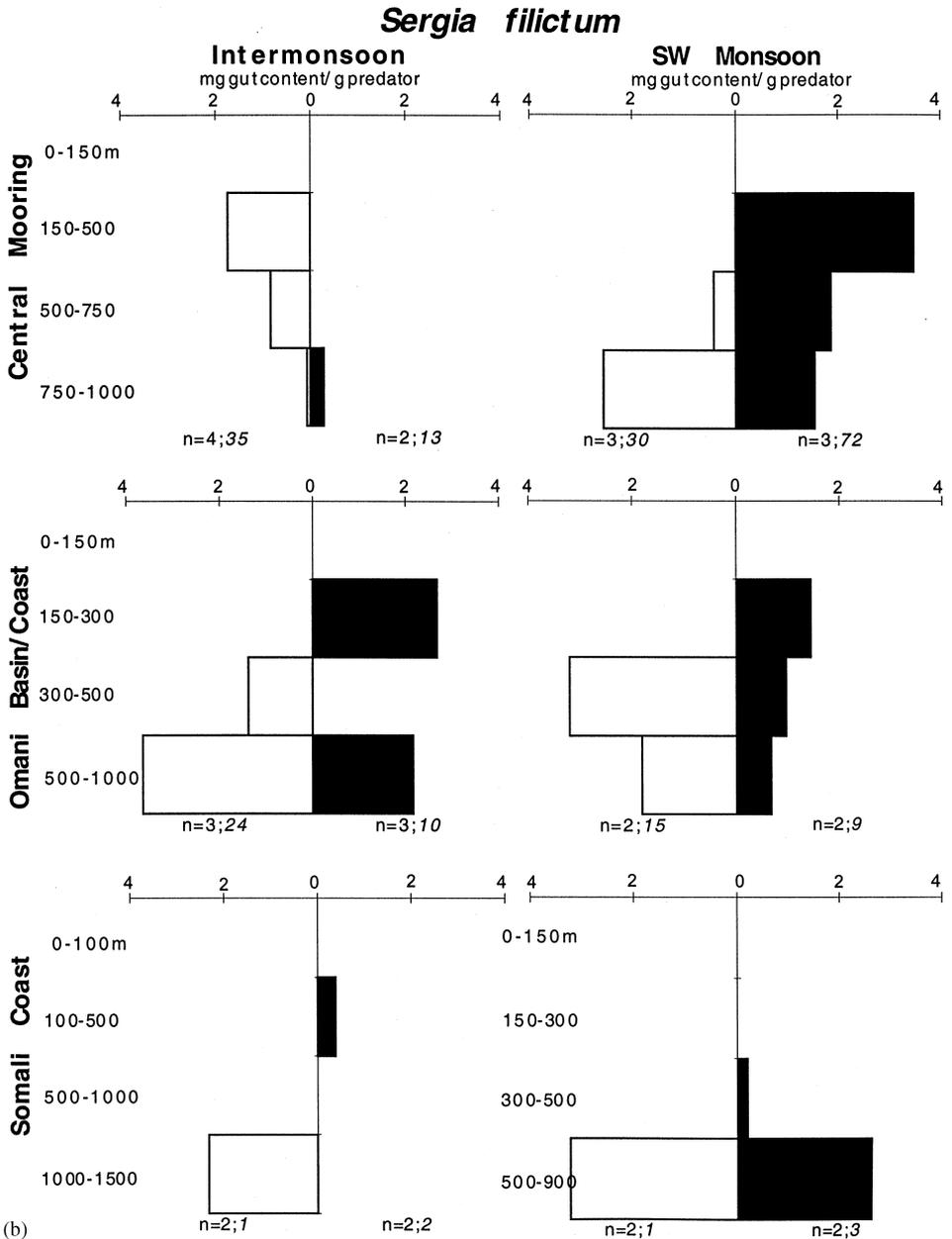
Fig. 5 (*continued*)

contents (Fig. 5a) mirrored the vertical distribution of the population (Fig. 2a), with full guts found at all depths where the species was captured. Despite these apparent trends, a four-factor repeated-measures ANOVA for weight-specific gut content yielded no significant depth, day/night, regional or seasonal effects for this species (Table 4).
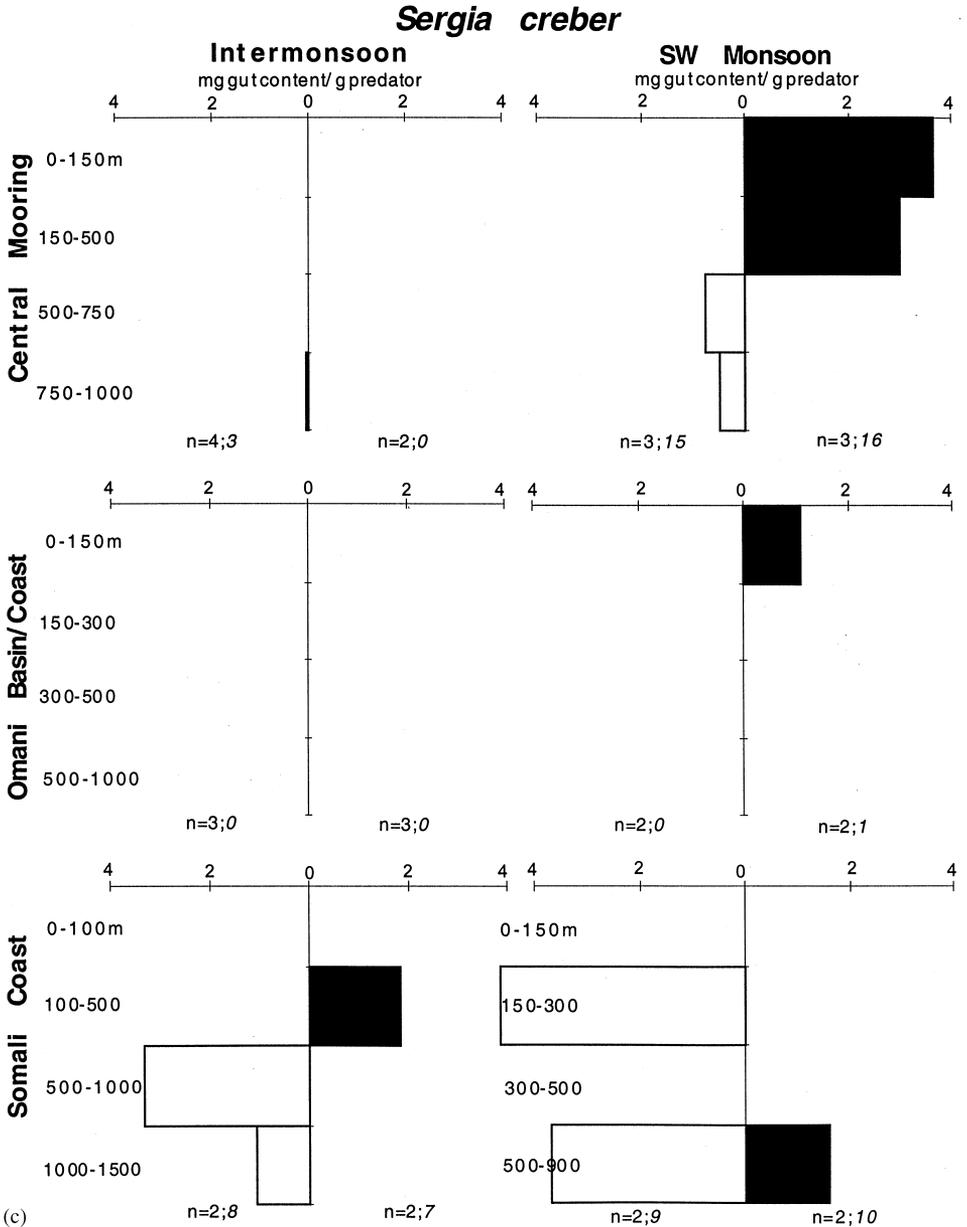
Fig. 5 (*continued*)

Although day/night differences in vertical distribution were not observed for *Sergia filictum* at the central mooring (Fig. 2b), diel changes in gut fullness were noticeable (Fig. 5b). During the Spring Intermonsoon season, guts were fuller nearer
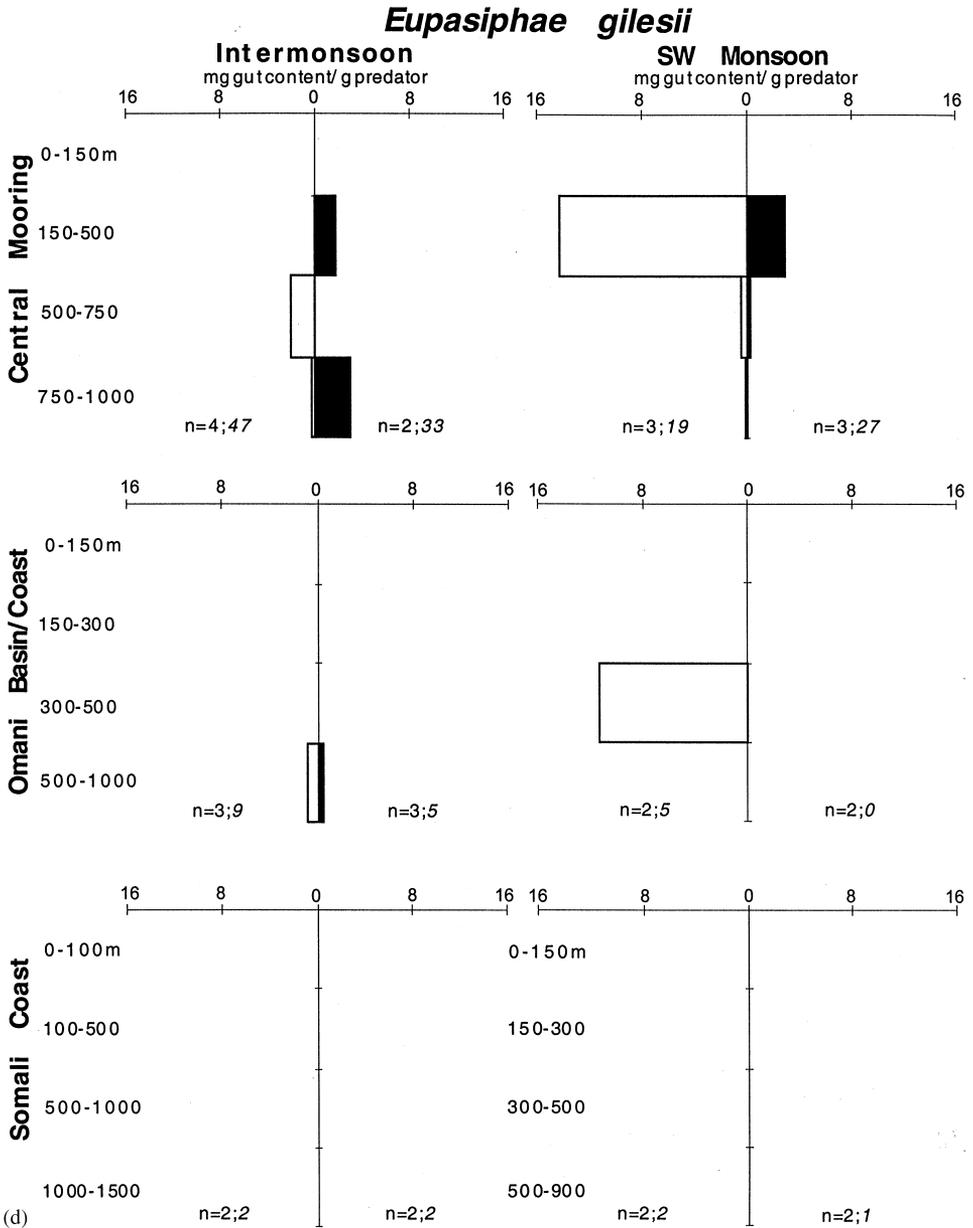
Fig. 5 (*continued*)

the surface by day (mostly 150–500 m), and largely empty at night. During the SW Monsoon, the pattern was reversed, with fuller guts higher in the water column by night, and at depth ( > 500 m) by day. At the Omani Basin/coast stations, gut fullness

Table 4
Summary of results for four-factor repeated measures ANOVA of weight-specific gut contents (mg gut content/g predator), with depth as the repeated measures factor. (d.f. = degrees of freedom, $F$ = $F$-value, $P$ = significance)

| Weight-specific gut content | d.f. | $F$ | $P$ |
|---|---|---|---|
| *Gennadas sordidus* | | | |
| Depth | 3.54 | 1.345 | 0.269 |
| Day/Night | 1.18 | 0.355 | 0.559 |
| Region | 2.18 | 1.347 | 0.285 |
| Season | 1.18 | 0.982 | 0.335 |
| Depth × Day/Night | 3.54 | 0.852 | 0.471 |
| Depth × Region | 6.54 | 1.552 | 0.179 |
| Depth × Season | 3.54 | 1.305 | 0.282 |
| | | | |
| *Sergia filictum* | | | |
| Depth | 3.54 | 5.946 | 0.001[a] |
| Day/Night | 1.18 | 0.104 | 0.751 |
| Region | 2.18 | 0.739 | 0.491 |
| Season | 1.18 | 0.895 | 0.357 |
| Depth × Day/Night | 3.54 | 2.273 | 0.090 |
| Depth × Region | 6.54 | 1.043 | 0.408 |
| Depth × Season | 3.54 | 0.461 | 0.711 |
| | | | |
| *Sergia creber* | | | |
| Depth | 3.54 | 0.844 | 0.476 |
| Day/Night | 1.18 | 0.570 | 0.460 |
| Region | 2.18 | 12.366 | < 0.001[a] |
| Season | 1.18 | 12.688 | 0.002[b] |
| Depth × Day/Night | 3.54 | 2.378 | 0.080 |
| Depth × Region | 6.54 | 2.061 | 0.073 |
| Depth × Season | 3.54 | 2.130 | 0.107 |
| | | | |
| *Eupasiphae gilesii* | | | |
| Depth | 3.54 | 0.675 | 0.571 |
| Day/Night | 1.18 | 0.960 | 0.340 |
| Region | 2.18 | 1.057 | 0.368 |
| Season | 1.18 | 0.982 | 0.335 |
| Depth × Day/Night | 3.54 | 0.507 | 0.679 |
| Depth × Region | 6.54 | 1.162 | 0.340 |
| Depth × Season | 3.54 | 0.737 | 0.535 |

[a]Significant at $\alpha \leqslant 0.001$.
[b]Significant at $\alpha \leqslant 0.01$.

(Fig. 5b) seemed to parallel patterns in abundance (Fig. 2b). Low numbers of *S. filictum* in the Somali coast region make it difficult to determine a pattern in gut fullness, but a few animals with very full guts were found at the deepest depths sampled (Fig. 5b). The repeated-measures ANOVA for weight-specific gut content of *S. filictum* showed a significant depth effect (Table 4), indicating that gut content was not equally

distributed throughout the water column as it was in *Gennadas sordidus*. The depth × day/night effect was nearly significant ($p = 0.09$), suggesting either day/night differences in the depth of feeding, or transport of gut content via diel vertical migration.

Vertical distribution patterns in weight-specific gut content for *Sergia creber* (Fig. 5c) also reflect patterns in abundance (Fig. 2c). During the SW Monsoon, when this species was substantially more abundant, relatively full guts were found wherever individuals were captured. At the central mooring station, weight-specific gut content was high in the surface and sub-surface layers (0–500 m) at night, and lower while the animals were at depth during the day. During the same season in the Somali coast region, the reverse was true, with abundance and gut fullness higher nearer the surface (150–300 m) by day, and at depth (500–900 m) by night. Results of the repeated measures ANOVA for this species showed significant regional and seasonal main effects on weight-specific gut contents (Table 4). (Depth × day/night) and (depth × region) effects were nearly significant ($p = 0.080$ and 0.073, respectively), indicating that there may have been diel changes in gut fullness with depth, as well as differences in vertical distribution of gut contents between regions.

Unlike the other shrimps, weight-specific gut content of *Eupasiphae gilesii* (Fig. 5d) did not correspond well to abundance patterns (Fig. 2d). For example, during the Spring Intermonsoon period at the central mooring station, maximum night-time abundances were found between 500 and 750 m (Fig. 2d), yet guts were all empty in this depth interval (Fig. 5d). During the SW Monsoon, maximum gut fullness was found in the 150–500 m depth range both day and night, while guts were virtually empty below 500 m, where the bulk of the population was found. A repeated measures ANOVA did not detect any significant depth, day/night, regional, or seasonal effects for this species (Table 4).

Adult individuals of *Charybdis smithii* were completely absent from all stations during the Spring Intermonsoon season, although larvae were present. During the SW Monsoon season, all adult individuals captured during the day were found in the surface layer (0–150 m) (Van Couwelaar et al., 1997), where weight-specific gut content was also high (Fig. 6). At night, the bulk of the population was still found at the surface with equally full guts, but some individuals with less full guts also were found at greater depths. A three-factor repeated measures ANOVA of weight-specific gut content yielded only a significant depth effect ($F = 17.748$; $p < 0.001$).

Time-series data from the central mooring station (Fig. 7) generally supported observations of feeding throughout the depths at which the animals were found, yet no consistent diel feeding patterns were observed in any species. *Gennadas sordidus* was found mainly below 500 m (Fig. 3a), with partially full guts throughout the day and night (Fig. 7a) during the Spring Intermonsoon period, but some less full guts were found in the 150–500 m layer around sunset. During the SW Monsoon, gut contents were detected throughout the water column at night (Fig. 7a), particularly in the deepest depths sampled, but all individuals were found > 150 m during the day (Fig. 3a).
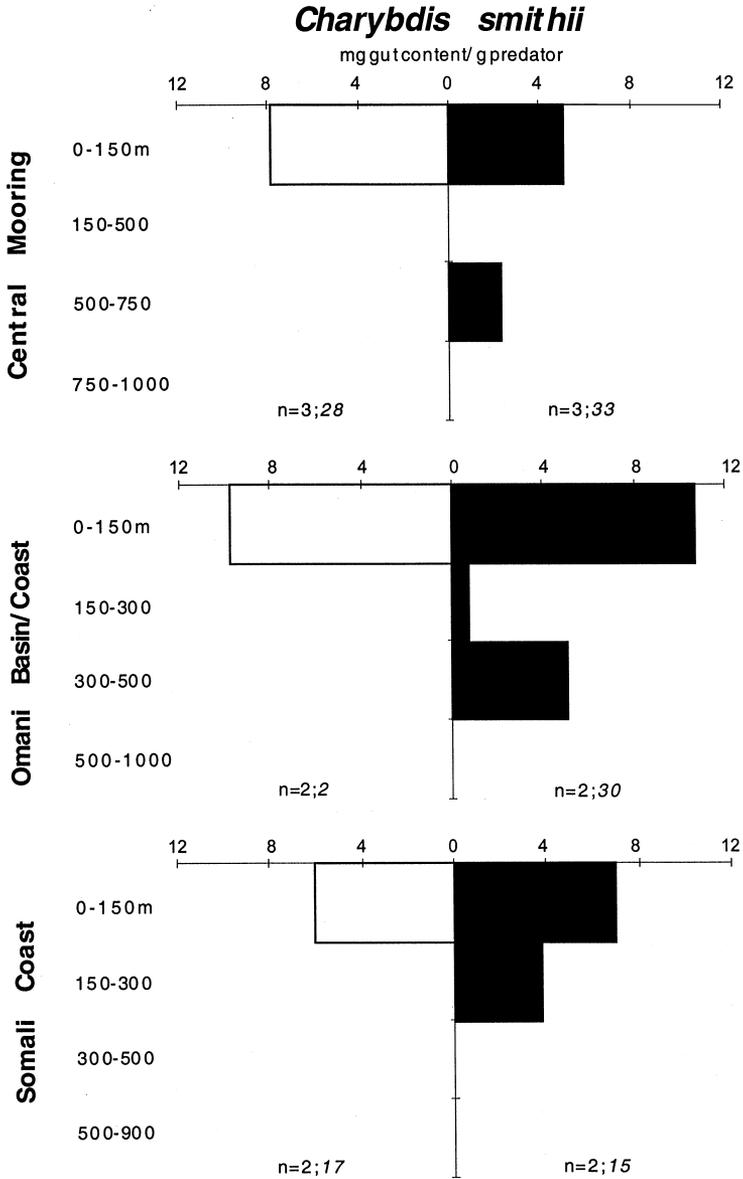
Fig. 6. Average weight-specific gut content (mg gut content/ g predator) for *Charybdis smithii* at each depth interval sampled during the SW Monsoon season. $n$ = number of tows; number of animals dissected. ($\square$ = day hauls, $\blacksquare$ = night hauls)

Feeding patterns were difficult to discern for *Sergia filictum, S. creber*, and *Eupasiphae gilesii* during the Spring Intermonsoon season due to low abundances, but diel feeding patterns with nighttime maxima were evident in the two sergestids during
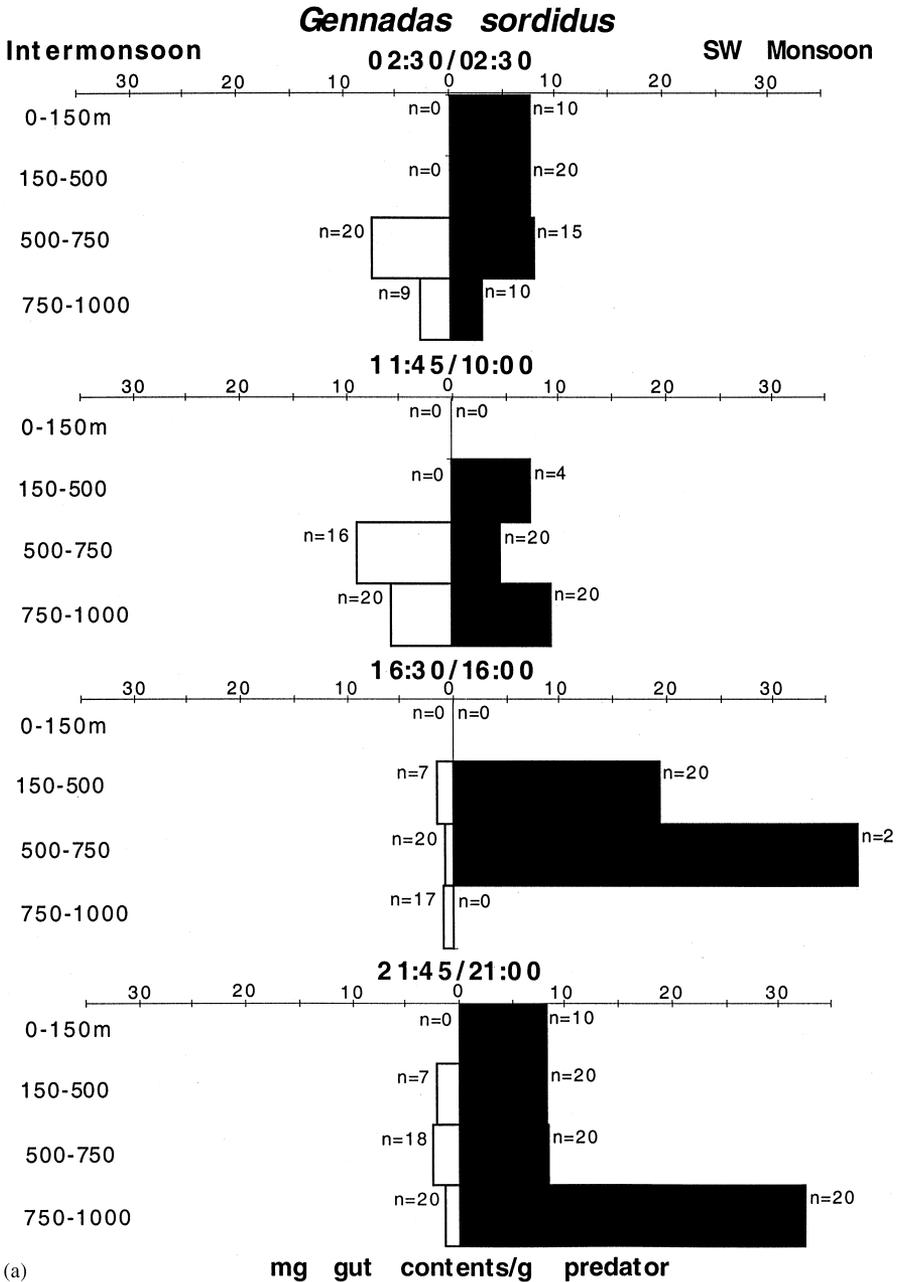
(a)

Fig. 7. Weight-specific gut content (mg gut content/ g predator) of (a) *Gennadas sordidus*, (b) *Sergia filictum*, (c) *Sergia creber*, and (d) *Eupasiphae gilesii* at each depth interval over a 24 h. period at the central mooring station. The left axes each show data from one haul during a 48 h. time series conducted during the Spring Intermonsoon season. The right axes show data from one haul at a comparable time of day or night during the SW Monsoon time series. Local time shown is equivalent to GMT + 4 h. $n =$ total number of individuals dissected.
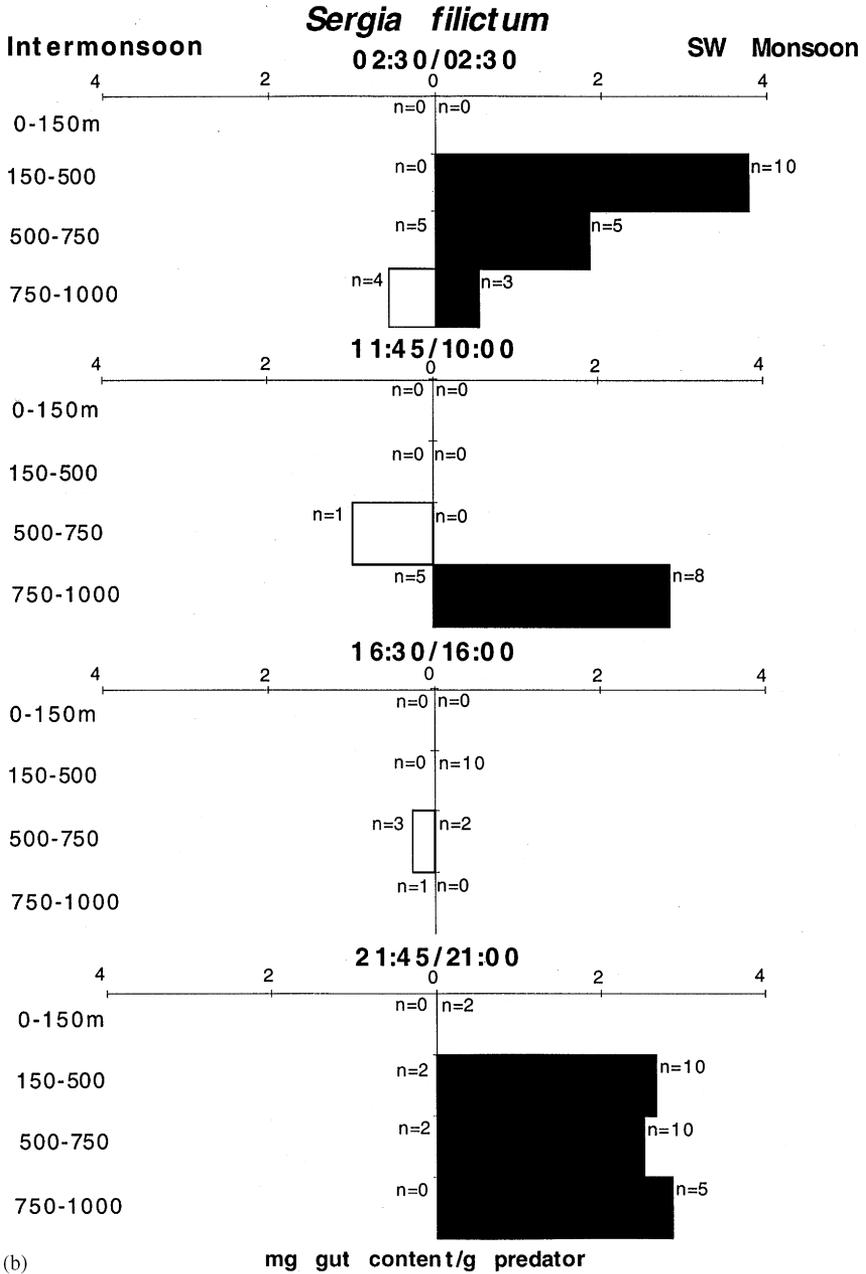
Fig. 7 (*continued*)

the SW Monsoon season. Few *S. filictum* were collected in the surface layer (Fig. 3b), but weight-specific gut content was high at all other depths throughout the night (Fig. 7b). The population had moved to depths > 750 m by late morning (10:00), yet
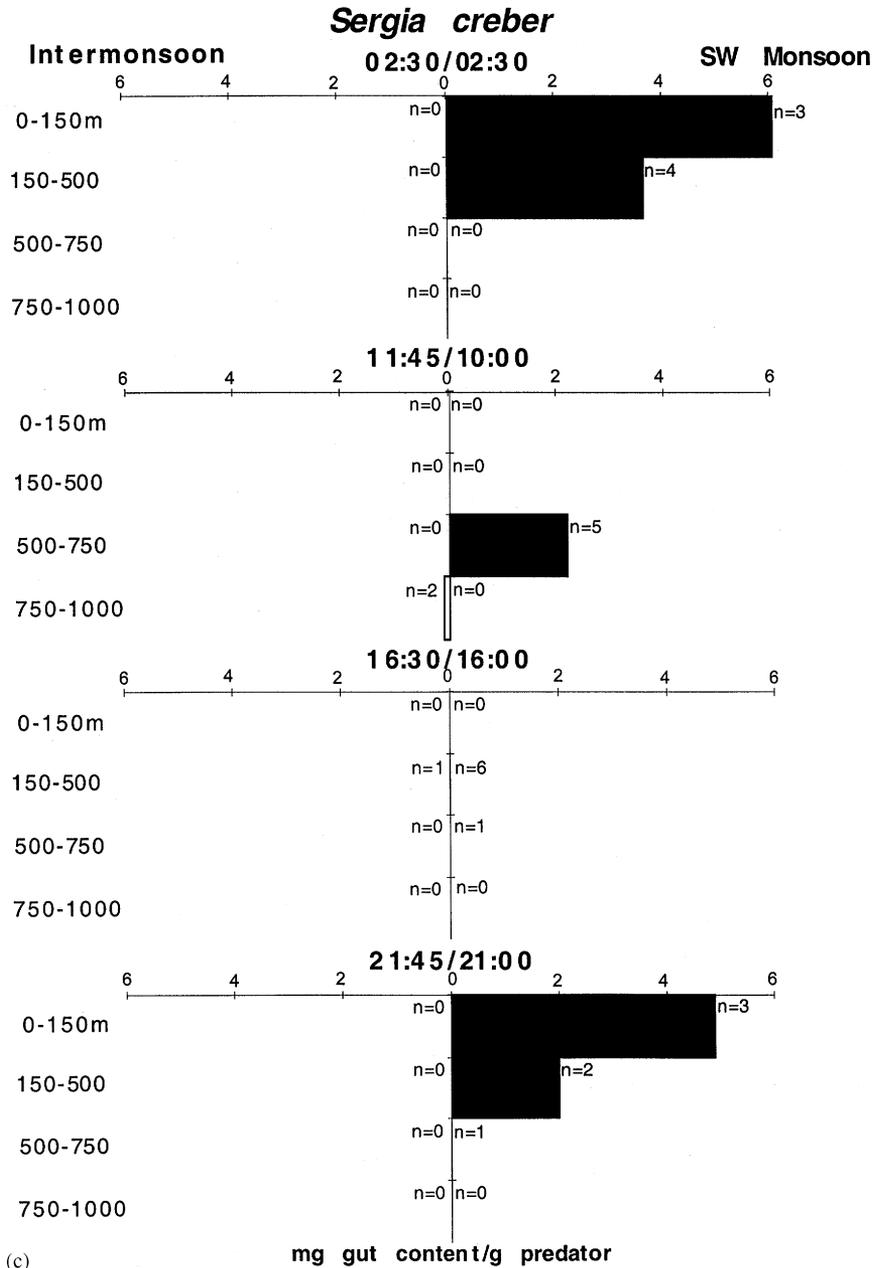
Fig. 7 (*continued*)

guts were still full. All guts were empty by late afternoon (16:00), but feeding appears to have begun again after sunset. Very full guts were found in *S. creber* in the upper 500 m late at night (21:00–02:30), less full guts were found at depth (500–750 m) by
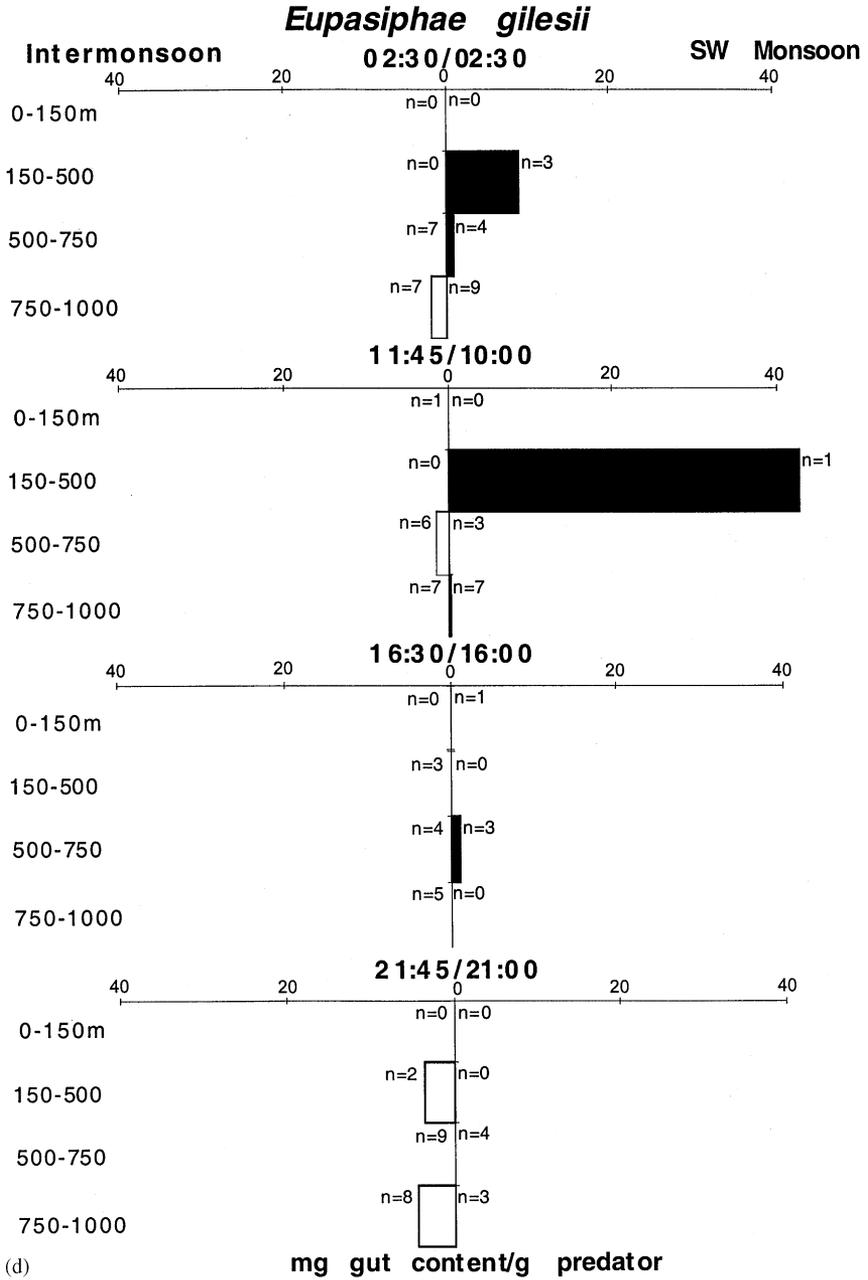
(d)

Fig. 7 (*continued*)

late morning (10:00), and guts were completely empty at all depths by late after-
noon (16:00) (Fig. 7c). Although the sample size was very small, *Eupasiphae gilesii*
appeared to feed primarily at mid-depths (150–500 m) during the SW Monsoon

## *Charybdis smithii*



**mg gut content/g predator**
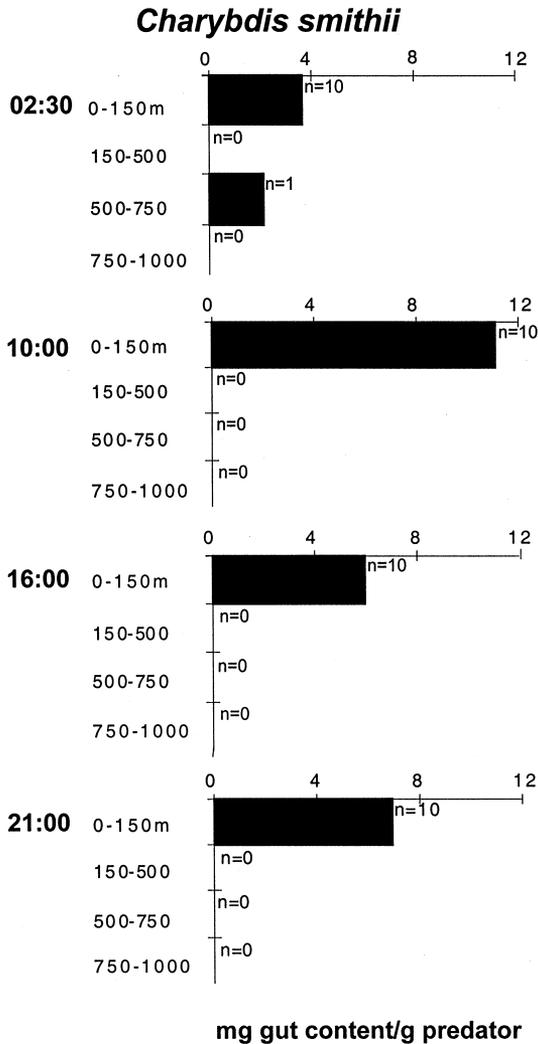
Fig. 8. Weight-specific gut content (mg gut content/g predator) of *Charybdis smithii* at each depth interval over a 24 h. period at the central mooring station during the SW Monsoon season. Local time shown is equivalent to GMT + 4 h. *n* = total number of individuals dissected.

(Fig. 7d), with high weight-specific gut content late at night (02:30) (Fig. 7d). Guts were nearly empty at all depths by late afternoon (16:00), and completely empty after sunset (21:00).

Again, adult *Charybdis smithii* were absent from the central mooring during the Spring Intermonsoon period. During the SW Monsoon, all feeding occurred at the surface, both day and night, with the exception of a single animal with a full gut captured late at night (02:30) in the 500–750 m-depth interval (Fig. 8).

## 4. Discussion

The penaeid *Gennadas sordidus* was by far the most abundant of the four shrimp species, ranging from a low value of 0.6 individuals 1000 m$^{-3}$ during the Spring Intermonsoon season to a high of 6.0 ind. 1000 m$^{-3}$ during the SW monsoon. *Sergia filictum* (0.03–1.5 ind. 1000 m$^{-3}$) and *Sergia creber* (0–0.2 ind. 1000 m$^{-3}$) were less abundant, followed by *Eupasiphae gilesii* (0.02–1.4 ind. 1000 m$^{-3}$). Hopkins et al. (1994) reported similar findings in the Gulf of Mexico, where the midwater decapod assemblage was dominated by *Gennadas valens,* with sergestids less abundant, and carideans the least abundant group. The mean abundance of all four taxa in the upper 1000 m of the NW Arabian Sea ranged from about 3.3 ind. 1000 m$^{-3}$ during the Spring Intermonsoon period to 3.9 ind. 1000 m$^{-3}$ during the SW Monsoon. The abundance of these taxa alone is comparable to the total abundance of all 29 species (3.1 ind. 1000 m$^{-3}$) comprising most of the decapod and mysid assemblage in the Gulf of Mexico (Hopkins et al., 1994).

At least five additional species of the genus *Gennadas* were collected in the Somali coast region during both seasons, including *G. clavicarpus, G. incertus, G. bouvieri, G. scutatus,* and *G. parvus. G. clavicarpus* was also relatively abundant in the Omani Basin/coast region during the Spring Intermonsoon season. None of these species were found at the central mooring station, where *G. sordidus* was most abundant, suggesting that *G. sordidus* may be particularly well adapted to the low-oxygen conditions found in the oligotrophic open-ocean waters, as well as along the Omani coast during the time of our sampling.

Adult *Gennadas sordidus* did not increase significantly in abundance between the two sampling seasons. *Eupasiphae gilesii*, *Sergia filictum*, and *S. creber* did increase in abundance to some extent, but the most notable change was at the oligotrophic central mooring station (Fig. 1). Why do some species not show increases in abundance or in gut fullness during periods of supposedly elevated primary productivity?

The absence of significant increases in either gut fullness or abundances of some of these decapods is notable and contrary to our expectations. Banse (1987) reported that the central Arabian Sea does experience a summer chlorophyll-*a* maximum (although see Gundersen et al., 1998); however, zooplankton do not always appear to keep up with the increased algal growth in the offshore regions of tropical seas. Seasonal appearance of large, fast-growing grazers during the SW Monsoon, particularly in upwelling regions, is thought to play a role in transferring increased production to higher trophic levels such as myctophids, which also undergo annual production cycles (Smith, 1995). However, myctophids migrate to more productive surface waters to feed (Kinzer et al., 1993), whereas this is less the case for the decapods examined in this study. Modest surface feeding was seen only in *S. creber* (Fig. 5c) and *G. sordidus* (Fig. 5a). *S. creber* alone showed a statistically significant increase in stomach contents during the SW Monsoon season (Table 4), suggesting that the other species were not directly affected by increased seasonal production. Phytoplankton productivity may simply be unavailable to the decapods because either they do not feed on phytoplankton due to its small size (Jerling and Wooldridge, 1995) or the material sinks out too quickly (Smetacek et al., 1978) for the algae to represent

a significant additional source of nutrition for the decapods. Alternatively, the seasonal appearance of large grazers, as noted by Smith (1995), may be accompanied by a seasonal increase in the number of trophic links such that the decapods are further removed from the primary production, and thus derive less of a benefit from it than might have been expected.

### 4.1. Vertical migration and feeding

Among the large crustaceans, there is high variability in diel vertical migration patterns. Some authors assert that nearly all mesopelagic species display vertical migration behavior, with few exceptions (Omori, 1974). Virtually all ($\sim 90\%$) micronektonic crustaceans in the Gulf of Mexico, including all *Gennadas* spp., that reside at daytime depths between 600 and 1000 m do show some vertical movement into shallower waters at night (Hopkins et al., 1994). Other authors have documented either weak or absent vertical migration in very deep-living decapod and euphausiid shrimps (Ponomareva, 1971; Fasham and Foxton, 1979; Angel et al., 1982; Hopkins et al., 1994). No clear and consistent diel migration patterns were found for any of the species considered in this study, although the data do suggest possible trends for some species in particular regions.

Both *Gennadas sordidus* (Fig. 2a) and *Sergia filictum* (Fig. 2b) appeared to spread upward at night, particularly during the SW Monsoon season. This diffuse type of migration has been observed in congeneric species residing at similar depths in the North Atlantic (Fasham and Foxton, 1979). *Sergia creber* showed a similar pattern at the central mooring (Fig. 2c), as well as an unexpected reverse migration during the SW Monsoon off the Somali coast. *Eupasiphae gilesii* did not appear to vertically migrate (Fig. 2d), but this species' range was probably not sampled in its entirety. Such deep-living carideans in tropical-subtropical waters are not known to be strong vertical migrators (Omori, 1974; Hopkins et al., 1989).

Some evidence suggests that the degree of vertical migration in mesopelagic species increases with size (Omori, 1974). Here, this trend was observed only in *Sergia creber*, with statistical evidence supporting the observation that larger individuals reside at depth by day and nearer the surface at night (significant depth × day/night interaction). For *Gennadas sordidus*, *Sergia filictum*, and *Eupasiphae gilesii*, differences in vertical distribution relative to size were likely a result of net-avoidance behavior. Small animals were caught more frequently near the surface than at depth, and during the day than at night, indicating that net avoidance behavior by some of the larger organisms during daylight hours probably confounded observations of vertical distribution. For *G. sordidus*, the average size of organisms in the water column during the day was smaller than at night, suggesting that, during daylight hours, larger organisms must either have migrated to depths below those sampled, or avoided the net. Given the size of the organisms and the size of the sampling gear, the latter explanation seems more plausible. Net avoidance behavior has been found to bias sampling of large crustaceans, including euphausiids (Cochrane et al., 1991; Sameoto et al., 1993) and carideans (Gibbons et al., 1994), and is reported to vary as a function of animal size (Hovekamp, 1989).

*Gennadas sordidus*, *Sergia filictum* and *Eupasiphae gilesii* remained between 150 and 1000 m depth, both day and night (Fig. 2a, b, and d, respectively). This depth range closely corresponds to the oxygen-minimum zone observed in this study (Fig. 4), and which is characteristic of the central Arabian Sea in particular (Olson et al., 1993). Indeed, these three species were most abundant in the low-oxygen waters of the central Arabian Sea. *Sergia creber*, in contrast, was most abundant in the Somali coast region, where suboxic conditions were not as severe. In the low-oxygen waters at the central mooring station, *S. creber* showed evidence of diel vertical migrations into the well-oxygenated surface layer during the night (Fig. 2c).

While the presence of oxygen minimum zones has been shown to affect the abundance and vertical distribution of some mesopelagic crustaceans and fishes (Vinogradov and Voronina, 1961; Sameoto, 1986; Kinzer et al., 1993), low-oxygen waters do support a surprising array of taxa (Banse, 1964; Longhurst, 1967). Childress (1975) described respiration in 28 species of midwater crustaceans and two species of midwater fish commonly found in the oxygen minimum layer off Southern California. All but three of these were able to regulate their oxygen consumption to respire aerobically down to the lowest oxygen levels at which they were found (0.13–0.20 ml $O_2 \, l^{-1}$). Of the remaining three species, one (the copepod *Gaussia princeps)* had remarkable anaerobic abilities and underwent extreme diel vertical migrations, thus gaining regular access to oxygenated waters where it could aerobically metabolize the byproducts of anaerobic metabolism accumulated at depth. *Sergia creber* could conceivably employ a similar strategy at the low-oxygen central mooring station.

The four decapod shrimps considered here fed largely, if not exclusively, within the oxygen-minimum layer (Fig. 5). Again, minimal surface feeding was observed only in *Gennadas sordidus* and *Sergia creber*. *G. sordidus* appeared to feed continuously throughout its depth range (Fig. 5a), as has been noted for other members of the genus (Roe, 1984), and did not display any consistent diel feeding pattern. *Sergia filictum* (Fig. 5b) and *S. creber* (Fig. 5c) also fed throughout their depth ranges, but time-series data suggest diel feeding cycles for both these species (Fig. 7b and c, respectively).

Teal (1971) reported that metabolism in midwater decapods tends to remain constant with depth because the effects of decreasing temperature are offset by the effects of increasing pressure. Thus, he predicted that feeding would occur throughout the water column, even in species that vertically migrate, given the metabolic advantage of actively pursuing prey items at all depths. His study was not conducted on organisms found in low-oxygen environments; however, feeding at all depths within the oxygen-minimum layer has been reported in other species. The mysid *Gnathophausia ingens* has an unusually wide respiratory range, which allows it to conserve energy by swimming slowly most of the time while retaining the ability to achieve sudden bursts of speed necessary for prey capture and predator evasion (Childress, 1971). Such adaptations may exist in Arabian Sea organisms, enabling them to persist solely within the deeper low-oxygen layers and avoid surfacing at all.

Vertical migration patterns and corresponding feeding cycles seem to vary a great deal among mesopelagic crustaceans, and no specific information on feeding chronology could be found for the five species considered in this report. Other migrating and non-migrating members of these genera have been described, many of which are said

to feed throughout their depth ranges (Omori, 1974; Roe, 1984), and only some of which display diel feeding patterns (Omori, 1974; Walters, 1976). In general, decapods tend to feed more actively at night, and some sort of relationship appears to exists between feeding behavior and diel vertical migration, particularly in the shallower ( < 500 m) living species (Omori, 1974; Foxton and Roe, 1974; Roe, 1984). Among euphausiids, some species that migrate little have been reported to have more pronounced feeding rhythms (Roger, 1975), while others are said to exhibit no diel feeding patterns (Ponomareva, 1971). Conflicting evidence for a relationship between vertical migrations and feeding periodicity may be attributed to high variability in gut passage time. According to Murtaugh (1984), average gut passage time in the mysid *Neomysis mercedis* is negatively correlated with ingestion rate, and ranges from 1 to 13 h. Although little or no diel change in gut fullness may appear to represent continuous feeding over a 24-h period, high variability in gut passage times might actually mask a true diel cycle. Our results should be viewed in this light.

An additional point relevant to these gut content analyses is the possibility of net feeding. A major dietary component of *Gennadas sordidus* and the two *Sergia* spp. was copepods ( < 1 mm), which were not captured by the 3-mm mesh of the MOCNESS trawl. Euphausiid and myctophid remains were recovered from some of the larger individuals, particularly in *Eupasiphae gilesii*, yet these were rarely in excess of 3 mm in length. While some authors claim that net feeding should be a major concern (Omori, 1974), others, using sampling gear comparable to that used here, indicate that net feeding is unimportant in large crustaceans (Foxton and Roe, 1974; Walters, 1976; Roe, 1984; Hopkins et al., 1994). Our results suggest that it is unimportant for the shrimps. However, after our first few hauls of the SW Monsoon cruise were completed, damage to other organisms provided evidence that *Charybdis smithii* was actively feeding in the cod end of the MOCNESS. In an effort to minimize net feeding by this species, the nets were modified with a "crab trap" that filtered out the crabs before they reached the cod end, and the crabs were handled separately from the rest of the catch once recovered from the net.

### 4.2. Implications for vertical flux

Monsoonal weather systems dramatically increase sedimentation rates in the Arabian Sea, with particle fluxes during the SW Monsoon season accounting for as much as 50–70% of the total annual flux, even in the central regions not heavily influenced by seasonal upwelling (Nair et al., 1989). Large zooplankton and micronekton must play some role in increased particle flux due to their production of large, fast–sinking fecal pellets (Fowler and Small, 1972; Small et al., 1979; Paffenhöfer and Knowles, 1979; Angel et al., 1982). Further, if these large organisms release fecal pellets at depth, those fecal pellets have an increased likelihood of reaching the deep sea and its benthos given the shorter transit time and decreased chance for bacterial degradation. We have combined our observations of stomach content mass with literature-derived estimates of assimilation efficiencies and gut passage times to yield estimates for daily contribution of decapod fecal pellet production to the vertical particulate flux.

Table 5
Dry weight of gut content per unit area (mg/m²) for four decapod shrimps and *Charybdis smithii* in each region and each season sampled

| | Gennadas sordidus | | | | Sergia filictum | | | | Sergia creber | | | | Eupasiphae gilesii | | | | Charybdis smithii | | | |
| | Inter-monsoon | | SW Monsoon | | Inter-monsoon | | SW Monsoon | | Inter-monsoon | | SW Monsoon | | Inter-monsoon | | SW Monsoon | | Inter-monsoon | | SW Monsoon | |
| | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Central Mooring** | | | | | | | | | | | | | | | | | | | | |
| 0–150 m | 0.001 | 0 | 0 | 0.02 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.02 | 0 | 0 | 0 | 0 | 0 | 0 | 1.49 | 1.00 |
| 150–500 m | 0.03 | 0.005 | 0.04 | 0.15 | 0.003 | 0 | 0 | 0.14 | 0 | 0 | 0 | 0.04 | 0 | 0.004 | 0.04 | 0.01 | 0 | 0 | 0 | 0 |
| 500–750 m | 0.05 | 0.08 | 0.05 | 0.08 | 0.02 | 0 | 0.02 | 0.08 | 0 | 0 | 0.01 | 0 | 0.03 | 0 | 0.01 | 0.001 | 0 | 0 | 0 | 0.19 |
| 750–1000 m | 0.07 | 0.02 | 0.04 | 0.21 | 0.002 | 0.01 | 0.10 | 0.04 | 9.16 | 0 | 0.01 | 0 | 0.01 | 0.14 | 0.001 | 0.001 | 0 | 0 | 0 | 0 |
| Water Column Total | 0.15 | 0.11 | 0.13 | 0.45 | 0.02 | 0.01 | 0.11 | 0.26 | 9.16 | 0 | 0.02 | 0.06 | 0.04 | 0.15 | 0.06 | 0.01 | 0 | 0 | 1.49 | 1.18 |
| **Omani Basin/Coast** | | | | | | | | | | | | | | | | | | | | |
| 0–150 m | 0 | 0.02 | 0.001 | 0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.003 | 0 | 0 | 0 | 0 | 0 | 0 | 0.55 | 5.64 |
| 150–300 m | 0.01 | 0.03 | 0.001 | 0.02 | 0 | 0.02 | 0 | 0.03 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.15 |
| 300–500 m | 0.01 | 0.04 | 0.11 | 0.04 | 0.01 | 0 | 0.02 | 0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0.04 | 0 | 0 | 0 | 0 | 1.13 |
| 500–1000 m | 0.01 | 0.04 | 0.01 | 0.03 | 0.04 | 0.03 | 0.02 | 0.01 | 0 | 0 | 0 | 0 | 0.04 | 0.001 | 0 | 0 | 0 | 0 | 0 | 0 |
| Water Column Total | 0.03 | 0.13 | 0.12 | 0.11 | 0.05 | 0.05 | 0.04 | 0.05 | 0 | 0 | 0 | 0.003 | 0.04 | 0.001 | 0.04 | 0 | 0 | 0 | 0.55 | 6.91 |
| **Somali Coast** | | | | | | | | | | | | | | | | | | | | |
| 0–100/0–150 m | 0.003 | 0 | 0 | 0.02 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.75 | 2.24 |
| 100–500/150–300 m | 0 | 0.08 | 0 | 0.03 | 0 | 0.002 | 0 | 0 | 0 | 0.04 | 0.02 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.29 |
| 500–1000/300–500 m | 0.06 | 0.04 | 0.004 | 0.04 | 0 | 0 | 0 | 0.0004 | 0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1000–1500/500–900 m | 0.01 | 0 | 0.04 | 0.03 | 0.05 | 0 | 0.01 | 0.005 | 0.02 | 0 | 0.04 | 0.03 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Water Column Total | 0.08 | 0.12 | 0.04 | 0.11 | 0.05 | 0.002 | 0.01 | 0.01 | 0.03 | 0.04 | 0.05 | 0.03 | 0 | 0 | 0 | 0 | 0 | 0 | 1.75 | 2.53 |

Table 5 shows total dry weight of gut content (mg m$^{-2}$) in each region and season sampled for each of the five species studied here. Assuming an 80% assimilation efficiency (Thomas et al., 1984), the mass of gut content can be multiplied by 0.2 to give the mass of material likely to be defecated, and thus the potential contribution to particulate flux. These calculations will likely underestimate fecal pellet production due to varied degrees of digestion of gut contents at time of capture. Gut content data can be converted from dry weight to carbon units using an approximate conversion factor of 35% (Wiebe et al., 1975; Donnelly et al., 1993; Madin et al., 2000). However, such conversions should be made with caution, since this value is for whole organisms. Percent carbon and nitrogen content of the gut content will vary with food source and degree of digestion at time of measurement.

Gut passage times reported for decapod crustaceans are highly variable, ranging from about 1–13 h under normal circumstances to 2–3 days when organisms are starved (Omori, 1974; Murtaugh, 1984). Our efforts to estimate defecation rates through a series of ship-board experiments resulted in a high degree of variability, even among individuals of the same species. Thus, we have used an average value from the literature of 6 h.

Estimated fecal pellet production during the Spring Intermonsoon season by the abundant *Gennadas sordidus* ranged from a high of 0.20 mg dry weight m$^{-2}$ d$^{-1}$ at the central mooring station to a low of 0.13 mg m$^{-2}$ d$^{-1}$ in the Omani Basin/coast region. During the SW Monsoon, fecal pellet production by this species was more than four times higher at the central mooring station (0.47 mg m$^{-2}$ d$^{-1}$), and approximately equal to the Spring Intermonsoon season in the other regions. Estimates for *Sergia filictum* were comparable to those for the smaller but more abundant *G. sordidus*, with values at the central mooring ranging from 0.02 during the Spring Intermonsoon to 0.3 by the SW Monsoon season. Average fecal pellet flux in the other regions remained at about 0.06 mg m$^{-2}$ d$^{-1}$ during both seasons. *Charybdis smithii* surpassed both of these shrimp species, although it was only present during the SW Monsoon season. Assuming the same literature-derived assimilation efficiency and gut passage time used for the shrimps, *C. smithii* would have defecated a minimum of 2.1 mg dry weight m$^{-2}$ d$^{-1}$ at the central mooring station and a maximum of 6.0 mg m$^{-2}$ d$^{-1}$ in the Omani Basin/coast region. These values were quite similar to our ship-board measurements of crab defecation rates. At the central mooring, we measured 2.2 mg m$^{-2}$ d$^{-1}$.

Average vertical flux of particulate material, as measured by sediment traps at 1000 m, has been reported by Nair et al. (1989); see also Lee et al. (1998) for organic carbon fluxes). Comparing these data with our estimates, we found that *Gennadas sordidus* could account for 2.1% of the particulate flux in the central Arabian Sea during the Spring Intermonsoon period, and 0.4% during the SW Monsoon. In the upwelling regions, fecal pellets of *G. sordidus* probably accounted for 0.5–0.7% of the particulate flux during the Spring Intermonsoon period, and 0.1% during the SW Monsoon season. *Sergia filictum* accounted for only 0.25% of the flux at the central mooring station during both seasons. In the upwelling regions, this species contributed 0.2–0.4% during the Spring Intermonsoon period, and < 0.01–0.03% during the SW Monsoon. *Charybdis smithii*, on the other hand, could potentially have made

a more significant contribution to the particulate flux during the SW Monsoon season. Fecal pellet production in this species could account for 1.8% of the particulate flux in the central Arabian Sea, and 1.8–3.0% in upwelling regions. As a group, these five species are estimated to have contributed 4.0% of the vertical flux at the central mooring station during the Spring Intermonsoon season, and 2.6% during the SW Monsoon. In upwelling regions, their contribution was 1.0% during the Spring Intermonsoon period, and ranged from 1.8–3.2% during the SW Monsoon.

The average depth of occurrence of decapod stomach contents in this study was approximately 500 m, whereas the best available historical data on total particle flux were collected at 1000 m (Nair et al., 1989). Loss terms such as coprophagy (Noji et al., 1991) and bacterial degradation could have caused us to overestimate the percentage of total flux at 1000 m. However, we assume that such loss terms will be counterbalanced by processes that would lead to underestimates, e.g., contributions from juvenile forms. Further, it is likely that only minimal degradation of decapod fecal pellets would occur between 500 and 1000 m since macrozooplankton fecal pellets have been found here and elsewhere (Fowler and Small, 1972) to sink rapidly (ca. 1000 m per day), and the low oxygen levels at these depths (Fig. 4) would retard bacterial degradation (Hansell and Naqvi, 1995).

Again, most of the species in this study were not strong vertical migrators, nor did they display clear and consistent diel feeding patterns. However, *Gennadas sordidus* and *Sergia filictum* both had full guts at depths in excess of 150 m during the day and at night – in fact, nearly all the gut contents collected in these species were found below the mixed layer. Thus, fecal pellets are probably being produced at depth, making them more likely to reach the deep sea before they are degraded (Angel et al., 1982; Emerson and Roff, 1987). Although *Charybdis smithii* appeared to have a more substantial impact on the particulate flux, fecal pellets of this species were produced largely within the surface layer, leaving them somewhat more susceptible to recycling.

## 5. Summary

Of the three regions sampled in this study, the mooring station in the central Arabian Sea had the highest abundance of *Gennadas sordidus*, *Sergia filictum*, and *Eupasiphae gilesii*. *Sergia creber* was most abundant in the Somali upwelling region. Only *S. filictum* and *S. creber* increased significantly in abundance between the Spring Intermonsoon and SW Monsoon seasons.

No clear and consistent diel vertical migration patterns were seen in any of the shrimp species studied here. *Gennadas sordidus* and *Sergia filictum* did appear to spread upward at night, especially during the SW Monsoon, but this movement did not include the entire population. *Sergia creber* showed signs of diel vertical migration in some areas, but *Eupasiphae gilesii* did not vertically migrate. The degree of vertical migration in *S. creber* appeared to increase with body size. For the other three species, net avoidance behavior was probably the cause of observed differences in depth distribution relative to size. All species, except, to some degree, *S. creber*, lived almost

exclusively within the oxygen-minimum zone, and may have respiratory adaptations that allow them to persist under such conditions.

*Gennadas sordidus* appeared to feed continuously throughout the day and night, and throughout its vertical range. *Sergia filictum* and *Sergia creber* showed weak day/night differences in gut fullness. Empty guts were common in *eupasiphae gilesii*, making patterns difficult to detect. *Charybdis smithii* fed largely in the surface layer throughout the day and night, with some full guts also found down to 500 m at night. Net feeding did not appear to be an important source of bias in the shrimps, nor in *C. smithii* after modifications to the sampling gear were made.

Estimated contribution of fecal material to vertical flux ranged from < 0.01–2.1% of particulate flux at 1000 m for each of the shrimps and 1.8–3.0% for *C. smithii*. The total contribution of all five species ranged from 2.6–4.0% of the vertical flux at 1000 m in the central Arabian Sea, and 1.0–3.2% in upwelling regions. The relative contribution of shrimp fecal pellets to total vertical flux was estimated to be higher during the Spring Intermonsoon period than during the SW Monsoon and in the central Arabian Sea than in upwelling regions, whereas the contribution of *C. smithii* was proportionately higher in the upwelling regions.

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