

Structure and trophic ecology of a low latitude midwater decapod and mysid assemblage

Thomas L. Hopkins¹, Mark E. Flock², John V. Gartner Jr³, Joseph J. Torres¹

¹Department of Marine Science, 140 Seventh Avenue South, University of South Florida, St. Petersburg, Florida 33701-5016, USA

²Florida Marine Research Institute, Department of Environmental Protection, 100 8th Street S.E., St. Petersburg, Florida 33701, USA

³St. Petersburg Junior College, Natural Science, 6605 5th Avenue N., St. Petersburg, Florida 33710, USA

ABSTRACT: The micronektonic crustacean assemblage in the eastern Gulf of Mexico is an extension of the low latitude Atlantic and Caribbean faunas. Species showed highly varying diel distribution patterns ranging from a strong vertical migration to the epipelagic zone to absence of any migration resulting in a permanent residence deep in the mesopelagic zone. As in other low latitude areas, decapod species with variegated pigment patterns centered above 650 m during the day, whereas 'all-red' species centered below this depth. Standing stocks were estimated at 0.18 g dry wt m⁻² and 3 ind. m⁻² in the upper 1000 m. Diet analysis revealed that crustaceans dominate as the main food biomass of sergestids (e.g. copepods, ostracods, euphausiids) while aristeids (*Gennadas* spp.) and carideans feed heavily on both fish and crustaceans. Among mysids, *Gnathophausia ingens* ingests mostly fish while eucopiids are primarily copepod feeders. Other common diet items of the micronektonic crustacean assemblage are chaetognaths, molluscs (pteropods, heteropods) and large phaeodarian radiolarians. Olive-green debris containing phytoplankton and protists was encountered in the diets of all but 2 caridean species and the mysids. It was most prevalent in the diets of the *Sergia* species and the aristeids. A likely source of this material is 'marine snow'. The predation impact of the decapod and mysid population on zooplankton is estimated at 1% of standing stocks and 18% of biomass production d⁻¹. Combined results from cluster analyses of vertical distribution (space and time niche dimensions) and diet (food niche dimension) characteristics indicate that resource partitioning among the shrimp assemblage in the eastern Gulf of Mexico occurs at the between-species level.

KEY WORDS: Crustacean · Decapod · Mysid · Feeding

INTRODUCTION

Micronektonic crustaceans are a major component of pelagic oceanic ecosystems and, as such, would be expected to play an important role in trophic dynamics at intermediate levels in the food web. For example, in waters off Hawaii midwater decapods and mysids constitute approximately one-fifth of the numbers and biomass of epi-mesopelagic micronekton (Maynard et al. 1975); in the eastern Gulf of Mexico they account for nearly a third (Hopkins & Lancaft 1984). Only midwater fishes rank higher in both areas. The trophic role of micronektonic crustaceans is primarily as zooplanktivores, with their diets being comprised largely of other crustaceans (Foxton & Roe 1974, Omori 1974, Donaldson 1975, Walters 1976, Heffernan & Hopkins

1981, Roe 1984, Nishida et al. 1988, Flock & Hopkins 1992). The predation impact of the micronektonic crustacean population on zooplankton, however, is unknown, though the biomass ingested is undoubtedly large given the abundance of these organisms in the oceanic ecosystem. Micronektonic crustaceans also support upper trophic levels in the ecosystem, acting as food for cephalopods, midwater fishes, commercially important epipelagic fishes, and cetaceans (Borodulina 1972, Judkins & Fleminger 1972, Omori 1974, Clarke 1982). In this paper we consider the abundance, vertical distribution, feeding ecology and predation impact of 29 midwater decapod and mysid species (large euphausiids excluded; see Kinsey & Hopkins 1994) prevalent in the eastern Gulf of Mexico. The species in this study constitute over 95% of the

numbers and biomass of the decapod and mysid assemblage in the upper 1000 m.

HYDROGRAPHIC SETTING

The eastern Gulf of Mexico is a subtropical regime characterized by warm surface temperatures throughout the year (20 to 30 °C), a shallow mixed layer of 25 to 50 m and a thermocline extending to ~150 m (15 to 18 °C at depth). Gulf temperatures at 500 and 1000 m, respectively, are 8 to 9 °C and 4 to 5 °C (Lancraft et al. 1988). The water column is well oxygenated, with the minimum occurring in a broad zone at 450 to 800 m ($>2.7 \text{ ml O}_2 \text{ l}^{-1}$; Bennett & Hopkins 1989). The most dynamic feature of the eastern Gulf is the Loop Current, of Caribbean origin, which intermittently enters the Gulf through the Yucatan Straits and on occasion approaches the Mississippi delta (Maul 1977, Sturges & Evans 1983). The Loop Current axis, however, lies west of the sampling location (27° N, 86° W) and was encountered during only 2 of 18 cruises. Most of our sampling, consequently, was in residual eastern Gulf water. Because of large density differences, there is apparently little mixing (G. A. Maul, Atlantic Oceanographic and Meteorological Laboratories, Miami, FL, USA, pers. comm.) between Loop and residual water. Hence the fauna in residual eastern Gulf water has evolved its own identifying characteristics in terms of community structure, with this being most apparent in species dominance patterns (Michel & Foyo 1976, Gartner et al. 1987, Passarella & Hopkins 1991, Flock & Hopkins 1992). Zooplankton standing stock is low, $1.2 \text{ g dry wt m}^{-2}$ in the upper 1000 m, and typical of oligotrophic boundary currents (Hopkins 1982). Faunal diversity is high, with species composition being little different from Caribbean and adjacent Atlantic waters.

METHODS

The micronektonic crustaceans (decapods and mysids) used for this study were collected in the vicinity of 27° N, 86° W during a series of 18 cruises made from 1972 to 1990. Sampling was with opening-closing Tucker trawls with mouth areas of 3, 4 or 6 m². The trawl body was of 4 mm mesh and cod-end nets were of 0.5 or 1 mm mesh. Towing speed for all nets was 1.5 to 3 knots and volume filtered was estimated with flowmeters. Details of construction and towing strategies are in earlier papers (Hopkins et al. 1973, Hopkins & Baird 1975, Gartner et al. 1987).

All catches were prorated to volume of water filtered. Individual species day and night vertical distribu-

tions were computed as percent of the total population number of that species occurring in each 50 m depth zone from the surface to 1000 m (20 zones). The vertical distributions of these species were based on a composite of all size classes of post-metamorphic decapods and mysids larger than 1 cm taken with our trawl nets and thus obscure intraspecific size versus depth of occurrence trends. The term 'population center' used in Results is defined as the depth above and below which 50% of the species population occurs. Species vertical distributions were compared using Bray-Curtis (1957) dissimilarity indices and UPGMA (unweighted pair-group method using arithmetic averages) hierarchical cluster analysis (Romesburg 1990). Species sample pairs matrices consisting of the Bray-Curtis indices were generated for day and night periods, then the matrices were clustered to determine species vertical groupings for day and night, respectively. Clusters were delineated at the 40% dissimilarity level in vertical distribution (Zaret & Rand 1971, Berkes 1976; see also 'Discussion' in Hopkins & Gartner 1992).

Diet analysis was on carideans and large mysids and on species of 2 families of penaeoidean shrimps, the Penaeidae and Aristeidae. Also, an earlier data set on the Sergestidae (Flock & Hopkins 1992) was incorporated into the study subsequent to converting diet results from incidence of food types to biomass of food types. Food biomass, despite difficulties and uncertainties in its estimation, was used in this analysis rather than incidence of occurrence of food types in guts because of its greater usefulness in trophodynamic calculations and value in defining species feeding-niche parameters. All specimens used in diet analysis were measured to the nearest millimeter from posterior eye orbit to middorsal posterior end of the carapace as an estimate of carapace length, and from posterior eye orbit to telson tip as an estimate of body length. The length data were used to establish crustacean dry weight regressions (unpubl.) on carapace length for estimating biomass. Dry weight for individuals of those species for which there were no regressions were estimated using the available regressions for species of similar morphology. The crustacean digestive tracts were removed from the thorax (foregut and anterior part of intestine) and gut contents were examined on microscope slides at 40 to 600× magnification. Food items were counted and measured when possible. In instances where prey were fragmented, body parts useful in estimating prey size were measured. For example, crustacean food predominated in guts and key body parts such as mandibles (copepods, ostracods, euphausiids), antennae (basipod of ostracod second antenna) and intact sections of metasomes and abdomens (copepods, euphausiids, amphipods) were

in most instances available for estimating prey size when crustaceans were present in gut contents. Accuracy in estimating prey size varied, with measurements based on mandible width (the most frequently measured body part) being the most reliable. It was impractical to obtain size conversions for key body parts for each of the hundreds of zooplankton species occurring in the upper 1000 m. Data on body parts for a wide spectrum of species, including a broad range of body types, were obtained, however, and measurements for each prey item were converted to prey size using tables or regressions based on species with the most similar morphology. Size data were then converted to prey dry weight using zooplankton size vs dry weight curves (unpubl. data).

Fishes were considered a diet item only when remains in foreguts included more than fish scales (e.g. skeletal fragments, eye lenses, otoliths) since scales can be readily shed from damaged fish and ingested both in the water column and trawl cod-ends (Hopkins & Baird 1975). When possible, the size of fish prey was estimated by measuring intact body parts such as eyes, otoliths and stomachs, then using body part versus fish standard length regressions (unpubl.). Diet data from the entire assemblage indicated that the average size of fish eaten was 1.2 cm. Most of the piscivorous shrimps centered well below 100 m at night and occurred deep in the mesopelagic zone during the day. This distribution placed them below the zone of abundance for larval and early stage post-metamorphic myctophids, but in the zone of the abundant *Cyclothone* gonostomatids. *Cyclothone* has been reported as a frequent diet item for mesopelagic shrimps, especially oplophorids (Roe 1984). A 1.2 cm *Cyclothone* weighs approximately 1 mg dry wt (Maynard 1982), and this weight was used in all incidences where fish remains were encountered in foreguts.

Olive-green debris containing phytoplankton and protozoans (e.g. tintinnids, radiolarians, foraminiferans) frequently occurred in guts, with incidence being especially high in the Aristeidae (*Gennadas* spp.), and appeared to account for a large fraction of the food volume. The biomass of this material was difficult to assess and its contribution to food biomass was not included in the diet composition calculations. Similarly, cnidarian nematocysts, also a common diet item, were not included in diet biomass computations.

Food was assigned to 11 diet categories: copepods, ostracods, euphausiids, decapods, cephalopods, other molluscs, chaetognaths, siphonophores, large radiolarians, fishes and other food. These food categories are broad because decapods and mysids chew their food and it was impossible to consistently obtain quantitative data on prey at even the taxonomic level of family. The biomass of food in each diet category for an indi-

vidual size class of a decapod or mysid species was calculated as a percentage of total food found in guts of the sample. The diet compositions of species were then grouped using Bray-Curtis indices and UPGMA cluster analysis as described above. Bray-Curtis and UPGMA procedures were also used to group species according to the size distribution of their prey where the biomass contained in each size class of prey (<1 to 9.9 mm in 2 mm intervals; 10 to 14.9 mm; 15 to 19.9 mm; >20 mm) was calculated as a percent of the total. All diet analyses were at the size class level where each size class of a decapod or mysid species examined was treated as an independent unit; this was required because of potential changes in diet with ontogeny. However, initial cluster analyses were unable to separate intraspecific size classes of the species considered either by food composition or food size. Consequently, the cluster results presented in this paper are based on the combined size class data for each micronekton species.

A potential source of bias in diet studies based on gut analysis is postcapture feeding in nets. However, a comparison of decapods (unpubl. data on *Gennadas valens*, *Systellaspis debilis* and *Acanthephyra purpurea*) returned in coarse (4 mm) and fine (1 mm) mesh trawl cod-ends revealed little difference in foregut contents. Especially significant was that the taxonomic composition and size distribution of prey such as copepods were quite similar in the foreguts of the 2 groups of shrimps examined even though this small prey was not retained in the coarse mesh codend. Consequently, we concur with those (e.g. Foxton & Roe 1974, Donaldson 1975, Walters 1976, Roe 1984) who suggest that net feeding is a minor source of bias in analyzing the diets of micronektonic crustaceans.

RESULTS

Abundance and vertical distribution

The crustaceans considered here (Table 1) totalled 3.1×10^6 ind. km^{-2} in the upper 1000 m. These 29 species constitute all but 5% of the decapod and mysid population in this depth zone. Their combined biomass was 183 kg dry wt km^{-2} . Of the taxonomic groups considered, the Penaeoidea (Aristeidae, Penaeidae) were the most numerous (50%), followed by Sergestoidea (34%), Mysidacea (9%) and Caridea (6%). Penaeoidea were also predominant in biomass (59%), with Sergestoidea ranking second (35%), followed by Caridea (31%) and Mysidacea (5%). Individual carideans on the average were larger than most other shrimps, hence their biomass percentage in comparison to their numerical fraction was disproportionately

Table 1. Abundance and biomass of midwater decapods and mysids at 27° N, 86° W in the eastern Gulf of Mexico

| Species | Code | Abundance (ind. km ⁻²) | Biomass (kg dry wt km ⁻²) |
|-------------------------------------|------|---------------------------------------|--|
| Penaeoidea | | | |
| <i>Gennadas bouvieri</i> | GBOV | 88 000 | 5.6 |
| <i>Gennadas capensis</i> | GCAP | 187 500 | 13.1 |
| <i>Gennadas scutatus</i> | GSCU | 31 000 | 1.3 |
| <i>Gennadas valens</i> | GVAL | 1 237 500 | 85.7 |
| <i>Funchalia villosa</i> | FVIL | 8 130 | 2.1 |
| Sergestoidea | | | |
| <i>Sergestes armatus</i> | SARM | 23 000 | 0.7 |
| <i>Sergestes atlanticus</i> | SATL | 97 000 | 1.6 |
| <i>Sergestes curvatus</i> | SCUR | 5 000 | 0.7 |
| <i>Sergestes edwardsii</i> | SEDW | 36 400 | 0.3 |
| <i>Sergestes henseni</i> | SHEN | 90 800 | 5.2 |
| <i>Sergestes paraseminudus</i> | SPAR | 43 600 | 3.8 |
| <i>Sergestes pectinatus</i> | SPEC | 271 600 | 2.2 |
| <i>Sergestes sargassi</i> | SSAR | 63 300 | 0.9 |
| <i>Sergestes vigilax</i> | SVIG | 33 800 | 0.6 |
| <i>Sergia robustus</i> | SROB | 68 500 | 3.8 |
| <i>Sergia splendens</i> | SSPL | 333 400 | 15.3 |
| Caridea | | | |
| <i>AcanthePHYra acanthitelsonis</i> | AACA | 6 700 | 3.1 |
| <i>AcanthePHYra curtirostris</i> | ACUR | 21 800 | 4.1 |
| <i>AcanthePHYra purpurea</i> | APUR | 33 750 | 7.2 |
| <i>AcanthePHYra stylorostrata</i> | ASTY | 6 780 | 1.3 |
| <i>Notostomus gibbosus</i> | NGIB | 1 600 | 0.5 |
| <i>Oplophorus gracilirostris</i> | OGRA | 4 950 | 0.6 |
| <i>Parapandalus richardi</i> | PRIC | 36 500 | 1.9 |
| <i>Pasiphaea merriami</i> | PMER | 7 350 | 0.6 |
| <i>Systellaspis debilis</i> | SDEB | 70 000 | 11.8 |
| Mysidacea | | | |
| <i>Eucopeia australis</i> | EAUS | 22 900 | 1.0 |
| <i>Eucopeia unguiculata</i> | EUNG | 167 600 | 3.6 |
| <i>Eucopeia sculpticauda</i> | ESCU | 91 670 | 3.1 |
| <i>Gnathophausia ingens</i> | GING | 6 346 | 1.1 |

large. The most abundant species in the upper 1000 m was the aristeid *Gennadas valens*, which alone constituted 40% of the midwater shrimp numbers and 47% of the biomass. Other abundant species ($>1 \times 10^5$ ind. km⁻²) were *Sergia splendens*, *Sergestes pectinatus* and the mysid *Eucopeia unguiculata*. Caridean species were much less numerous than the abundant aristeid, sergestid and mysid species, with the 4 most common ($>2 \times 10^4$ ind. km⁻²) being *Systellaspis debilis*, *Parapandalus richardi*, *AcanthePHYra purpurea* and *A. curtirostris*. As the samples used in this study were from the upper kilometer, the abundances of some species have been underestimated because much of their populations reside below 1000 m (e.g. *A. acanthitelsonis*, *A. curtirostris*, *A. stylorostrata*, *Notostomus gibbosus*, the 3 eucopiid species). The vertical distribution patterns of all 29 species examined are shown in Fig. 1 and cluster analyses based on these distributions are in Figs. 2 & 3. Cluster analysis of night vertical distributions (Fig. 2) yielded 14 clusters. Eight were single spe-

cies clusters whereas 6 clusters grouped 2 or more species. Species (15) with night depth distribution centers in the epipelagic zone were in clusters N4 to N9. In this group of clusters were all but one sergestid species (*Sergia robustus*), the strongly migrating oplophorids (*Oplophorus gracilirostris*, *Systellaspis debilis*), *Parapandalus richardi*, *Pasiphaea merriami* and *Funchalia villosa*. Species (7) centering in the upper mesopelagic zone (200 to 600 m) occurred in clusters N10 to N14. This group included the Aristeidae (*Gennadas* spp.), *Sergia robustus*, *AcanthePHYra purpurea* and *Gnathophausia ingens*. Deep dwelling, weakly migrating species (7) having population centers below 800 m at night were grouped in clusters N1 to N3. These included 3 species of *AcanthePHYra*, the eucopiid mysids and *Notostomus gibbosus*.

There were 12 daytime depth clusters (Fig. 3), 6 single species and 6 multiple species clusters. Species (13) with population depth centers shallower than 600 m were grouped in clusters D6 to D8 and D10 to D12. Included

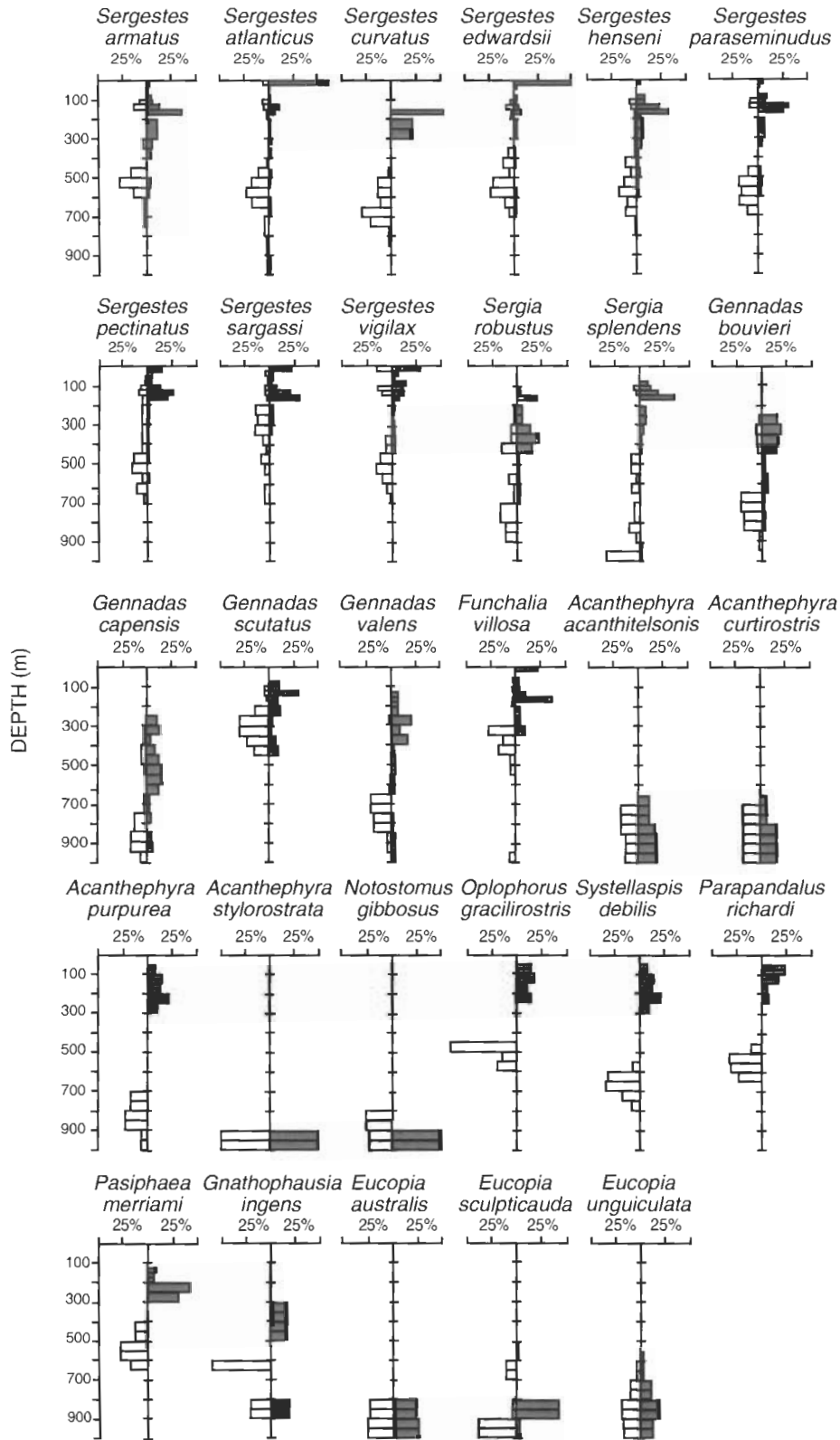


Fig. 1. Vertical distributions of 29 species of midwater decapods and mysids in the eastern Gulf of Mexico. Open and shaded bars, respectively, represent day and night

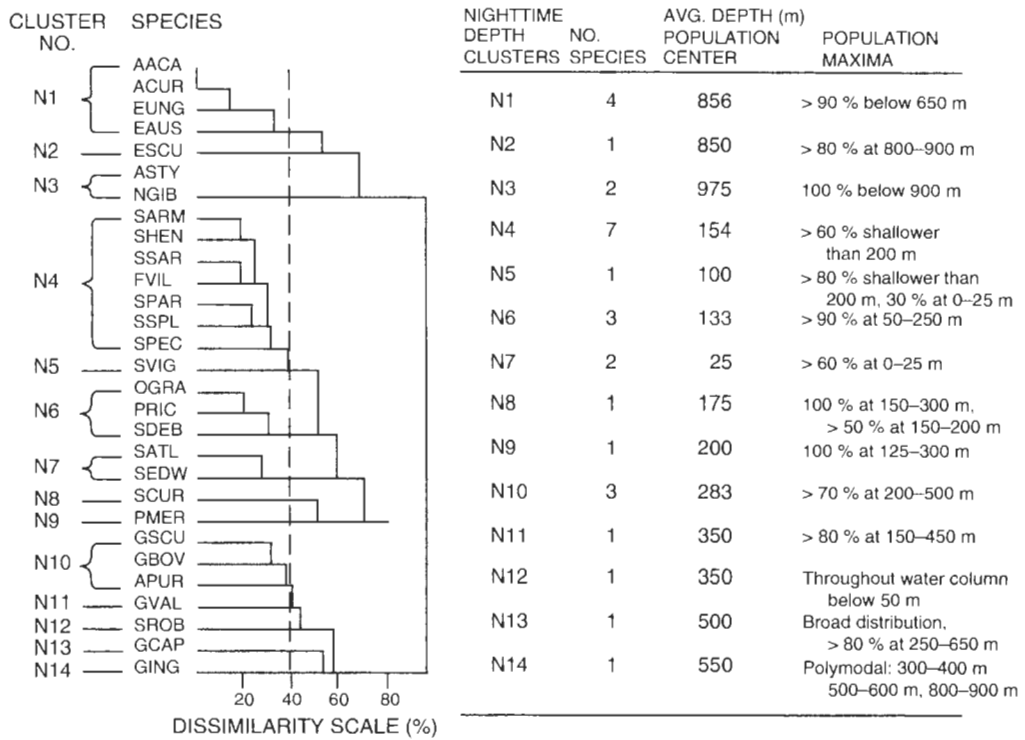


Fig. 2. Cluster analysis of the nighttime vertical distributions of eastern Gulf midwater decapods and mysids in the upper 1000 m. Cluster separation at 40% dissimilarity level. Species name code in Table 1

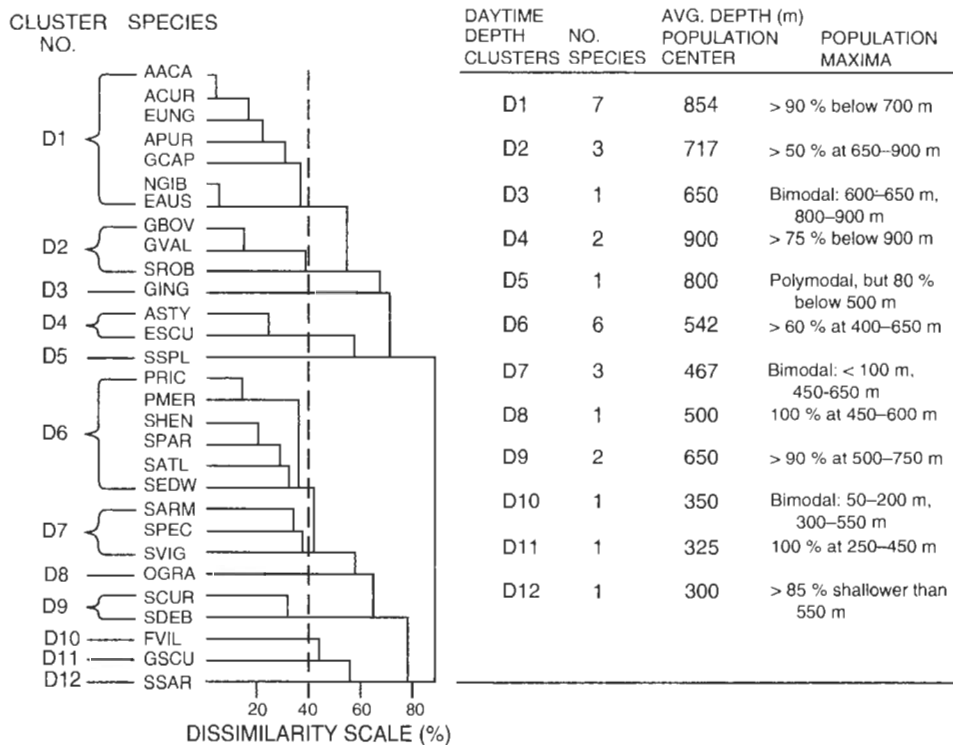


Fig. 3. Cluster analysis of the daytime vertical distributions of eastern Gulf midwater decapods and mysids in the upper 1000 m. Cluster separation at 40% dissimilarity level. Species name code in Table 1

here were 8 of the 11 sergestids, *Gennadas scutatus*, *Funchalia villosa*, *Oplophorus gracilirostris*, *Parapandalus richardi* and *Pasiphaea merriami*. All of these are strong vertical migrators and account for most of the species occurring in the epipelagic zone at night. The remaining clusters, D1 to D5 and D9, contain the species (16) which center below 600 m during the day. With 3 exceptions, *Sergestes curvatus*, *Sergia splendens* and *Systellaspis debilis*, the species grouped in these clusters center below the epipelagic zone at night.

Feeding

The diet composition of the 29 species in terms of biomass is given in Table 2. This data set served as the basis for the pie distribution diagrams in Fig. 4 which summarize diet composition by family. The Sergestidae ingested primarily euphausiids (38.9%) and copepods (36.5%). Most of the remaining diet biomass (20.2%) was composed of chaetognaths, ostracods and radiolarians. All sergestid species fed on olive-green debris containing phytoplankton and protists (Table 2, columns 4 and 5), with this material being especially prevalent in the 2 *Sergia* species. Cnidarian nematocysts also occurred in most sergestids, but again were most prevalent in the diets of the *Sergia* species.

The aristeids had fish (31.7%) and euphausiids (27.3%) as principal food categories, with copepods, chaetognaths and radiolarians being important diet elements as well. Their foreguts also contained especially large quantities of olive-green debris interspersed with phytoplankton and protists. Nematocysts were frequently encountered as well.

The pie diagram for the Penaeidae represents only the diet of *Funchalia villosa*. Over half (54.5%) of the food biomass was fish, with most of the balance (44.2%) being chaetognaths and euphausiids. Olive-green debris and to a lesser extent nematocysts were also diet items.

A third (33.2%) of the diet of the Oplophoridae was fish and another 41.2% was chaetognaths and euphausiids. Olive-green debris was often noted in foreguts of *Acanthephyra curtirostris* and *Systellaspis debilis*, and nematocysts from *A. curtirostris*, *A. purpurea* and *S. debilis*. The diet of *Parapandalus richardi*, the only representative of the Pandalidae, was largely fish (46.3%), with siphonophores, euphausiids and chaetognaths together contributing an equivalent share (45.3%). Both olive-green debris and nematocysts were common in its diet. *Pasiphaea merriami*, the single species of Pasiphaeidae examined, fed mostly on euphausiids (62.1%), with the balance (34.8%) of the diet being primarily fishes and decapods. Olive-

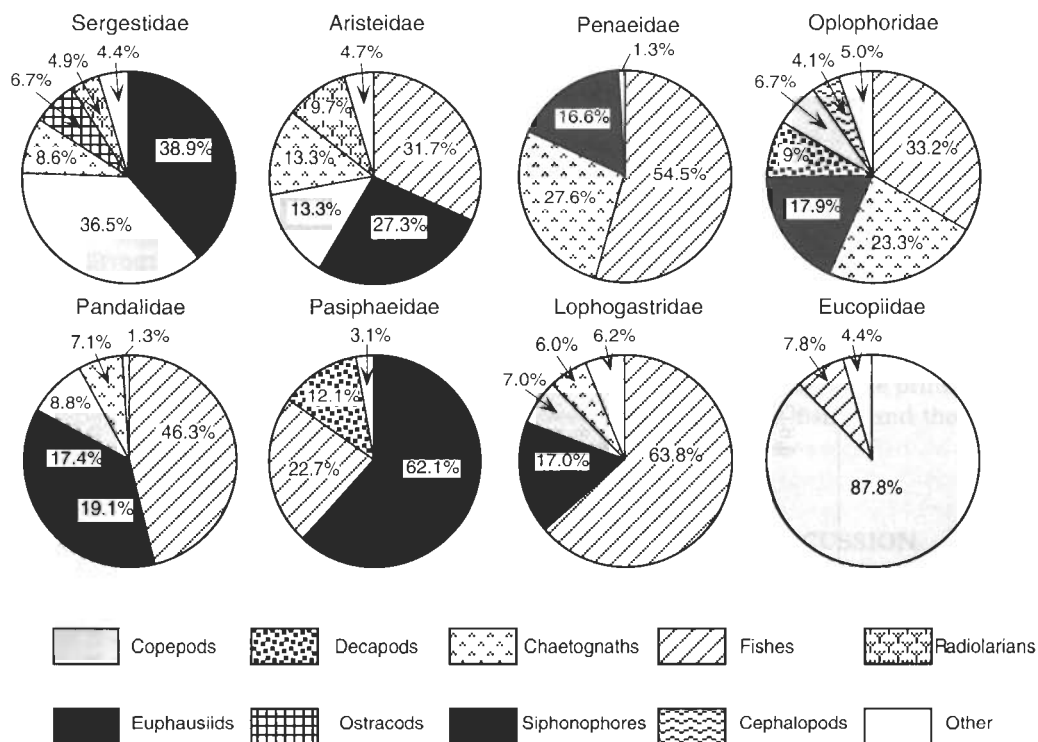


Fig. 4. Diet composition of the dominant families of midwater decapods and mysids in the eastern Gulf of Mexico. Percentages are of food biomass

Table 2. Diet composition of the dominant midwater decapods and mysids in the eastern Gulf of Mexico. -: absent from diet, +: <0.1% of diet

| Species | Feeding sample size: total length in cm (range) | Percent of diet biomass | | | | | | | | | | | | | | |
|-------------------------------------|---|--------------------------------------|--|---|-------------------------------|----------|-----------|-------------|----------|-------------|----------------|--------------|---------------|--------------------|--------|-------|
| | | No. of ind. used in diet analysis | Incidence of phytoplankton & protozoans (no. of guts) | Incidence of cnidarians debris (no. of guts) | Items No. of metazoan food | Copepods | Ostracods | Euphausiids | Decapods | Cephalopods | Other molluscs | Chaetognaths | Siphonophores | Large radiolarians | Fishes | Other |
| Sergestidae | | | | | | | | | | | | | | | | |
| <i>Sergestes armatus</i> | 3.6 (3.1-4.0) | 15 | 2 | 0 | 13 | 17.8 | - | 68.0 | - | - | 7.2 | - | 5.8 | - | 1.2 | |
| <i>Sergestes atlanticus</i> | 2.1 (1.8-3.0) | 20 | 4 | 4 | 68 | 38.9 | 3.5 | 45.3 | - | 0.3 | 6.7 | - | 5.3 | - | - | |
| <i>Sergestes curvatus</i> | 4.9 (4.2-5.3) | 12 | 1 | 4 | 34 | 42.4 | 3.8 | 26.5 | - | 0.2 | 8.0 | - | 6.4 | 12.7 | - | |
| <i>Sergestes edwardsii</i> | 1.5 (1.1-1.8) | 10 | 2 | - | 19 | 10.4 | - | 77.3 | 11.0 | - | 0.2 | - | - | - | 1.1 | |
| <i>Sergestes henseni</i> | 3.0 (1.8-4.6) | 25 | 5 | 8 | 54 | 22.5 | 4.3 | 57.4 | - | - | 15.0 | - | - | - | 0.8 | |
| <i>Sergestes paraseminudus</i> | 3.0 (2.3-3.2) | 25 | 4 | 11 | 41 | 37.8 | 8.8 | 34.9 | - | - | 12.6 | - | 4.9 | - | 1.0 | |
| <i>Sergestes pectinatus</i> | 1.5 (1.1-2.0) | 24 | 1 | 6 | 65 | 90.7 | 9.3 | - | - | - | - | - | - | - | - | |
| <i>Sergestes sargassi</i> | 2.4 (1.9-2.8) | 18 | 4 | 4 | 46 | 83.8 | 3.7 | 12.5 | - | - | - | - | - | - | - | |
| <i>Sergestes vigilax</i> | 1.9 (1.6-2.3) | 25 | 5 | - | 32 | 19.4 | - | 78.5 | 0.5 | - | 0.6 | - | - | - | - | |
| <i>Sergia robustus</i> | 5.3 (3.4-7.8) | 40 | 19 | 36 | 153 | 22.0 | 20.0 | 17.9 | - | 0.1 | 25.4 | 0.9 | 12.7 | - | 1.0 | |
| <i>Sergia splendens</i> | 2.5 (1.5-3.2) | 80 | 56 | 57 | 187 | 15.1 | 20.4 | 9.8 | 9.8 | 2.8 | 18.7 | 3.3 | 18.5 | - | 1.6 | |
| Aristeidae | | | | | | | | | | | | | | | | |
| <i>Gennadas bouvieri</i> | 2.3 (2.0-2.9) | 25 | 21 | 10 | 146 | 16.2 | 1.1 | 20.4 | 1.7 | 1.7 | 12.0 | - | 14.1 | 32.3 | 0.3 | |
| <i>Gennadas capensis</i> | 2.6 (2.0-3.6) | 25 | 22 | 12 | 204 | 12.2 | 1.0 | 22.3 | 8.5 | - | 14.9 | - | 5.1 | 36.0 | - | |
| <i>Gennadas scutatus</i> | 2.1 (1.8-2.8) | 25 | 19 | 4 | 85 | 14.6 | + | 38.7 | - | - | 9.4 | - | 6.3 | 30.9 | - | |
| <i>Gennadas valens</i> | 3.4 (2.5-4.2) | 79 | 68 | 23 | 255 | 10.1 | 0.9 | 28.4 | 2.1 | - | 16.7 | - | 13.1 | 28.0 | 0.5 | |
| Penaeidae | | | | | | | | | | | | | | | | |
| <i>Funchalia villosa</i> | 5.0 (3.0-7.8) | 85 | 47 | 11 | 19 | 1.0 | - | 16.6 | - | - | 0.3 | 27.6 | - | 54.5 | - | |
| Ophiophoridae | | | | | | | | | | | | | | | | |
| <i>Acanthephyra acanthitelsonis</i> | 6.9 (3.1-10.9) | 49 | 2 | 8 | 141 | 8.4 | - | 3.5 | 27.2 | 6.2 | 2.1 | 20.4 | 0.1 | 31.4 | 0.7 | |
| <i>Acanthephyra curtirostris</i> | 4.7 (3.0-7.7) | 74 | 22 | 29 | 198 | 7.6 | 1.0 | 9.8 | 9.0 | 1.1 | 0.4 | 23.1 | - | 45.4 | 2.6 | |
| <i>Acanthephyra purpurea</i> | 5.4 (3.8-7.5) | 53 | 7 | 18 | 179 | 3.0 | 0.3 | 31.2 | 6.2 | 3.7 | 0.8 | 26.3 | - | 0.3 | 28.0 | 0.2 |
| <i>Acanthephyra stylostrata</i> | 3.0 (2.2-4.1) | 14 | 3 | 3 | 33 | 7.2 | 3.2 | 13.6 | 6.8 | - | 0.6 | 11.3 | - | 57.3 | - | |
| <i>Notostomus gibbosus</i> | 6.5 (3.0-11.5) | 13 | 4 | 6 | 17 | 1.8 | - | 16.1 | 5.4 | - | 46.0 | - | 25.3 | 5.4 | - | |
| <i>Ophiophorus gracilirostris</i> | 4.7 (3.0-6.8) | 41 | - | 6 | 174 | 8.7 | + | 13.1 | 3.6 | 10.7 | 19.1 | 18.2 | 0.1 | 26.2 | 0.3 | |
| <i>Systellaspis debilis</i> | 3.9 (2.1-6.0) | 121 | 45 | 77 | 677 | 10.2 | 2.3 | 38.0 | 4.5 | 7.1 | 1.1 | 18.2 | - | 18.6 | + | |
| Pandalidae | | | | | | | | | | | | | | | | |
| <i>Parapandalus richardi</i> | 3.0 (2.6-4.0) | 69 | 38 | 47 | 83 | 8.8 | - | 17.4 | - | - | 1.3 | 7.1 | 19.1 | 46.3 | - | |
| Pasiphaeidae | | | | | | | | | | | | | | | | |
| <i>Pasiphaea merriami</i> | 6.2 (3.5-8.5) | 22 | - | 1 | 18 | 1.2 | - | 62.1 | 12.1 | - | - | - | 1.9 | 22.7 | - | |
| Lophogastridae | | | | | | | | | | | | | | | | |
| <i>Gnathophausia ingens</i> | 5.2 (2.0-10.7) | 45 | - | - | 68 | 7.0 | 0.2 | 17.0 | 2.9 | - | 1.7 | 6.0 | - | 1.4 | 63.8 | - |
| Eucopeiidae | | | | | | | | | | | | | | | | |
| <i>Eucopeia australis</i> | 4.2 (3.5-5.3) | 49 | - | - | 42 | 90.4 | - | - | - | - | - | - | - | 8.7 | 0.9 | |
| <i>Eucopeia unguiculata</i> | 3.2 (1.9-5.6) | 117 | - | - | 68 | 79.6 | 0.4 | - | - | - | - | 4.7 | 0.7 | 14.6 | - | |
| <i>Eucopeia sculpticauda</i> | 2.8 (1.8-4.9) | 155 | - | - | 53 | 93.4 | - | - | - | - | - | 6.6 | - | - | - | |

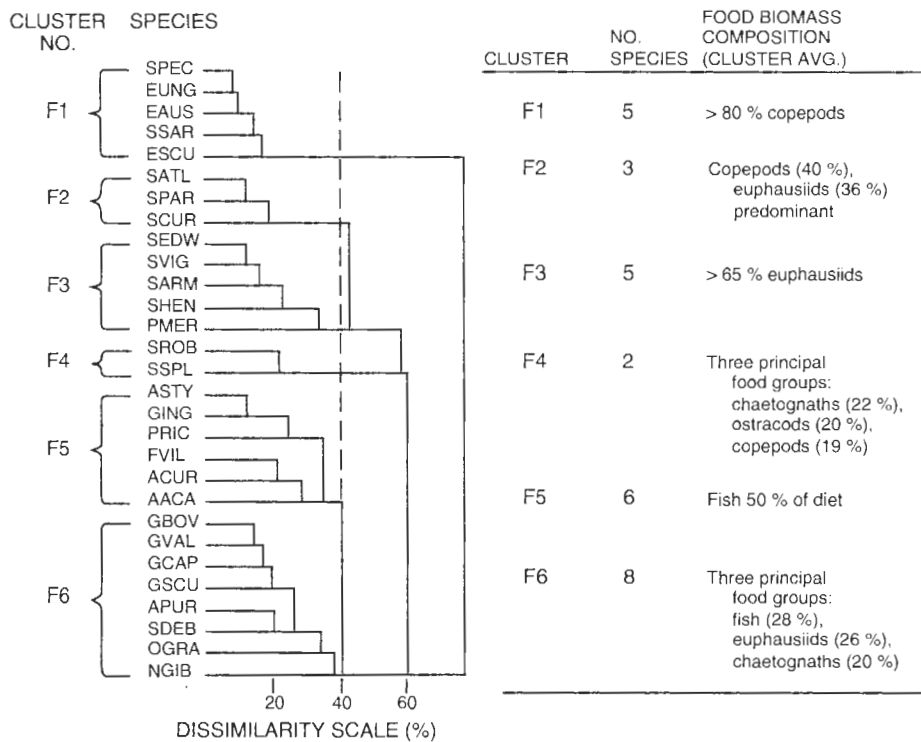


Fig. 5. Cluster analysis of the taxonomic composition of the diets of eastern Gulf midwater decapods and mysids. Cluster separation at 40% dissimilarity level. Species name codes in Table 1

green debris and nematocysts were infrequently recorded.

The diet of the lophogastrid mysid *Gnathopausia ingens* consisted largely (63.8%) of fish, with an additional 30% contributed by euphausiids, copepods and chaetognaths. Eucopiid mysids fed on little else but copepods (87.8%). No olive-green debris or nematocysts were recorded from foreguts of mysids in either family.

The clustering of diet composition data (Fig. 5), based on the information in Table 2, revealed 6 feeding guilds. All were multispecies clusters. Cluster F1 was a guild of copepod feeders (>80% of the diet) which included the eucopiid mysids and 2 sergestids. The 3 sergestid species constituting cluster F2 had diets which were three-fourths copepods and euphausiids. Cluster F3 consisted of 5 species with primarily euphausiid diets. Included here were 4 sergestid species and *Pasiphaea merriami*. The diet of the 2 *Sergia* species in cluster F4 was relatively diverse, with the principal food groups being chaetognaths, ostracods and copepods. The 6 species in cluster F5, a mixture of taxa which included 3 oplophorids, *Gnathopausia ingens*, *Parapandalus richardi* and *Funchalia villosa*, were largely piscivorous (50% of the diet). Cluster F6 included 8 species, half aristeids and

half oplophorids, which fed primarily on 3 food categories, fish, euphausiids and chaetognaths.

Cluster analysis of food size distribution (Fig. 6) yielded 6 clusters. Species in clusters S1 to S3 obtained most of their diet biomass from crustacean prey smaller than 8 mm in length such as copepods, ostracods and small euphausiids. These clusters included 8 of the 11 sergestids and the eucopiid mysids. In clusters S4 to S6 were species which had most of their diet biomass as food larger than 8 mm. These clusters grouped the carideans, aristeids, the remaining 3 sergestid species and *Gnathopausia ingens*. The principal food of these species was decapods, fishes and the larger chaetognaths and euphausiids.

DISCUSSION

Eastern Gulf assemblage

The midwater decapod and mysid assemblage of the eastern Gulf of Mexico is an extension of the tropical-subtropical western North Atlantic and Caribbean faunas, with many species that are pan-oceanic at low latitudes (see Hopkins et al. 1989, Flock & Hopkins 1992). The principal group, as in the North Atlantic from tem-

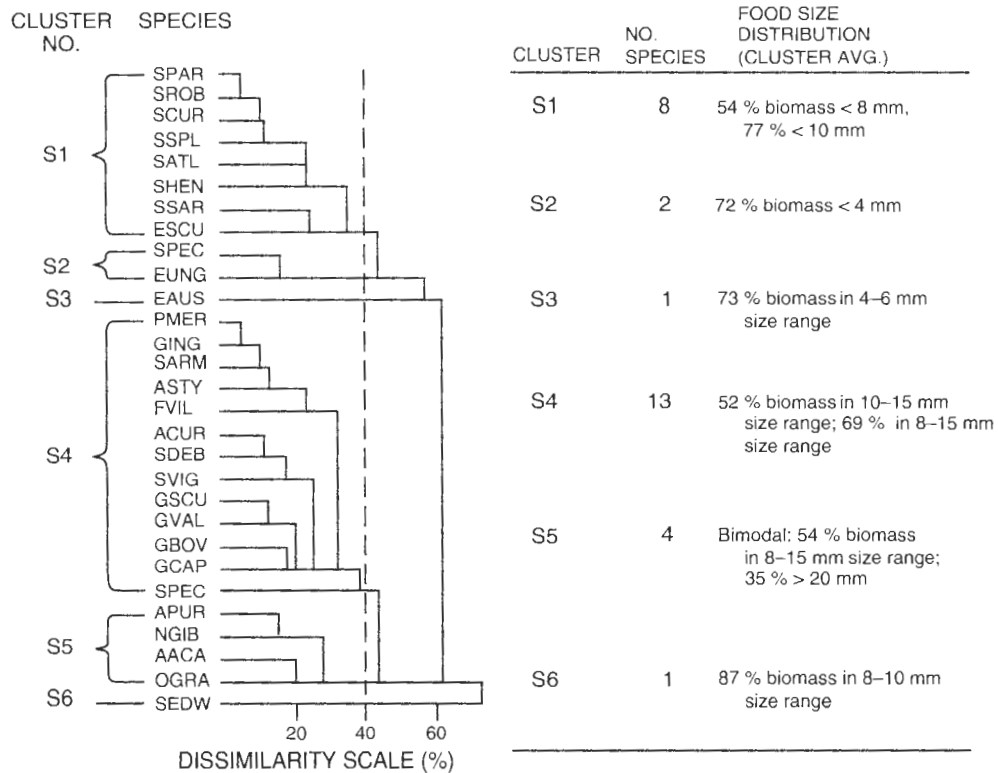


Fig. 6. Cluster analysis of the size distribution of prey biomass in the diets of eastern Gulf midwater decapod and mysid species. Cluster separation at 40 % dissimilarity level. Species name codes in Table 1

perate to tropical latitudes (Foxton 1970b, Hargreaves 1985), is the Aristeidae which accounts for nearly 60 % of the midwater decapod and mysid numbers and biomass. The overwhelmingly dominant species in the eastern Gulf is *Gennadas valens* which contributed $0.09 \text{ g dry wt m}^{-2}$ (47 %) to total assemblage biomass. This approximates the standing stock of the entire myctophid fish assemblage ($0.08 \text{ g dry wt m}^{-2}$) and underscores the trophic significance of this species. The total midwater decapod and mysid biomass in the upper 1000 m is estimated at $0.18 \text{ g dry wt m}^{-2}$ which is similar to that reported for other middle and low latitude environments such as off Hawaii ($0.15 \text{ g dry wt m}^{-2}$; Maynard et al. 1975; conversion factor $0.15 \times$ wet wt) and in the Kuroshio Current (0.06 to $0.19 \text{ g dry wt m}^{-2}$; Aizawa 1974; wet wt conversion).

While decapod and mysid vertical distribution patterns (Figs. 1 & 2) in the eastern Gulf are generally similar to those in other mid- to low latitude areas (e.g. Chace 1940, Foxton 1970a, b, Donaldson 1975, Ziemann 1975, Walters 1976), there are apparent distributional features unique to this region. For example, the sergestid population is found at somewhat shallower depths during the day in the eastern Gulf than in the western North Atlantic near Bermuda and in the Pacific off Hawaii. This may be related to light

penetration as Secchi disk readings indicate eastern Gulf waters are less transparent than in the other 2 regions (Flock & Hopkins 1992). The 'all-red' component of the decapod and mysid assemblage, as observed in both the Atlantic and Pacific (Foxton 1970b, Omori 1974, Walters 1976), tends to have deeper distributions, especially during the daylight hours, than do species with variegated patterns of mixed red/orange pigmentation and semi-transparency. The transition depth in the eastern Gulf appears to be 650 m. Semi-transparency and/or variegated colored species such as members of the genera *Sergestes*, *Funchalia*, *Parapandalus*, *Pasiphaea*, *Systellaspis* (early juvenile stages) and *Oplophorus* have populations centering shallower than this depth, day and night. The 'all-red' decapods and mysids center below 650 m during the day while at night much of the population of this group (e.g. *Sergia*, *Gennadas*, late-stage *Systellaspis debilis*, *Acantheephyra purpurea*, *Gnathophausia ingens*) migrate into the upper mesopelagic and epipelagic zones (see also Hefferman & Hopkins 1981, Hopkins et al. 1989, Flock & Hopkins 1992). The remaining 'all-red' genera included in this study, *Notostomus*, *Acantheephyra* (most species) and *Eucopeia*, center below 650 m day and night, with much of their populations ranging well

below 1000 m (Fasham & Foxton 1979, Hargreaves 1985, Domanski 1986, Krygier & Murano 1988), and hence out of our sampling coverage. The salient feature of the micronektonic crustacean population in the upper 1000 m is vertical migration, with species which account for 90% of the numbers and biomass of the assemblage moving into shallower depths at night (Fig. 1, Table 1).

Trophic ecology

Considering the entire decapod and mysid population, the principal food is crustacean, which accounts for nearly half (46%) of the biomass consumed by the assemblage. This is predictable given that crustaceans predominate in the size range of plankton utilized by micronekton (Hopkins 1982). Within the Crustacea, euphausiids are the most important food (28%), followed by copepods (17%). The role of decapods and mysids in low latitude ecosystems, then, is similar to that of the dominant midwater fish groups, with these being zooplanktivorous and relying heavily as crustacean prey. Over 60% of the biomass of food consumed by myctophids, gonostomatids, sternoptychids and photichthyids in the eastern Gulf is crustacean (Hopkins & Baird 1981, 1985, Lancraft et al. 1988, Hopkins & Gartner 1992, Hopkins unpubl. data). The overall trophic position of midwater micronektonic crustaceans, however, is not identical to that of the dominant midwater fishes, in that fish, cnidarians and water column debris appear to play a more important role in the diets of micronektonic crustaceans than in the midwater fish groups mentioned above. These 3 diet components have also been recorded by others for a wide range of micronektonic crustaceans (Aizawa 1974, Foxton & Roe 1974, Omori 1974, Donaldson 1975, Roe 1984, Nishida et al. 1988). While the biomass contribution of small fishes to diets of decapods and mysids has been estimated in the present study (27% of the biomass consumed by the assemblage), that of the cnidarians and water column (olive-green) debris was not. Cnidarian remains were especially common in the foreguts of the decapod genera *Sergia*, *Genadas*, *Acanthephyra*, *Systellaspis* and *Parapandalus* but were usually represented by nematocyst clusters which are difficult to convert to food biomass. Consequently the biomass, and therefore, caloric importance of cnidarians to the diets of micronektonic crustaceans has been underestimated. The olive-green debris observed in foreguts could be fecal pellets (Omori 1974), material from the phaeodia vacuoles of large radiolarians (Roe 1984) and/or marine snow. The debris in diets closely resembles the marine snow described by Alldredge & Silver (1988) and was absent

only from the diets of *Oplophorus gracilirostris*, *Pasiphaea merriami* and the mysids. Highest incidences and greatest quantities occurred in the Aristeidae, the most abundant group in the assemblage. This indicates that some of the settling water column debris, perhaps mostly as marine snow, is entering the oceanic food web at the micronekton trophic level, and that micronektonic crustaceans play a role in retaining and recycling this organic matter in the upper layers of the ocean. It also suggests that micronektonic crustaceans are a component of the microbial loop since this olive-green material is heavily invested with phytoplankton and microheterotrophs.

The predation impact of micronektonic assemblages on zooplankton stocks is unknown. This is so because of the difficulty in determining natural feeding rates *in situ*, under laboratory conditions, or from preserved collections (i.e. through diet analysis). For the present, a general estimate of carbon utilization by the micronektonic crustacean assemblage can be calculated indirectly for the purpose of oceanic carbon flux modeling, by applying daily ration information available from other micronektonic groups having comparable weight-specific metabolic rates in the eastern Gulf. Myctophid fishes meet this criterion (Donnelly & Torres 1988), and estimates of their daily ration in terms of body weight percentage (BW), summarized in Palomares & Pauly (1989), fall in the range of 3 to 10% (avg. = 6%; n = 8 spp.). Decapod and mysid biomass in the upper 1000 m of the eastern Gulf of Mexico is 0.18 g dry wt m^{-2} , and assuming a daily ration of 6% BW for the assemblage, the zooplankton biomass ingested is 0.18×0.06 or 0.011 g dry wt m^{-2} (≈ 0.005 g C m^{-2}). Zooplankton biomass in the upper 1000 m is 1.2 g dry wt m^{-2} , hence daily predation by decapods and mysids on zooplankton stocks is 0.011×1.2 , or $\sim 1\%$. A daily production to biomass ratio (P:B) for meso- and macrozooplankton in low latitude oligotrophic systems has been reported at 0.05:1 (Shushkina 1973, 1985), which converts to a daily biomass production for eastern Gulf zooplankton of 0.05×1.2 , or 0.06 g dry wt m^{-2} . The portion of this production consumed by midwater decapods and mysids, then, is 0.011×0.06 or 18%. The daily consumption rate of the myctophid assemblage, using the same computational method, is estimated at 0.4% of zooplankton standing stocks (a downward revision of our earlier determination of 2%; Hopkins & Gartner 1992) and 8% of the zooplankton daily production. These 2 principal groups through predation account for only one-fourth of the zooplankton production, yet combined they constitute nearly half of the micronekton biomass taken with midwater trawls in the upper 1000 m of the eastern Gulf (Hopkins & Lancraft 1984). The question remains open, then, as to which taxonomic groups are accounting for most of the predation on the

meso- and macrozooplankton. Two likely important sources which have not been quantitatively investigated are predation from gelatinous megaplankton and that occurring within the zooplankton assemblage (i.e. zooplankton feeding on zooplankton).

Resource partitioning

Low latitude shrimp assemblages, as typified by that in the eastern Gulf, are characterized by a broad range of vertical distributions and diets. Others have suggested that resource partitioning of space and/or food does indeed occur among low latitude micronektonic shrimp and fish assemblages (e.g. Donaldson 1975, Clarke 1980, Roe 1984, Roe & Badcock 1984, Nishida et

al. 1988), with this being a mechanism for reducing competition. Evidence for resource partitioning should be more apparent in oligotrophic areas such as the eastern Gulf than in more productive areas where food is less limiting (Nishida et al. 1988). In our investigation of mysctophid food and space resource partitioning (Hopkins & Gartner 1992), we combined the results of cluster analyses into a master species-pairs matrix which enabled considering the food and space factors together. We found that resource partitioning in mysctophids based on these combined factors was at the species level rather than at the cohort or guild level. That is, species which co-occurred in space differed significantly in their diets and vice versa.

We prepared a similar combined factor species-pairs matrix (Fig. 7) for shrimps using the cluster results in

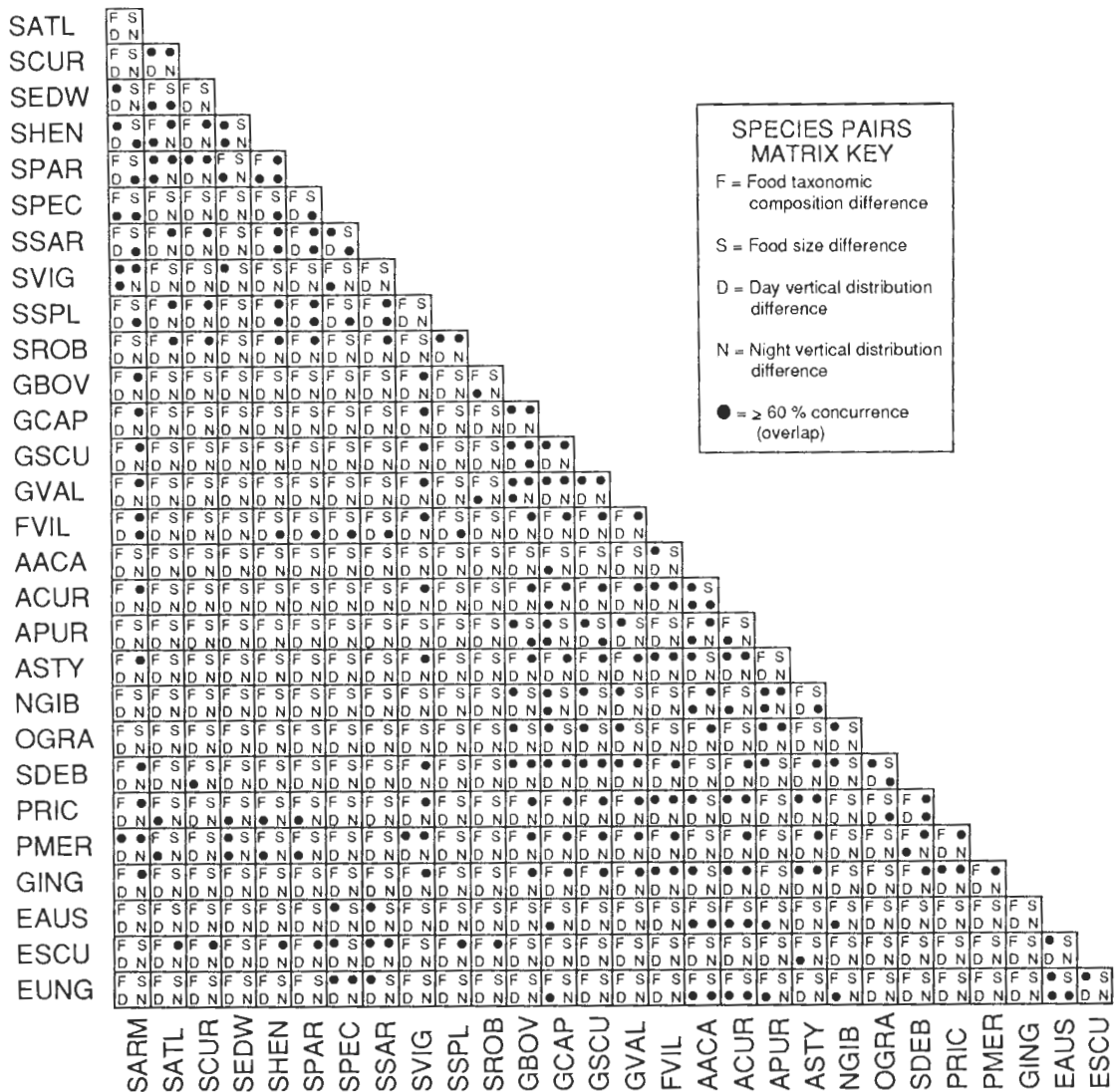


Fig. 7. Decapod and mysid species-pairs matrix summarizing the results of cluster analyses of diets and vertical distributions (see Figs. 2, 3, 5 & 6)

Figs. 2, 3, 5 & 6. The matrix shows, as in the case for myctophids, that when niche parameters are considered singly, cluster analysis results in a grouping primarily by cohorts or guilds. As more parameters are examined in combination, the trend is for smaller cohorts and for more separation at the species level. As an example, the diet component of the matrix reveals that 26 of 29 shrimp species had similar diets to other species or groups of species when food taxonomic composition and size are considered together. There are 28 species pairs, 1 guild of 3 species (SARM - SVIG - PMER) and 2 guilds of 5 species each (GBOV - GCAP - GSCU - GVAL - SDEB; FVIL - ACUR - ASTY - PRIC - GING) with similar diets. When considering diel vertical distribution, 11 species had day and night distribution patterns similar to other species or groups of species, with these forming 9 species pairs and 1 cohort of 4 species (ACUR - AACA - EAUS - EUNG). If these diet and spatial niche parameters are in turn combined and the matrix re-analyzed, the result is that no species pair is similar in both the diet and space niche parameters considered (i.e. each species pair differed in at least one of the parameters). Our data suggest, then, as in the case of one of the other major components of the eastern Gulf pelagial, the myctophid fishes, that resource partitioning in the midwater shrimp assemblage is at the between-species level.

Two major groups of micronekton, then, the midwater 'shrimps' and the myctophids, while showing high intrageneric (e.g. *Sergestes* and *Diaphus*) and overall species diversity, demonstrate species-specific niche separation in a physically 'structureless' ecosystem. The likely factors enabling the evolution of resource partitioning in low latitude oceanic environments are variations in the depth distribution of food (zooplankton), light and temperature. A necessary criterion, however, for these factors to operate in effecting niche separation, as Sanders (1968) suggested for benthic communities, is habitat stability over time. As noted by Lehman (1988) in his discussion of zooplankton community structure in marine and freshwater environments, the low latitude oceanic ecosystem is among the earth's most ancient.

Acknowledgements. This research was funded by National Science Foundation contracts DES 75-03845 and OCE 84-10787. We thank Tracey Sutton for running the cluster analyses, Lisa Thurm and Madeleine Marchy for manuscript preparation and Tom Lancraft and José Torres for manuscript review. We also thank the Florida Institute of Oceanography for their excellent shiptime services.

LITERATURE CITED

Aizawa, Y. (1974). Ecological studies of micronektonic shrimps (Crustacea, Decapoda) in the western north Pacific. *Bull. Ocean Res. Inst., Univ. Tokyo* 6: 1-84

- Aldredge, A. L., Silver, M. W. (1988). Characteristics, dynamics and significance of marine snow. *Prog. Oceanogr.* 20: 41-82
- Bennett, J. L., Hopkins, T. L. (1989). Aspects of the ecology of the calanoid copepod genus *Pleuromamma* in the eastern Gulf of Mexico. *Contrib. mar. Sci.* 31: 119-136
- Berkes, F. (1976). Ecology of euphausiids in the Gulf of St. Lawrence. *J. Fish Res. Bd Canada* 33: 1894-1905
- Borodulina, O. D. (1972). The feeding of mesopelagic predatory fish in the open ocean. *J. Ichthyol.* 12: 692-703
- Bray, J. R., Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-349
- Chace, F. A. Jr (1940). Plankton of the Bermuda Oceanographic Expeditions, IX: the bathypelagic caridean Crustacea. *Zoologica* 25: 117-209
- Clarke, T. A. (1980). Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters. *Fish. Bull. U.S.* 78: 619-640
- Clarke, T. A. (1982). Feeding habits of stomiatoid fishes from Hawaiian waters. *Fish. Bull. U.S.* 80: 287-304
- Domanski, P. A. (1986). The Azores front: a zoogeographic boundary? In: Pierrot-Bults, A. C., Zahuranec, B. J., Johnson, R. K. (eds.) *Pelagic biogeography*. UNESCO Tech. Pap. Mar. Sci. 49: 73-83
- Donaldson, H. A. (1975). Vertical distribution and feeding of sergestid shrimps (Decapoda: Natantia) collected near Bermuda. *Mar. Biol.* 31: 37-50
- Donnelly, J., Torres, J. J. (1988). Oxygen consumption of midwater fishes and crustaceans from the eastern Gulf of Mexico. *Mar. Biol.* 97: 483-494
- Fasham, M. J. R., Foxton, P. (1979). Zonal distribution of pelagic decapods (Crustacea) in the eastern north Atlantic and its relation to the physical oceanography. *J. exp. mar. Biol. Ecol.* 37: 225-253
- Flock, M. E., Hopkins, T. L. (1992). Species composition, vertical distribution, and food habits of the sergestid shrimp assemblage in the eastern Gulf of Mexico. *J. crust. Biol.* 12: 210-223
- Foxton, P. (1970a). The vertical distribution of pelagic decapods (Crustacea: Natantia) collected on the SONDA cruise 1965. I. The Caridea. *J. mar. biol. Ass. U.K.* 50: 939-960
- Foxton, P. (1970b). The vertical distribution of pelagic decapods (Crustacea: Natantia) collected on the SONDA cruise 1965. II. The Penaeidea and general discussion. *J. mar. biol. Ass. U.K.* 50: 961-1000
- Foxton, P., Roe, H. S. J. (1974). Observations on the nocturnal feeding of some mesopelagic decapod Crustacea. *Mar. Biol.* 28: 37-49
- Gartner, J. V. Jr, Hopkins, T. L., Baird, R. C., Milliken, D. M. (1987). The lanternfishes of the eastern Gulf of Mexico. *Fish. Bull. U.S.* 85: 81-98
- Hargreaves, P. M. (1985). The vertical distribution of Decapoda, Euphausiacea, and Mysidacea at 42° N, 17° W. *Biol. Oceanogr.* 3: 431-464
- Heffernan, J. J., Hopkins, T. L. (1981). Vertical distribution and feeding of the shrimp genera *Gennadas* and *Bentheogennema* (Decapoda: Penaeidea) in the eastern Gulf of Mexico. *J. crust. Biol.* 1: 461-473
- Hopkins, T. L. (1982). The vertical distribution of zooplankton in the eastern Gulf of Mexico. *Deep Sea Res.* 29: 1069-1083
- Hopkins, T. L., Baird, R. C. (1975). Net feeding in mesopelagic fishes. *Fish. Bull. U.S.* 73: 908-914
- Hopkins, T. L., Baird, R. C. (1981). Trophodynamics of the fish *Valenciennellus tripunctulatus*. I. Vertical distribution, diet and feeding chronology. *Mar. Ecol. Prog. Ser.* 4: 1-10

- Hopkins, T. L., Baird, R. C. (1985). Feeding ecology of four hatchetfishes (Sternoptychidae) in the eastern Gulf of Mexico. *Bull. mar. Sci.* 36: 260–277
- Hopkins, T. L., Baird, R. C., Milliken, D. M. (1973). A messenger operated closing trawl. *Limnol. Oceanogr.* 18: 488–490
- Hopkins, T. L., Gartner, J. V. Jr (1992). Resource-partitioning and predation impact of a low latitude myctophid community. 114: 185–197
- Hopkins, T. L., Gartner, J. V. Jr, Flock, M. E. (1989). The caridean shrimp (Decapoda: Natantia) assemblage in the mesopelagic zone of the eastern Gulf of Mexico. *Bull. mar. Sci.* 45: 1–14
- Hopkins, T. L., Lancraft, T. M. (1984). The composition and standing stock of mesopelagic micronekton at 27° N, 86° W in the eastern Gulf of Mexico. *Contrib. mar. Sci.* 27: 143–158
- Judkins, D. C., Fleminger, A. (1972). Comparison of foregut contents of *Sergestes similis* obtained from net collections and albacore stomachs. *Fish. Bull. U.S.* 70: 217–223
- Kinsey, S. T., Hopkins, T. L. (1994). Trophic strategies of euphausiids in a low latitude ecosystem. *Mar. Biol.* 118: 651–661
- Krygier, E. E., Murano, M. (1988). Vertical distributions and zoogeography of oceanic mysids from the northeastern Pacific Ocean. *Bull. Ocean Res. Inst., Univ. Tokyo* 26: 109–122
- Lancraft, T. M., Hopkins, T. L., Torres, J. J. (1988). Aspects of the ecology of the mesopelagic fish *Gonostoma elongatum* (Gonostomatidae, Stomiiformes) in the eastern Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 49: 27–40
- Lehman, J.T. (1988). Geological principles affecting community structure and secondary production by zooplankton in marine and freshwater environments. *Limnol. Oceanogr.* 33:931–945
- Maul, G. A. (1977). The annual cycle of the Gulf Loop Current. Part 1: observations during a one year time series. *J. mar. Res.* 35: 29–47
- Maynard, S. D. (1982). Aspects of the biology of mesopelagic fishes of the genus *Cyclothone* (Pisces: Gonostomatidae) in Hawaiian waters. Ph.D. dissertation, Univ. Hawaii, Honolulu
- Maynard, S. D., Riggs, F. V., Walters, J. F. (1975). Mesopelagic micronekton in Hawaiian waters: faunal composition, standing stock, and diel vertical migration. *Fish. Bull. U.S.* 73: 726–736
- Michel, H. B., Foyo, M. (1976). Caribbean zooplankton. Part I. Siphonophora, Heteropoda, Copepoda, Euphausiacea, Chaetognatha and Salpidae. Report to the Office of Naval Research. U.S. Govt. Print. Off., Washington, DC, Stock no. 608-051-00066-6, p. 1–549
- Nishida, S., Pearcy, W. G., Nemoto, T. (1988). Feeding habits of mesopelagic shrimps collected off Oregon. *Bull. Ocean Res. Inst., Univ. Tokyo* 26: 99–108
- Omori, M. (1974). The biology of the pelagic shrimps in the ocean. *Adv. mar. Biol.* 12: 233–342
- Palomares, M. L., Pauly, D. (1989). A multiple regression model for predicting the food consumption of marine fish populations. *Aust. J. mar. Freshwat. Res.* 40: 259–273
- Passarella, K. C., Hopkins, T. L. (1991). Species composition and food habits of the micronektonic cephalopod assemblage in the eastern Gulf of Mexico. *Bull. mar. Sci.* 49: 638–659
- Roe, H. S. J. (1984). The diel migrations and distributions within a mesopelagic community in the northeast Atlantic. 2. Vertical migrations and feeding of mysids and decapod Crustacea. *Prog. Oceanogr.* 13: 269–318
- Roe, H. S. J., Badcock, J. (1984). The diel migrations and distributions within a mesopelagic community in the northeast Atlantic. 5. Vertical migrations and feeding of fish. *Prog. Oceanogr.* 13: 389–424
- Romesburg, H. C. (1990). Cluster analysis for researchers. R. E. Krygier Publ. Co., Malabar, FL
- Sanders, H.L. (1968). Marine benthic diversity: a comparative study. *Am. Nat.* 102: 243–282.
- Shushkina, E. A. (1973). Evaluation of the production of tropical zooplankton. In: Vinogradov, M. E. (ed.) Life activity of pelagic communities in the ocean tropics. Akad. Nauk. SSSR, Moscow, p. 172–183
- Shushkina, E. A. (1985). Production of principal ecological groups of plankton in the epipelagic zone of the ocean. *Oceanology* 25: 653–658
- Sturges, W., Evans, J. C. (1983). On the variability of the Loop Current in the Gulf of Mexico. *J. mar. Res.* 41: 639–653
- Walters, J. F. (1976). Ecology of Hawaiian sergestid shrimps (Penaeidea: Sergestidae). *Fish. Bull. U.S.* 74: 799–836
- Zaret, T. M., Rand, A. S. (1971). Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* 52: 336–342
- Ziemann, D. A. (1975). Patterns of vertical distribution, vertical migration and reproduction in the Hawaiian mesopelagic shrimps of the family Ophrophoridae. Ph.D. thesis, Univ. Hawaii, Honolulu

This article was presented by R. L. Haedrich (Senior Editorial Advisor), St. John's, Nfld., Canada

Manuscript first received: June 16, 1993

Revised version accepted: February 16, 1994