

# The bathypelagic Decapoda, Lophogastrida, and Mysida of the eastern Gulf of Mexico

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**Abstract** The Earth's greatest living space is found in the bathypelagic zone of the oceans (depths >1,000 m), yet little research has been dedicated to these ecosystems. The micronekton of the bathypelagic zone in the eastern Gulf of Mexico (EGOM) was investigated with the goal of comparing its community structure with that of the well-studied mesopelagic micronekton. Herein is described a portion of that community, specifically species belonging to the orders Lophogastrida, Mysida, and Decapoda. A total of 46 species were collected, most of which have broad zoogeographic distributions. Seventeen of the species had not previously been collected above 1,000 m in the same location despite over 20 years of sampling. Compared to the mesopelagic zone, the bathypelagic community showed increased contributions to abundance and estimated biomass from the Oplophoridae and Eucopiidae, with a simultaneous decrease in the importance of the Dendrobranchiata. In addition, the bathypelagic zone was distinguished by a relatively high percentage of individuals that brood their eggs (77% vs. 15% in the mesopelagic zone). The results are interpreted as evidence that the bathypelagic zone contains a distinct pelagic community, with a biology and ecology fundamentally different from that of the mesopelagic zone.

## Introduction

Most of the earth's habitable volume is found in the open ocean, specifically, those areas with a bottom depth of >200 m. The average depth of the ocean is 3,800 m, meaning that about 88% of its volume lies below 1,000 m (Herring 2002). Consequently, the planet's largest ecosystem is that volume of the ocean between 1,000 m and the bottom—the bathypelagic zone. Despite the overwhelming volumetric dominance of the bathypelagic system, little effort has been dedicated to assessing even its most basic features. There are two principal reasons for this. First, most of the oceans' primary production takes place in surface waters; consequently shallow waters support most species of commercial importance. Second, exploration of the bathypelagic zone is logistically difficult and costly.

In contrast, a great deal of research has been dedicated to the oceans' upper 1,000 m. As an example, the mesopelagic zone of the eastern Gulf of Mexico (EGOM), which is ecologically similar to other low-latitude oceanic systems, has been the subject of regular sampling for over 30 years, and as a result, its community structure and trophic relationships are well described. The system supports a total micronekton biomass of 375–450 kg DW km<sup>-2</sup> (Hopkins and Lancraft 1984), and is characterized by the high-diversity typical of low-latitude oceanic systems. The community contains over 250 species of fish (Hopkins and Lancraft 1984; Gartner et al. 1987; Sutton and Hopkins 1996a; Hopkins et al. 1997), at least 30 species of decapods (Heffernan and Hopkins 1981; Hopkins et al. 1989; Flock and Hopkins 1992; Hopkins et al. 1994), and at least 47 species of cephalopods (Passarella and Hopkins 1991). Typically, micronektonic species vertically migrate on a diel basis, and diets within the community are planktivorous.

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Although this assemblage largely depends on zooplankton for food, its predation does not appear to have a large impact on that assemblage (Hopkins et al. 1997). Predation among micronekton groups, however, can often be intense (Sutton and Hopkins 1996b; Hopkins et al. 1997). One important result of research within the system is that, despite high diversity and little physical structure, niches are discernable when sufficient environmental factors are considered (Hopkins and Gartner 1992; Hopkins et al. 1994; Hopkins and Sutton 1998).

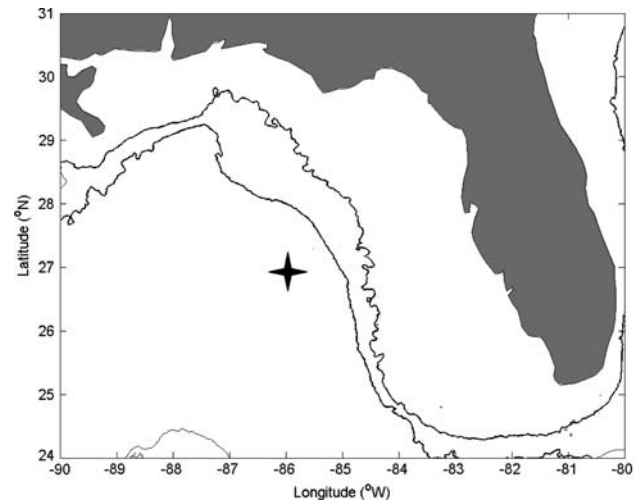
While oceanic mesopelagic systems seem homogenous compared to epipelagic and coastal waters, they are not entirely devoid of structure in that they contain vertical gradients in light, temperature, and food concentration. Below 1,000 m, gradients are less prominent; sunlight is absent, hence the system is far removed from a source of primary production (hydrothermal vents excepted), and there is little variation in temperature. Bathypelagic organisms reside in a unique environment characterized by high pressure and low temperature, low-temporal variability, and diffuse resources. Thus, it is reasonable to expect significantly lower diversity and more weakly defined niches. However, due to the small number of studies centered on the bathypelagic zone, community composition, and energy cycling is poorly understood.

Between 1996 and 2000, a trawling program was conducted to address this deficiency in fundamental information pertaining to the Earth's largest ecosystem by examining the community composition within the bathypelagic zone. The resulting data clearly establish the unique qualities of this extreme environment, and highlight its definition as a distinctive ecosystem. A search of bathypelagic literature indicates that this study is unique in that it treats the species composition, abundance and vertical distribution of micronektonic crustaceans in one comprehensive study.

## Methods

The study site was located in the EGOM within a 30 km radius of 27°N 86°W, a site that has been sampled by the University of South Florida for more than 22 years (Fig. 1). Previous work in the area suggests it may be used as an analog for low-latitude oceanic gyre systems (Hopkins and Gartner 1992; Hopkins et al. 1994), although productivity and standing stock levels are closer to that of oceanic boundary currents (Hopkins 1982; Remsen et al. 2003). All samples were collected between May and September.

Except for one cruise in 1999 (Table 1), samples were collected using an opening/closing rectangular mid-water trawl (Tucker Trawl) with a mouth area of 9 m<sup>2</sup> and 4-mm



**Fig. 1** Location of the study area in the eastern Gulf of Mexico

mesh tapering to a meter net with 1-mm mesh and a closed cod end. The cod end itself was lined with 1-mm mesh netting. The volume of every tow was measured using a General Oceanics flowmeter mounted in the mouth of the net, and some tows also included a nested plankton net (162- $\mu$ m mesh).

Depth of the Tucker Trawl was monitored in real-time during tows using either a MOCNESS depth sensor (1996, 1999, and 2000) or a depth sensor designed specifically for the trawl by the USF Center for Ocean Technology (COT) (Table 1). During the first four cruises, depth was also monitored with a TDR. On cruise P98, a cable failure prevented transmission of electronic data from the COT depth sensor and resulted in the use of a SeaBird CTD with data logging capability to record trawl depth, temperature, and salinity.

Two mechanisms were employed to close the trawl, ensuring discrete depth zone samples. Prior to 1999, trawls were opened and closed using electronic clock timers. The first cruise in 1999 utilized an entire MOCNESS system, while the later cruises in 1999 and 2000 utilized the MOCNESS electronics to open and close the trawl as well as monitor its depth (Table 1). When the clocks were in use, the net was first lowered to the bottom of the desired depth horizon until it opened. At the end of the trawl, the net was held at depth for a minimum of 30 min after the scheduled closing time before being brought to the surface to ensure closure prior to retrieval.

The water column below 1,000 m was divided up into 500-m discrete depth intervals (Table 1), and a majority of the trawls took place entirely within one of these intervals. The depth-monitoring device was utilized to keep the trawl within the targeted depth horizon as it was oscillated up and down during the tow. During the 1999 cruise on which the MOCNESS was used, only the 1,000–1,500-m zone

**Table 1** List of bathypelagic trawl samples with their corresponding depths, gear combinations, and volumes filtered

Cruise number	Trawl number	Depth	Net type	Monitoring system	Closing mechanism	Volume filtered (m <sup>3</sup> )
SC96	5	1,000–1,500	Tucker	MOCNESS	Clock	209,567
SC96	6	1,500–2,000	Tucker	MOCNESS	Clock	318,046
SC96	10	1,000–1,500	Tucker	MOCNESS	Clock	226,002
SC96	11	1,500–2,000	Tucker	MOCNESS	Clock	334,051
SC96 B	4	1,000–1,500	Tucker	MOCNESS	Clock	246,444
SC96 B	5	2,000–2,500	Tucker	MOCNESS	Clock	116,510
SC96 B	9	1,500–2,000	Tucker	MOCNESS	Clock	186,130
SC96 B	16	1,000–2,000	Tucker	MOCNESS	Clock	153,995
SC96 B	18	1,000–1,500	Tucker	MOCNESS	Clock	246,986
SC96 B	22	1,000–1,500	Tucker	MOCNESS	Clock	210,561
SC96 B	23	1,500–2,000	Tucker	MOCNESS	Clock	147,906
SC97	1	1,000–1,500	Tucker	COT depth sensor	Clock	88,087
SC97	2	1,000–1,500	Tucker	COT depth sensor	Clock	141,734
SC97	3	2,000–2,500	Tucker	COT depth sensor	Clock	284,345
SC97	4	1,500–2,000	Tucker	COT depth sensor	Clock	286,463
SC97	5	1,000–1,500	Tucker	COT depth sensor	Clock	184,070
SC97	6	1,000–1,500	Tucker	COT depth sensor	Clock	130,471
SC97	8	2,500–3,000	Tucker	COT depth sensor	Clock	257,020
SC97	9	1,500–2,500	Tucker	COT depth sensor	Clock	116,833
SC97	10	1,500–2,000	Tucker	COT depth sensor	Clock	327,072
SC97 B	2	1,000–1,500	Tucker	COT depth sensor	Clock	200,944
SC97 B	3	1,500–2,000	Tucker	COT depth sensor	Clock	197,664
SC97 B	4	1,500–2,000	Tucker	COT depth sensor	Clock	286,703
SC97 B	5	1,000–1,500	Tucker	COT depth sensor	Clock	249,005
SC97 B	6	1,500–2,000	Tucker	COT depth sensor	Clock	249,575
SC97 B	7	1,000–1,500	Tucker	COT depth sensor	Clock	338,579
SC97 B	9	1,500–2,000	Tucker	COT depth sensor	Clock	91,723
SC97 B	10	1,500–2,000	Tucker	COT depth sensor	Clock	387,644
P98	7	1,500–2,000	Tucker	Seabird	Clock	214,364
P98	11	1,500–2,000	Tucker	Seabird	Clock	360,292
P98	15	1,500–2,000	Tucker	Seabird	Clock	403,233
P98	20	2,000–3,000	Tucker	Seabird	Clock	378,280
P98	23	2,000–3,000	Tucker	Seabird	Clock	364,327
P98	30	1,000–2,000	Tucker	Seabird	Clock	167,914
SC98	1	1,000–1,500	Tucker	COT depth sensor	Clock	320,216
SC98	4	2,000–2,500	Tucker	COT depth sensor	Clock	271,974
SC98	9	1,500–2,000	Tucker	COT depth sensor	Clock	251,153
SC98	11	1,000–1,500	Tucker	COT depth sensor	Clock	363,321
SC98	15	1,500–2,000	Tucker	COT depth sensor	Clock	347,300
SC98	18	1,500–2,000	Tucker	COT depth sensor	Clock	360,232
SC98	21	1,000–1,500	Tucker	COT depth sensor	Clock	109,114
P99	2	1,000–1,500	MOCNESS	MOCNESS	Stepping motor	63,758
P99	12	1,000–1,500	MOCNESS	MOCNESS	Stepping motor	180,210
P99	17	1,000–1,500	MOCNESS	MOCNESS	Stepping motor	269,987
P99	21	1,000–1,500	MOCNESS	MOCNESS	Stepping motor	233,026
SC99	3	2,000–2,500	Tucker	MOCNESS	Stepping motor	108,165

was sampled, but was divided into 100-m intervals. Those smaller intervals were pooled for analysis. Thus, all trawls from that cruise were simply labeled as 1,000–1,500-m tows. Overall, the majority of sampling took place in the upper bathypelagic zone, with 20 tows sampling the 1,000–1,500-m and 16 sampling the 1,500–2,000-m depth horizons (Table 1). Seven tows successfully sampled depth intervals below 2,000 m, and for the purposes of analysis, these were grouped together and categorized as >2,000-m trawls. In addition, three trawls successfully opened and closed within the bathypelagic zone, but did not remain within one of the 500-m depth horizons, or below 2,000 m (for example, trawl SC97 09 fished between 1,500 and 2,500 m).

All organisms were counted, identified to lowest possible taxonomic level (usually species), and measured. Species that had not previously been recorded below 700 m in the EGOM were considered contaminants, and excluded from analysis. There were two probable sources of sample contamination. First, the closing mechanism may have failed to operate before the net rose above 1,000 m, however as stated above, retrieval of the net did not begin until at least 30 min after the scheduled closing time. Nets observed to be even partially open upon arrival at the surface were not counted as discrete depth tows, and therefore not included in the results, however, error resulting from a tow in which the net hung open temporarily (but closed completely before reaching the surface) would not have been detected. The second possible source of contamination is the net drifting above 1,000 m for a significant period of time while open. The ability to monitor the depth of the net in real time minimized such error, and tows, which strayed above 1,000 m for a significant period of time were discarded.

Due to the rare nature of many of the specimens, dry weight was estimated rather than measured using relationships between length and weight established from congeners or confamilials in the mesopelagic zone (Torres and Donnelly, unpublished; Hopkins, unpublished). Whenever possible, these regressions were generated using data obtained from non-preserved material (Torres and Donnelly, unpublished). Dry weights were obtained by adjusting for water content reported for the closest possible taxonomic group (Childress and Nygaard 1974; Donnelly and Torres 1988).

Mesopelagic data used as a basis of comparison was obtained from previous work conducted in the EGOM at the same location as the present study. Those results were presented previously in several papers that summarize the results of over 300 trawls taken between the years 1972 and 1990 (Heffernan and Hopkins 1981; Hopkins and Lancraft 1984; Hopkins et al. 1989; Flock and Hopkins 1992; Hopkins et al. 1994). Although access to only summary data from the mesopelagic zone prevented rigorous statis-

tical comparison between the two data sets, the descriptive comparisons were strengthened by the identical geographical location and the nearly identical gear employed in both zones (rectangular mid-water trawls equipped with the same mesh sizes). Both mesopelagic and bathypelagic data sets were compiled over a period of several years, decreasing the probability that interannual variability affected the conclusions drawn.

## Results

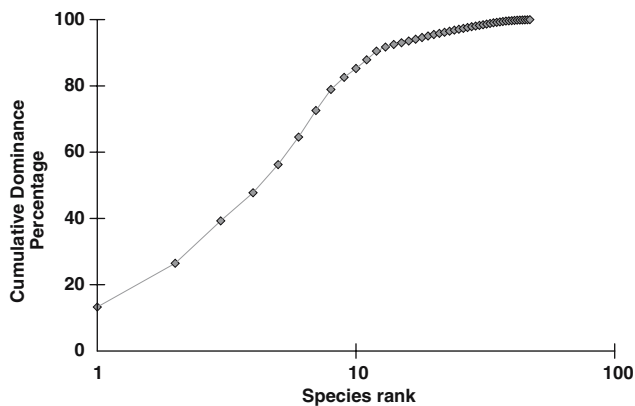
### Sample contamination

The total abundance of all species deemed to be mesopelagic contaminants amounted to 1.3% of the total number collected. The two species most clearly satisfying the criteria were *Pasiphaea merriami* (two individuals), and *Parapandalis richardi* (five individuals) (Hopkins et al. 1989). *Gennadas scutatus* and *G. talismani* were also classified as contaminants (see Heffernan and Hopkins 1981), and both were present in very low numbers (six specimens in four samples between the two of them). The largest source of contamination (25 individuals) was due to individuals of *Sergestes* (Heffernan and Hopkins 1981; Flock and Hopkins 1992).

### Crustacean faunal composition

This paper deals only with the three dominant crustacean orders in our catches: Lophogastrida, Mysida, and Decapoda (following Martin and Davis 2001). Other crustacean groups, namely euphausiids and amphipods, were encountered in very low numbers (34 and 38 total individuals, respectively) and with very few exceptions were too small to be considered micronekton (<2 cm TL). The total abundance of euphausiids and amphipods combined was 1% that of all other crustacean groups. In total, we collected 46 species from six different families. Figure 2 shows that all but the rarest species were collected, indicating the assemblage was sufficiently sampled for characterization. Included among the species was *Pseudochalaraspidium hanseni*, a species previously reported only in the Pacific Ocean (Richter 2003), and thus a new record for the Atlantic basin.

The most speciose family was the Oplophoridae with 23 different species identified among the samples. Oplophorids were commonly encountered, with every tow containing at least one individual. Thirteen different species had sample-occurrence rates >10% (Table 2), three of which were encountered in at least half of the samples: *Hymenodora glacialis* (89.1%), *Acanthephyra stylostratis* (73.9%), and *Acanthephyra curtirostris* (56.5%). *H. glacialis*



**Fig. 2** Species dominance plot of bathypelagic crustacean micronekton in the eastern Gulf of Mexico

was absent from only five tows and was the most commonly encountered species overall.

Representatives of the Oplophoridae accounted for about one quarter of the individuals collected. Two oplophorids, *A. stylostratis* (24,600 individuals  $\text{km}^{-3}$ ) and *H. glacialis* (25,800 individuals  $\text{km}^{-3}$ ), were found in numbers  $>20,000$  individuals  $\text{km}^{-3}$  (Table 2). Six oplophorids were among the 20 most abundant shrimp taxa overall: *H. glacialis* (4th), *A. stylostratis* (7th), *A. curtirostris* (10th), *Hymenodora gracilis* (12th), *Acanthephyra gracilipes* (15th), and *Acanthephyra purpurea* (17th), although 16 of the 24 species within the family were represented by ten or fewer specimens.

Benthescymidae, with five species, was the second most speciose family. *Bentheogennema intermedia* occurred in 69.6% of the tows, and was the most commonly encountered species within the family. *Gennadas valens* also occurred in more than half the samples (54.3%). The third most commonly encountered member of the family was *Gennadas capensis* (39.1% of samples). *Gennadas bouvieri* was found in more than 10% of the samples, but generally as solitary individuals, resulting in its low abundance.

Together, benthescymids accounted for 18.8% of the total numbers. The most abundant member of the family was *B. intermedia* which, at an average of 25,800 individuals  $\text{km}^{-3}$ , was the fifth most abundant crustacean overall. None of the other benthescymids were present in numbers  $>20,000$  individuals  $\text{km}^{-3}$ , although *G. valens* (19,400 individuals  $\text{km}^{-3}$ ), the eighth most abundant overall, was nearly so.

Five species of *Sergia* were positively identified, the most common being *Sergia splendens*, occurring in 39.1% of the samples. All other species of *Sergia* had sample occurrence rates of  $<15\%$ . The Sergestidae accounted for 6.2% of the total numbers, and with the exception of *S. splendens*, which had an abundance of 11,200 individuals  $\text{km}^{-3}$  (ninth most abundant species overall), all species

had abundances  $<10,000$  individuals  $\text{km}^{-3}$ . The second most abundant taxon within the family was unidentified individuals of the genus *Sergia* that were either immature or too damaged to be identified to species.

The four species within the Eucopiidae were among the most commonly collected organisms. Only three trawls contained none, and all occurred in at least half of the samples. The two most frequently collected species within the family were *Eucopeia australis* (87.0%) and *Eucopeia sculpticauda* (84.8%). Only the oplophorid *H. glacialis* was collected with greater frequency. In addition, *E. grimaldii* (67.4% of samples) was the sixth most commonly encountered species and *Eucopeia unguiculata* (50.0% of the samples) was the ninth most common.

In addition to being commonly encountered, the eucopiids were the most abundant family, collectively accounting for 46.2% of the total numbers. All four species were among the ten most abundant. *E. sculpticauda*, *E. australis*, and *E. grimaldii* were all present in numbers  $>30,000$  individuals  $\text{km}^{-3}$ , while *E. unguiculata* occurred at 25,300 individuals  $\text{km}^{-3}$ . The four species were the first, second, third, and sixth most abundant, respectively.

The families Mysidae, Pasiphaeidae, and Bresiliidae provided small contributions to the catch, combining to add four taxa to the list (Table 2). While two taxa, *Boreomysis* spp. and *Lucaya bigelowi*, were encountered in more than 20% of the trawls, all of the members of these families were present in numbers  $<2,000$  individuals  $\text{km}^{-3}$ .

#### Estimated shrimp biomass

The entire assemblage totaled an estimated 60 kg DW  $\text{km}^{-3}$ . Oplophorids accounted for over half (59.6%) of the biomass, although they comprised only about a quarter of the numbers. Among the more prominent species, 6 of the top 10, and 12 of the top 20 contributors belonged to this family. Despite the collection of only eight specimens, *Acanthephyra acutifrons* had the highest estimated biomass (Table 2), accounting for 15.6% of the total. Similarly, *Ephyrina benedicti*, *E. ombango*, *A. acanthitelsonis*, and *Notostomus gibbosus*, while collected in very low numbers (7, 14, 10, and 14 specimens, respectively), contributed disproportionately due to their large size.

The family Benthescymidae, with a combined 18% of the total, was estimated to have the second largest biomass and had three species among the top 20 contributors. This was principally due to *B. intermedia*, which had the second highest biomass of all species (7.4 kg DW  $\text{km}^{-3}$ ), and accounted for 12.6% of the total (Table 2). The other two species among the top 20 included *G. valens*, which accounted for 3.4% of the total, and *G. capensis* (1.4%).

The four species of *Eucopeia* combined for 13.1% of estimated biomass with the largest contribution being that



**Table 2** Taxonomic roster of micronektonic crustaceans collected from the bathypelagic zone of the eastern Gulf of Mexico listed in order of abundance

	% Occurrence in samples	Individuals km <sup>-3</sup>	% of numbers	kg DW km <sup>-3</sup>	% of estimated biomass
<i>Eucopia sculpticauda</i>	84.8	40,500	12.9	1.6	2.1
<i>Eucopia australis</i>	87.0	40,200	12.8	3.1	5.2
<i>Eucopia grimaldii</i>	67.4	39,100	12.4	1.9	3.1
<i>Bentheogennema intermedia</i>	69.6	25,800	8.2	7.4	12.6
<i>Hymenodora glacialis</i>	89.1	25,800	8.2	2.5	4.2
<i>Eucopia unguiculata</i>	50.0	25,300	8.1	1.2	2.0
<i>Acanthephyra stylostratis</i>	73.9	24,600	7.8	3.3	5.6
<i>Gennadas valens</i>	54.3	19,400	6.2	2.1	3.4
<i>Sergia splendens</i>	39.1	11,200	3.6	0.8	1.3
<i>Acanthephyra curtirostris</i>	56.5	8,200	2.6	3.5	5.8
<i>Gennadas capensis</i>	39.1	8,000	2.5	0.9	1.4
<i>Hymenodora gracilis</i>	43.5	8,000	2.5	1.0	1.7
<i>Gennadas</i> spp.	28.3	5,100	1.6	0.3	0.4
<i>Acanthephyra gracilipes</i>	37.0	3,700	1.2	0.8	1.4
<i>Sergia</i> spp.	10.9	2,300	0.7	0.6	1.0
<i>Acanthephyra purpurea</i>	21.7	2,300	0.7	0.8	1.4
<i>Boreomysis</i> sp.	23.9	1,700	0.5	<0.1	<0.1
<i>Sergia regalis</i>	10.9	1,600	0.5	0.6	1.0
<i>Sergia wolffi</i>	10.9	1,600	0.5	0.7	1.1
<i>Lucaya bigelowi</i>	21.7	1,600	0.5	<0.1	0.1
<i>Parapasiphaea sulcatifrons</i>	15.2	1,300	0.4	1.0	1.6
<i>Ephyrina ombango</i>	17.4	1,300	0.4	1.2	2.0
<i>Notostomus gibbosus</i>	15.2	1,300	0.4	6.5	11.0
<i>Meningodora mollis</i>	17.4	1,000	0.3	1.1	1.9
<i>Gnathophausia gigas</i>	17.4	900	0.3	0.4	0.7
<i>Acanthephyra acanthitelsonis</i>	15.2	900	0.3	2.5	4.3
<i>Meningodora vesca</i>	21.7	900	0.3	0.3	0.5
<i>Gnathophausia gracilis</i>	13.0	800	0.3	0.2	0.4
<i>Sergia japonica</i>	13.0	800	0.3	0.3	0.5
<i>Systellaspis debilis</i>	8.7	800	0.3	0.2	0.3
<i>Acanthephyra acutifrons</i>	13.0	700	0.2	9.3	15.7
<i>Gnathophausia zoea</i>	10.9	600	0.2	0.1	0.2
<i>Gennadas bouvieri</i>	13.0	600	0.2	<0.1	0.1
<i>Acanthephyra</i> spp.	8.7	600	0.2	0.2	0.3
<i>Ephyrina benedicti</i>	10.9	600	0.2	1.5	2.7
<i>Janicella spinicauda</i>	6.5	600	0.2	<0.1	<0.1
<i>Sergia grandis</i>	8.7	500	0.1	0.2	0.4
<i>Parapasiphaea macrodactyla</i>	10.9	500	0.1	0.1	0.1
<i>Acanthephyra quadrispinosa</i>	6.5	500	0.1	0.3	0.6
<i>Pseudochalaraspidium hanseni</i>	8.7	400	0.1	0.1	0.1
<i>Systellaspis braueri</i>	6.5	300	0.1	0.3	0.5
<i>Systellaspis pellucida</i>	6.5	300	0.1	<0.1	<0.1
<i>Acanthephyra pelagica</i>	4.3	200	0.1	0.1	0.1
<i>Gnathophausia ingens</i>	2.2	<100	<0.1	0.2	0.3
<i>Acanthephyra exima</i>	2.2	<100	<0.1	<0.1	<0.1
<i>Meningodora marptocheles</i>	2.2	<100	<0.1	<0.1	<0.1
<i>Meningodora miccylla</i>	2.2	<100	<0.1	<0.1	<0.1
<i>Systellaspis cristata</i>	2.2	<100	<0.1	<0.1	<0.1

of *E. australis* (5.2%), which had the sixth highest biomass among all species. The other three species from the family (*E. grimaldii*, *E. sculpticauda*, and *E. unguiculata*) had the 10th, 11th, and 13th highest totals, reflecting their similar size and abundance.

Sergestids were the only remaining family to comprise over 5% of the total estimated biomass (5.2%). The largest contribution came from *S. splendens* (0.8 kg DW km<sup>-3</sup>; 1.3% of total), while *S. regalis*, *S. wolffi*, and unidentified members of *Sergia* all accounted for ~1%. The remaining two species, *S. grandis* and *S. japonica* had very low estimated totals.

Two families, Lophogastridae and Pasiphaeidae, made similar contributions to the estimated biomass of the assemblage (1.8 and 1.7%, respectively), and between them, only the pasiphaeid *Parapasiphaea sulcatifrons* was among the top 20 species. The largest contributor from the Lophogastridae was *Gnathophausia gigas*, which had an estimated biomass of 0.4 kg DW km<sup>-3</sup> (0.7% of the total). The remaining two families, Mysidae and Bresiliidae, contributed little to the assemblage biomass (each amounting to 0.1% or less).

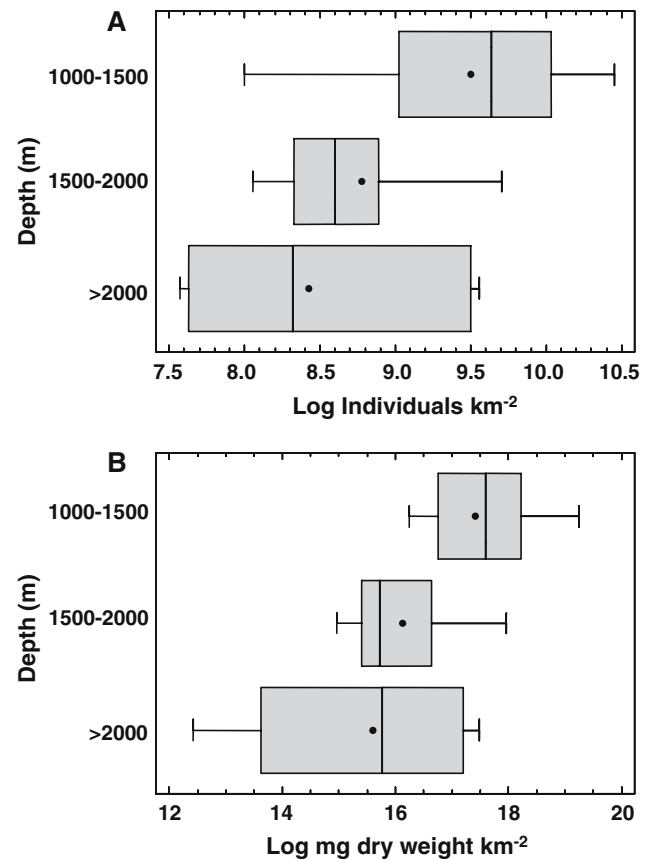
#### Vertical distribution

For statistical comparison, all tows were divided into three depth categories: 1,000–1,500, 1,500–2,000, and >2,000 m. The three tows whose depths did not fit into one of these three categories were discarded. Considering the total assemblage, according to Fisher's LSD procedure, log transformed abundance was highest in the 1,000–1,500-m depth zone (Fig. 3a) as was estimated biomass (Fig. 3b). An identical procedure was applied individually to the abundance of each species numbering >2,000 individuals km<sup>-3</sup>. About 5 of the 14 did not show significant trends in abundance with depth (Table 3), although for one, *G. capensis*, there was a significant trend at the *P*-0.1 level (*P* = 0.0608) in which abundance was highest in the 1,000–1,500-m depth zone. Only one of the ten most abundant species, *H. glacialis*, displayed no significant trend in depth distribution. For six of the nine species that did show significant trends, abundance was highest in the 1,000–1,500-m depth zone, while no difference was evident between the lower two zones. In the remaining three cases, no differences were discerned between the shallowest and deepest depth zones.

## Discussion

#### Biomass estimates

The high-estimated biomass contributions of some species with low-abundances implied that energy processing



**Fig. 3** Vertical distribution of abundance (a) and estimated biomass (b) of bathypelagic crustacean micronekton in the eastern Gulf of Mexico

through a small number of large micronektonic individuals may be important in the bathypelagic zone. Numerically important species, such as those in the genera *Eucopia* and *Hymenodora*, were still significant contributors in terms of biomass (and thus energy cycling), but less so than their abundance would indicate.

Relationships between size and biomass were derived using data collected from mesopelagic shrimp in the EGOM (Torres et al. unpublished). In the EGOM, the trend is for water content of crustaceans to increase with increasing minimum depth of occurrence (MDO) (Donnelly et al. 1993). For example, the water content of *A. purpurea* (MDO 300 m) averages 73.6%, while that of *A. acutifrons* (MDO 800 m) averages 85.2%. According to the same work, the migratory behavior of the species in question also has an effect on water content, evidenced by the lower water content of migratory compared to that of non-migratory species (73.1 ± 3.8% vs. 82.0 ± 7.9%, respectively). Consequently, even within a given genus, the variation in relationships between carapace length and dry weight can be considerable and the application of equations arrived at from mesopelagic migrating shrimp species will

**Table 3** Vertical distribution results for the 14 most abundant species of bathypelagic crustaceans using Fisher's LSD procedure

Species	1,000–1,500 and 1,500–2,000	1,000–1,500 and >2,000	1,500–2,000 and >2,000
<i>Eucopia sculpticauda</i>	X	X	NS
<i>Eucopia australis</i>	X	X	NS
<i>Eucopia grimaldii</i>	X	NS	NS
<i>Eucopia unguiculata</i>	X	X	NS
<i>Hymenodora glacialis</i>	NS	NS	NS
<i>Bentheogennema intermedia</i>	X	X	NS
<i>Acantheephyra stylostratis</i>	X	X	NS
<i>Gennadas valens</i>	X	NS	NS
<i>Sergia splendens</i>	X	X	NS
<i>Acantheephyra curtirostris</i>	X	NS	NS
<i>Gennadas capensis</i>	NS	NS	NS
<i>Hymenodora gracilis</i>	NS	NS	NS
<i>Acantheephyra gracilipes</i>	NS	NS	NS
<i>Acantheephyra purpurea</i>	NS	NS	NS

NS indicates no significant difference

X—indicates a significant difference ( $P < 0.05$ )

invariably lead to an overestimate of biomass for bathypelagic, non-migrators such as *B. intermedia*, *Hymenodora* spp., *Notostomus* spp., and some species of *Acantheephyra*. The problem may be greatest in the Ophlophoridae as the same equation was applied across several genera. However, biomass for all species of shrimp was calculated in the same manner and thus, downward adjustments would include virtually all species to some degree, including those that are smaller and more numerous. Thus, while the absolute values of biomass may vary depending on the method used, the conclusion that relatively small numbers of large organisms are important to energy cycling in the bathypelagic zone would remain unaltered.

#### Comparison between the mesopelagic and bathypelagic communities

The division between mesopelagic and bathypelagic zones in the ocean is based mainly on light attenuation (Herring 2002), but little evidence has been advanced regarding the ecological validity of this boundary. Recently, there has been some effort devoted to resolving this, although it has tended to focus on plankton, particularly copepods (Yamaguchi et al. 2002, 2004, 2005). Collectively, those studies have found significant changes with depth in community composition, chemical composition, and ontogenetic vertical migration patterns. In an extensive review on the vertical distribution of plankton, Vinogradov (1997) suggested that, while not representing a firm ecological border, the boundary has some significance at lower latitudes where vertical stratification is more evident. Childress et al. (1980) compared life history strategies among fishes living in different depth zones and found deep-living, non-migratory species were different. Due to

the large body of work published on the EGOM mesopelagic ecosystem, a direct comparison between the two zones at this location is possible. Again, while access to only summary data precludes rigorous statistical comparison, there is enough information to establish patterns.

To begin, there is overlap in the fauna of both zones. For example, four species, *G. valens*, *S. splendens*, *E. sculpticauda*, and *E. unguiculata*, ranked among the ten most numerous in both zones. Further, six species were among the 20 highest biomass contributors to both assemblages: *A. curtirostris*, *G. valens*, *E. sculpticauda*, *E. unguiculata*, *G. capensis*, and *A. purpurea*. Finally, of the 67 species found in the EGOM, almost half have distributions that span the 1,000-m isobath. As mentioned above, several of those species were prominent in both sets of samples, indicating that the distributions of several important micronektonic crustacean species have vertical distributions that are best characterized as deep meso- to bathypelagic.

Other authors have reported species distributions including both depth zones. Foxton (1970) found that some large males and large ovigerous females of *A. purpurea* reside below 1,000 m during the day, and move above this depth at night. Vereshchaka (1994) and Donaldson (1975) similarly found that some species of *Sergia* migrate from the bathypelagic zone to the mesopelagic zone on a diel basis, while others had broad distributions including both zones. Thus, the delineation between mesopelagic and bathypelagic is often not absolute, however, there are several obvious differences between the two assemblages.

In the EGOM, crustacean groups examined were much more numerous above than below 1,000 m. In the mesopelagic zone, shrimps totaled  $3.1 \times 10^6$  individuals  $\text{km}^{-2}$  (Hopkins et al. 1994), while in the bathypelagic zone there were  $1.5 \times 10^5$  individuals  $\text{km}^{-2}$ . However, of the 67 total

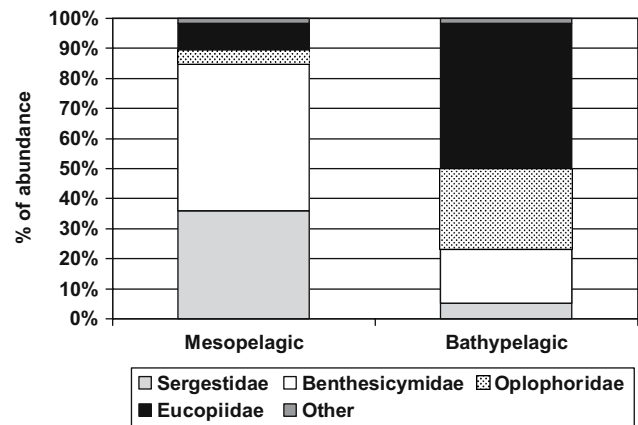


species reported from the area, 28 have a greater abundance below 1,000 m than above it. In 17 of the 28 taxa, the species belong to the Oplophoridae. Another key difference was 17 species found in the present study were not collected in the mesopelagic zone despite years of sampling. Those included four of the nine lophogastrids (Lophogastridae and Eucopiidae), as well as *Boreomysis sp.* Also, three of the 17, *A. gracilipes*, and both species of *Hymenodora*, were present in numbers >2,000 individuals km<sup>-3</sup>. The bathypelagic samples added ten species of oplophorids to the list of those reported in the EGOM, as well as the new record for *P. hanseni* in the Atlantic.

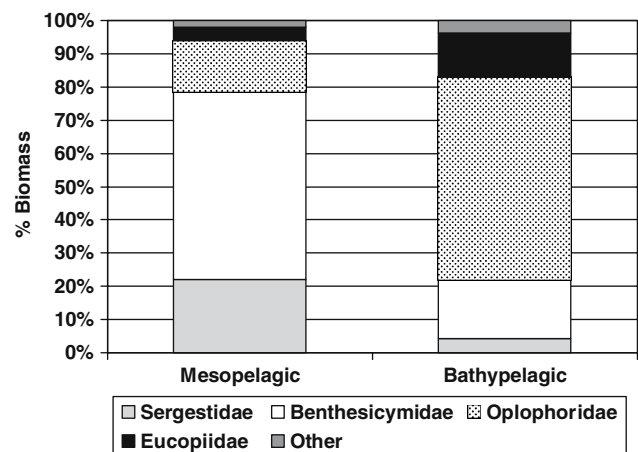
There were also obvious changes in the dominant organisms within families, most prominently in the Benthescycymidae and Oplophoridae. Above 1,000 m, *G. valens* was clearly not only the dominant benthescycymid, but the dominant shrimp in the EGOM. This single species accounted for almost 50% of the micronektonic crustacean biomass, and nearly equaled that of the entire family Myctophidae (Hopkins et al. 1994). While *G. valens* was still present in high numbers below 1,000 m, its abundance decreased by more than two orders of magnitude. Conversely, *B. intermedia*, present in very low numbers above 1,000 m, became the most abundant benthescycymid (more than three times as numerous as *G. valens*) and, along with *H. glacialis*, ranked fourth in abundance (Table 2). Within the Oplophoridae the three most abundant mesopelagic species were *Systellaspis debilis*, *A. purpurea*, and *A. curtirostris* while below 1,000 m the numerical dominants were *H. glacialis*, *A. curtirostris*, and *A. stylostratis*.

The difference in assemblage composition was further highlighted when the contribution of each species to overall abundance was considered. In the mesopelagic zone, six species contributed 5% or more to total numbers (*Sergestes pectinatus*, *S. splendens*, *G. valens*, *G. capensis*, and *E. unguiculata*) while below 1,000 m, the number increased to eight (*B. intermedia*, *G. valens*, *A. stylostratis*, *H. glacialis*, *E. australis*, *E. grimaldii*, *E. sculpticauda*, and *E. unguiculata*). The similarity in gear used to sample both zones allowed for diversity comparisons, and showed a somewhat higher measure of species evenness in the bathypelagic zone ( $J'$  0.6179 vs. 0.7094). A matching trend was observed for biomass, with four species contributing more than 5% above 1,000 m and six species contributing more than 5% below 1,000 m.

Perhaps the most obvious difference between the two zones is the sharp contrast in abundance and biomass contributions considered at the family level. The composition of the mesopelagic shrimp assemblage in the EGOM was dominated by the Benthescycymidae (due mainly to *G. valens*) and Sergestidae (Figs. 4, 5), with the two families accounting for about 85% of the individuals and 78% of the biomass. In contrast, the Eucopiidae and Oplophoridae



**Fig. 4** Relative abundance of micronektonic crustacean families between the mesopelagic and bathypelagic zones in the eastern Gulf of Mexico



**Fig. 5** Relative biomass of micronektonic crustacean families between the mesopelagic and bathypelagic zones in the eastern Gulf of Mexico

were the most numerous bathypelagic families (72.6% combined—Fig. 4), while the Oplophoridae and Benthescycymidae were the two highest contributors of estimated biomass (77.5% combined—Fig. 5). While benthescycymids were still important below 1,000 m, their estimated biomass fraction decreased from 56 to 17.9%. At the same time, the biomass contribution of the Eucopiidae increased from an estimated 4 to 13.1%. Between the mesopelagic and bathypelagic zones, then, the dominant families change from Benthescycymidae and Sergestidae, to the Oplophoridae and Eucopiidae.

The shifts in faunal structure illustrate the distinctive nature of the two assemblages, and indicate fundamental biological differences between the two communities. Above 1,000 m, 85% of the numbers and 79% of the biomass was due to species that broadcast their eggs

(Sergestidae and Benthescycymidae), while this was true for only 23% of the numbers and 22% of the biomass in the bathypelagic zone. Furthermore, the majority of the numbers and biomass of broadcast spawners in the bathypelagic zone were accounted for by only three species: *S. splendens*, *G. valens*, and *B. intermedia* (18.0% of the numbers, 17.3% of the estimated biomass). Of these three species, *S. splendens* and *G. valens* were also prominent members of the mesopelagic community and are strong diel vertical migrators, leaving *B. intermedia* as the only characteristic bathypelagic inhabitant to broadcast its eggs. The increased prominence of carideans and lophogastrids indicates that the primary reproductive strategy among bathypelagic species is the brooding of eggs (Omori 1974; Mauchline 1980), and may often include semelparity (Childress and Price 1978). There appears to be a similar trend in the eastern Pacific as Krygier and Pearcy (1981) found none of the dendrobranchiate shrimp species had distribution centers below 1,000 m, while several carideans did. Likewise, Walters (1976) found that, among the penaeids, only *Petalidium suspiciosum* had significant fraction of the population below 1,000 m. Among bathypelagic crustaceans then, there is an apparent shift away from “income” breeding toward “capital” breeding (Stearns 1992).

The prevalence of brooders in the bathypelagic zone is likely related to distance from productive surface waters. Dendrobranchiate shrimp hatch as nauplii and develop in epipelagic waters (Omori 1974). Eggs and early developmental stages are thus constrained to develop in shallow waters where they are exposed to predators and a patchy food supply for an extended period of time. Species that brood fewer but larger eggs hypothetically reduce risk to younger stages (Mauchline 1972; Bauer 2004) since the young of such species hatch at a later stage of development (Aizawa 1974; Bauer 2004). As Omori (1974) states, this abbreviated larval development, “...imparts to the larvae greater independence of possible food shortages, greater swimming and feeding abilities, and greater safety from predators.” The lophogastrids and mysids provide an even more extreme example in that they eliminate larval stages entirely by hatching as juveniles (Mauchline 1980). Based on the assemblage composition then, from the time of hatching, the young of bathypelagic crustaceans are closer (developmentally and spatially) to joining the adult population.

#### Zoogeographic comparisons

Little study has been dedicated to descriptions of the bathypelagic fauna, making comparisons with other areas difficult; however, there is a handful of other papers available addressing species composition. Two studies (Fasham and Foxton 1979; Hargreaves 1985) used principal

component analysis to identify faunal groups in the eastern North Atlantic, and both were able to identify distinct species groups with bathypelagic distributions. Hargreaves (1985) found a faunal break at 1,000 m that appeared in decapods, euphausiids, and mysids. Below 1,000 m, the numerically dominant decapods were the oplophorids *H. gracilis* and *H. glacialis*, while the most numerous lophogastrids were *E. unguiculata*, *E. grimaldii*, *E. australis*, *Gnathophausia* spp., and *Boreomysis* spp. Species with bathypelagic centers of distribution included: *Acanthephyra pelagica*, *H. gracilis*, *H. glacialis*, *Sergia japonicus*, *Ephyrina bifida*, *B. intermedia*, *Systellaspis braueri*, *E. grimaldii*, *E. sculpticauda*, *E. australis*, *Boreomysis microps*, *B. incisa*, *B. acuminata*, and *G. gigas*. The division between meso- and bathypelagic found by Fasham and Foxton (1979) was less clear. Looking at only decapods, they identified a total of fourteen faunal groups, three of which were centered below 1,000 m. The species comprising these groups were *A. prionota*, *A. curtirostris*, *A. acutifrons*, *Physetocaris micropthalma*, *Meningodora miccylla*, *E. bifida*, *H. gracilis*, *S. braueri*, *A. stylostratis*, *Petalidium obesum*, *B. intermedia*, and *Sergestes submaximus*.

Donaldson's (1975) examination of the sergestids in the western Atlantic included some sampling within the upper bathypelagic zone. As in both the meso- and bathypelagic zones in the EGOM, *S. splendens* was found to be the most abundant species. In addition, several species had vertical distributions that extended below 1,000 m, including some found in our samples: *S. splendens*, *S. japonica*, and *S. grandis*. Of the species reported, *S. japonica* had the deepest vertical distribution.

In the eastern Pacific, Krygier and Pearcy (1981) found 29 species of decapods (Dendrobranchiata and Caridea) down to depths of 2,400 m. The assemblage was dominated by *Sergestes similis*, a species with a mesopelagic distribution that made up 94% of the shrimp collected, while below 1,000 m the most prevalent species were *Hymenodora frontalis* and *H. gracilis*. Only five of their 29 species had bathypelagic centers of distribution. These included *Parapasiphaea cristata*, *H. gracilis*, *H. glacialis*, *H. acanthitelsonis*, *S. braueri*, and *Acanthephyra* sp. (an unknown species). Among the lophogastrids in the same area, *Eucopia* was reported as being “the most abundant meso- to bathypelagic mysid in all the oceans,” (Krygier and Murano 1988), and both *E. sculpticauda* and *E. australis* were reported as having a deep meso- to bathypelagic distribution. It should be noted they considered it possible that *E. australis*, *E. unguiculata*, *E. grimaldii*, and *E. hanseni* were part of a single species complex, and they therefore referred to all of them collectively as the “*E. australis* complex,” a practice that has not been followed here.

**Table 4** Oceanic distributions of bathypelagic crustacean species found in the eastern Gulf of Mexico

	Atlantic	Pacific	Indian	Antarctic	Source
<b>Lophogastridae</b>					
<i>Gnathophausia gigas</i>	X	X	X	X	Müller (1993)
<i>Gnathophausia gracilis</i>	X	X	X		Müller (1993)
<i>Gnathophausia ingens</i>	X	X	X		Müller (1993)
<i>Gnathophausia zoea</i>	X	X	X		Müller (1993)
<i>Pseudochalaraspidium hanseni</i>		X			Richter (2003)
<b>Eucopiidae</b>					
<i>Eucopia australis</i>	X	X	X	X	Müller (1993)
<i>Eucopia grimaldii</i>	X	X	X	X	Müller (1993)
<i>Eucopia sculpticauda</i>	X	X	X	X	Müller (1993)
<i>Eucopia unguiculata</i>	X	X	X	X	Müller (1993)
<b>Benthesicytidae</b>					
<i>Bentheogennema intermedia</i>	X	X	X		Pérez Farfante and Kensley (1997)
<i>Gennadas bouvieri</i>	X	X	X		Pérez Farfante and Kensley (1997)
<i>Gennadas capensis</i>	X	X	X		Pérez Farfante and Kensley (1997)
<i>Gennadas scutatus</i>	X	X	X		Pérez Farfante and Kensley (1997)
<i>Gennadas talismani</i>	X				Pérez Farfante and Kensley (1997)
<i>Gennadas valens</i>	X				Pérez Farfante and Kensley (1997)
<b>Sergestidae</b>					
<i>Sergia grandis</i>	X		X		Pérez Farfante and Kensley (1997), Vereshchaka (1994)
<i>Sergia japonica</i>	X	X	X		Pérez Farfante and Kensley (1997), Vereshchaka (1994)
<i>Sergia regalis</i>	X	X	X		Pérez Farfante and Kensley (1997), Vereshchaka (1994)
<i>Sergia splendens</i>	X				Pérez Farfante and Kensley (1997), Vereshchaka (1994)
<i>Sergia wolffi</i>	X				Pérez Farfante and Kensley (1997), Vereshchaka (1994)
<b>Pasiphaeidae</b>					
<i>Parapasiphaea sulcatifrons</i>	X	X	X		Krygier and Percy (1981), Iwasaki and Nemoto (1987), Wasmer (1993)
<b>Oplophoridae</b>					
<i>Acanthephyra acanthitelsonis</i>	X				Chace (1986)
<i>Acanthephyra acutifrons</i>	X	X	X		Chace (1986), Krygier and Wasmer (1988)
<i>Acanthephyra curtirostris</i>	X	X	X		Chace (1986), Krygier and Wasmer (1988)
<i>Acanthephyra exima</i>	X	X	X		Chace (1986), Krygier and Wasmer (1988)
<i>Acanthephyra gracilipes</i>	X				Chace (1986), Krygier and Wasmer (1988)
<i>Acanthephyra pelagica</i>	X	X	X	X	Chace (1986), Iwasaki and Nemoto (1987), Wasmer (1993)
<i>Acanthephyra purpurea</i>	X				Chace (1986)
<i>Acanthephyra quadrispinosa</i>	X	X	X		Chace (1986), Iwasaki and Nemoto (1987)
<i>Acanthephyra stylostratis</i>	X	X	X?		Chace (1986)
<i>Ephyrina benedicti</i>		X	X		Chace (1986), Krygier and Wasmer (1988)
<i>Ephyrina ombango</i>	X	X	X		Chace (1986)
<i>Hymenodora glacialis</i>	X	X	X	X	Chace (1986), Wasmer (1993)
<i>Hymenodora gracilis</i>	X	X	X	X	Chace (1986), Wasmer (1993)
<i>Janicella spinicauda</i>	X	X	X		Chace (1986)
<i>Meningodora marptocheles</i>	X	X			Chace (1986)
<i>Meningodora miccyla</i>	X				Chace (1986)
<i>Meningodora mollis</i>	X	X	X		Chace (1986), Krygier and Wasmer (1988)
<i>Meningodora vesca</i>	X	X	X		Chace (1986), Krygier and Wasmer (1988)
<i>Notostomus gibbosus</i>	X	X	X		Chace (1986), Krygier and Wasmer (1988)
<i>Systemaspis braueri</i>	X	X	X		Chace (1986), Krygier and Wasmer (1988)

**Table 4** continued

	Atlantic	Pacific	Indian	Antarctic	Source
<i>Stellaspis cristata</i>	X	X	X		Chace (1986), Krygier and Wasmer (1988)
<i>Stellaspis debilis</i>	X	X	X		Chace (1986), Iwasaki and Nemoto (1987), Wasmer (1993)
<i>Stellaspis pellucida</i>	X	X	X		Chace (1986)

A majority of the species collected in this study have been reported in more than one ocean basin (Table 4). Of the ten most abundant shrimp species found in this study, only two, *G. valens* and *S. splendens*, are restricted to the Atlantic. In addition, only 8 of the 44 species for which zoogeographical data are available are thus far found to be restricted to the Atlantic. Many species have distributions that could be considered as pantropical/subtropical, and a few appear to be distributed globally (Table 4). Chace (1986) discussed ranges of the oplophorids and found several species ranged from tropical to subtropical areas of the Indian, Pacific, and Atlantic Oceans, including several species found to be numerous in the EGOM such as *A. curtirostris*, *H. glacialis*, *H. gracilis*, and *A. acutifrons*. According to Müller (1993), the distributions of all four species of *Eucopeia* from this study are nearly pan-global, as are those of all four species of *Gnathophausia*. Although direct comparisons between different regions are hindered by the scarcity of bathypelagic studies, it is clear that most of the bathypelagic shrimp species found in the EGOM have broad geographic distributions limited primarily by latitude.

## Conclusion

This study of the bathypelagic crustacean assemblage revealed some commonality between the species present in the mesopelagic and bathypelagic zones in the EGOM. Almost half of the species identified were found in both environments, including some species, such as *G. valens*, *E. unguiculata*, *E. sculpticauda*, and *S. splendens*, that are prominent in both zones. Our data indicate there is no abrupt faunal transition between the two zones. However, based on the following evidence, viewing the two zones as separate faunal assemblages is useful and valid:

1. There were obvious shifts in the relative abundances of species in each zone. Some numerous bathypelagic species, such as *B. intermedia*, *A. stylorostris*, *H. glacialis*, *H. gracilis*, and *E. grimaldii* were either absent from the mesopelagic assemblage, or present only in low numbers.
2. There was a high percentage of species whose vertical distributions were restricted to the bathypelagic zone (~35%).

3. Important differences in assemblage composition occurred at the family level, implying biological differences between the communities. An important example was a reduced contribution by those species that disperse their eggs (Dendrobranchiata) in favor of those that brood them (Caridea, Lophogastrida, and Mysida).

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