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Midwater fishes and shrimps as competitors and resource partitioning in low latitude oligotrophic ecosystems

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ABSTRACT: Oligotrophic tropical-subtropical oceanic regimes constitute the largest and most ancient ecosystem on earth, with these enormous areas being characterized by high faunal diversity. The stability and age of the ecosystem have enabled the evolution of many similar species niches where there is considerable overlap in niche parameters such as food and space, resulting in high species packing, especially in the epi- and mesopelagic zones. Competition for limited resources undoubtedly exists and has been described by MacArthur (1972; *Geographical ecology*, Harper and Row, New York) as diffuse competition where each species is impacted by many other species sharing the environment. Most studies of resource partitioning in the oceanic pelagial have been restricted to specific taxonomic groups, such as copepods, fishes, shrimps, or cephalopods, and intergroup relationships have not been examined. The 2 dominant (numbers and biomass) components of low latitude midwater micronekton communities, based on trawl catches, are fishes and shrimps, and the present study reveals that species from each of these 2 assemblages occur in the same feeding guilds and hence potentially compete for food resources. However, as additional niche parameters are included in the analysis, such as food size and predator vertical distribution, groups of species with matching niche characteristics become increasingly smaller. Results of this study suggest that as additional information on individual life histories is obtained, such as data on seasonality of reproduction and population dynamics, the same pattern will emerge as we have found for fishes and shrimps considered separately, i.e. that resource partitioning occurs at the species level despite the pressures of diffuse intra- and intergroup competition. This minimizes competitive exclusion and enables the maintenance of a high-diversity fauna in resource-poor low latitude ecosystems.

KEY WORDS: Gulf of Mexico · Oceanic ecosystem · Decapods · Myctophids · Food web · Vertical distribution

INTRODUCTION

Of enduring interest to pelagic oceanic ecologists is the phenomenon of high faunal diversity in low latitude oligotrophic oceans (e.g. Hutchinson 1959, 1961). This occurs in a seemingly low structure environment, with light, temperature and pressure demonstrating the only major physical changes with depth. For example, the micronekton assemblage in the eastern Gulf of Mexico (EGOM) is comprised of over 200 species of midwater fishes, over 50 species of decapod and mysid

shrimps and approximately 60 species of cephalopods and large heteropods in the upper 1000 m, with most occurring in the upper 200 to 300 m at night. Many of these species share the same vertical zones and food resources, and the obvious question is how diversity is maintained with a presumed minimum loss of species from the system due to competitive exclusion. MacArthur (1972, see also Pianka 1974) suggested that individual species in complex ecosystems are impacted by many other species, the results being cumulative 'diffuse competition'. Most studies addressing resource partitioning in the midwater pelagial have been limited to discrete taxonomic groups such as fishes (Clarke 1978, Domanski 1984, Hopkins & Gartner

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1992), shrimps (Donaldson 1975, Walters 1976, Hefferman & Hopkins 1981, Flock & Hopkins 1992, Hopkins et al. 1994) or cephalopods (Passarella & Hopkins 1991), whereas diffuse competition may include species from widely disparate taxonomic groups which competitively interact. Previous studies (e.g. Maynard et al. 1975, Hopkins & Lancraft 1984) have shown that the 2 dominant components of low latitude micronekton communities are shrimps and fishes, and that these 2 components show spatial concurrence and dietary similarities. In this paper, we examine aspects of diet and vertical distribution of the midwater fishes and shrimps in the EGOM, a low latitude oligotrophic environment, and apply cluster analyses to assess the amount of niche overlap in these 2 groups. Our objective is to enable further insight in the phenomenon of rich faunal diversity in the low latitude pelagial.

MATERIALS AND METHODS

Information on midwater fish and shrimp assemblage structure has been accumulated over a 20 yr sampling period (25 cruises) at 27°N 86°W, a station of 3200 m depth in the EGOM. The various types of opening-closing midwater trawls used, including a MOCNESS (Wiebe et al. 1976), are described in Hopkins et al. (1973), Hopkins & Baird (1975), Gartner et al. (1987) and Hopkins et al. (1996). Our sampling (1155 discrete trawl samples) has enabled us to resolve vertical distributions in the upper 1000 m to contiguous 25 m depth intervals. Diet information used in this study was from 4991 fish specimens from 26 species (range per species: 40 to 450; mean number per species: 192) and 1070 shrimp specimens from 21 species (range: 10 to 155; mean: 51). Fish and shrimp gut contents were examined microscopically in water or fuchsin-acid-stained glycerin. Contents were identified to the lowest possible taxonomic level and food measurements (to the nearest 0.1 mm) were converted to estimates of dry organic weight of undigested prey using procedures described in Hopkins & Gartner (1992), Hopkins et al. (1994, 1996), and Sutton & Hopkins (1996a).

A principal consideration in the present analysis is post-capture feeding in trawl net cod ends. As stated in Hopkins et al. (1996), and others (Clarke 1978, 1980, Roe & Badcock 1984), net feeding appears to be a minor source of bias because (1) it is usually readily recognized as such when it occurs, (2) gut fullness shows diel periodicity even though prey is always abundant in the cod end, (3) consistent differences are observed in diets of species occurring in the same trawl catches, (4) most micronektonic fishes and shrimps were small, fragile and arrived on deck to some degree damaged or moribund, and (5) stomach and intestinal

contents (the latter presumably with a pre-trawl catch residence time) were similar.

Species in the present investigation were compared for each of 3 niche parameters, diet composition (% of food biomass of each of 15 prey categories: copepod, ostracod, amphipod, euphausiid, decapod, larvacean, salp, siphonophore, unidentified gelatinous tunic, polychaete, gastropod, cephalopod, chaetognath, fish, and other food), prey size (% of food biomass in each of 13 size categories: <1.0, 1–1.9, 2–2.9, 3–3.9, 4–4.9, 5–5.9, 6–6.9, 7–7.9, 8–8.9, 9–9.9, 10–14.9, 15–19.9, >20 mm) and species nighttime vertical distribution (% of species population numbers in each 25 m zone from the surface to a depth of 1000 m). For each niche parameter, Bray-Curtis (1957) dissimilarity indices were calculated for all combinations of cluster unit pairs, then these indices were subjected to hierarchical unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis (Romesburg 1990) to determine taxonomic groupings for each of the 3 parameters. Clusters were defined at the 40% dissimilarity level as in previous studies (Zaret & Rand 1971, Berkes 1976, Hopkins & Gartner 1992).

The comparisons involved many more cluster units of fishes than shrimps (77 vs 21 units), this being a result of diet changes with ontogeny in fishes [detected by previous cluster analyses (see Hopkins et al. 1996)]. Many fish species were considered by size class, and numerical designations after fish species names (see Table 1) represent size class in 10 mm intervals of standard length (SL) (for example, 2: 20–29 mm SL, 3: 30–39 mm SL, and pairs of numbers separated by a slash, e.g. 10/19, represent pooled data for several size classes, in this case 100–199 mm SL). Pooling was applied to very large fish species [e.g. *Gonostoma elongatum*, the Stomiidae (*sensu* Fink 1985)] which have a large size range. Changes in diet with ontogeny in shrimps are highly probable, but were not detectable through cluster analysis (Hopkins et al. 1994). This contrast in ontogenetic diet patterns for fishes and shrimps in part results from differences in the way prey is manipulated in these 2 groups—fish swallow prey whole, so prey size is limited by mouth size, whereas shrimps masticate their food.

Data from the 3 cluster analyses were combined in a trellis matrix (e.g. see Fig. 7 in Hopkins et al. 1994) which compared all combinations of cluster unit pairs. The matrix grid was tallied square by square for cluster unit pairs which demonstrated no niche separation, or niche separation by a single parameter, by 2 parameters, or by all 3 parameters. The term 'cluster unit' is used rather than 'species' in describing cluster and trellis matrix composition because in the case of fishes more than 1 size class could occur in a single cluster and/or in several different clusters. The trellis matrix

and parameter cluster analyses are summarized in tables rather than included in the paper because of their large dimensions in relation to journal page size.

RESULTS

Prey item composition

The species treated in cluster analyses are listed in Table 1. These species combined represent 90 and 99%, respectively, of the numbers of fishes and shrimps in the upper 1000 m of the EGOM. The cluster analysis summary for diet composition (Table 2), based on 20 183 and 3302 prey items of fish and shrimp, respectively, revealed 2 large clusters (Clusters 1 and 2), 2 of intermediate size (Clusters 11 and 14) with most of the remainder (14 clusters) containing only 1 to 4 cluster units. All 4 of the large- and intermediate-sized clusters included both fishes and shrimps.

Cluster 1, the largest (29 cluster units), combined predators which fed almost entirely on small crustaceans (food biomass range: 80 to 100%; mean: 97%), with copepods the overwhelmingly dominant prey (range: 67 to 99%; mean: 86%). The potential for competition between fishes and shrimps for the same resource is apparent in Table 3, which lists the principal copepod genera in the diets of myctophids and sergestids, 2 of the dominant families in the fish and shrimp assemblages, respectively. Eleven of the 15 (including 4 of the top 5) copepod prey genera appeared in both lists. It should be noted that 89 and 81% of the copepods encountered in the digestive tracts of myctophids and sergestids, respectively, were identified at least to genus. Hence, any bias due to unidentified copepods was small. At the head of each list is the copepod genus *Pleuromamma* (of which there are 4 abundant species in the EGOM), with *P. abdominalis* and *P. xiphias* contributing the most biomass to the diets of both myctophids and sergestids. Cluster 2, with 21 cluster units, aggregated fishes and shrimps which fed on small crustaceans (range: 66 to 100%; mean: 87%) including copepods, ostracods and amphipods, along with small euphausiids and decapods. Copepods were again the principal food biomass (range: 29 to 57%; mean: 45%), but contributed proportionately less to diets than in Cluster 1.

Table 1. List of species of midwater fishes and shrimps from the eastern Gulf of Mexico used in cluster analyses. Numbers in parentheses are size classes of fishes examined (see 'Materials and methods' for size code)

Fishes	Shrimps
Family Myctophidae	Family Sergestidae
<i>Benthoosema suborbitale</i> (1, 2)	<i>Sergestes armatus</i>
<i>Ceratoscopelus warmingii</i> (1, 2, 3, 4)	<i>Sergestes atlanticus</i>
<i>Diaphus dumerilii</i> (1, 2, 3)	<i>Sergestes edwardsii</i>
<i>Diaphus lucidus</i> (3, 4, 5, 6)	<i>Sergestes henseni</i>
<i>Diaphus mollis</i> (2, 3, 4)	<i>Sergestes paraseminudus</i>
<i>Lampanyctus alatus</i> (1, 2, 3, 4)	<i>Sergestes pectinatus</i>
<i>Lepidophanes guentheri</i> (1, 2, 3, 4, 5, 6)	<i>Sergestes sargassi</i>
<i>Myctophum affine</i> (1, 2, 3)	<i>Sergestes vigilax</i>
<i>Notolychnus valdiviae</i> (1, 2)	<i>Sergia robustus</i>
<i>Notoscopelus resplendens</i> (2, 3, 4, 5)	<i>Sergia splendens</i>
Family Gonostomatidae	Family Aristeidae
<i>Cyclothone acclinidens</i> (1, 2, 3)	<i>Gennadas bouvieri</i>
<i>Cyclothone alba</i> (1, 2)	<i>Gennadas capensis</i>
<i>Cyclothone braueri</i> (1, 2)	<i>Gennadas scutatus</i>
<i>Cyclothone pallida</i> (2/3, 4)	<i>Gennadas valens</i>
<i>Cyclothone pseudopallida</i> (1, 2, 3)	Family Oplophoridae
<i>Gonostoma elongatum</i> (1/2, 3/4, 5/7, 8/9, 10/12)	<i>AcanthePHYRA curtirostris</i>
Family Phosichthyidae	<i>AcanthePHYRA purpurea</i>
<i>Vinciguerria nimbaria</i> (1, 2, 3)	<i>Systellaspis debilis</i>
<i>Vinciguerria poweriae</i> (1, 2, 3)	Family Pandalidae
Family Sternoptychidae	<i>Parapandalus richardi</i>
<i>Argyropelecus aculeatus</i> (1, 2, 3, 4/5)	Family Eucopiidae (mysid)
<i>Argyropelecus hemigymnus</i> (1, 2)	<i>Eucopia australis</i>
<i>Sternoptyx diaphana</i> (1, 2, 3)	<i>Eucopia sculpticauda</i>
<i>Sternoptyx pseudobscura</i> (1, 2, 3, 4/5)	<i>Eucopia unguiculata</i>
<i>Valenciennellus tripunctulatus</i> (1, 2, 3)	
Family Stomiidae	
<i>Chauliodus sloani</i> (2/20)	
<i>Photostomias guernei</i> (3/12)	
<i>Stomias affinis</i> (2/19)	

Cluster 11, with 10 cluster units, was another mixed group of fishes and shrimps which fed primarily on crustaceans (range: 76 to 99%; mean: 88%), but with larger prey such as euphausiids playing a more important role in diets (range: 40 to 79%; mean: 59%). Fishes occurred in the diet of some of these predators as well (maximum 25% in the diet of *Gonostoma elongatum* 5/7). Cluster 14, mostly a shrimp cohort (8 of 9 species), was characterized by a mixed diet of both crustacean (range: 26 to 55%; mean: 42%) and non-crustacean (range: 45 to 73%; mean: 58%) food, with larger elongate prey such as chaetognaths (mean: 14%), euphausiids (mean: 26%) and fishes (mean: 34%) contributing the most to food biomass.

It is apparent from Table 2 that different size classes of many fish species (e.g. *Gonostoma elongatum*, *Ceratoscopelus warmingii*, *Argyropelecus aculeatus*, *Sternoptyx diaphana*, *S. pseudobscura*) fall into different clusters. This primarily resulted from changes in diet composition with ontogeny. Also, what appears to be marine snow was prominent in the stomachs of certain shrimps, e.g. the 4 aristeid *Gennadas* spp. and

Table 2. Cluster analysis summary of diet composition (% of food biomass of each prey type) of the fish and shrimp assemblages in the upper 1000 m of the eastern Gulf of Mexico. Cluster units listed in the sequence they occurred in each cluster. Numbers after species names indicate size class

Cluster 1	<i>Cyclothone acclinidens</i> -2, <i>Cyclothone acclinidens</i> -3, <i>Cyclothone braueri</i> -2, <i>Cyclothone pseudopallida</i> -3, <i>Sergestes pectinatus</i> , <i>Cyclothone pseudopallida</i> -1, <i>Cyclothone pseudopallida</i> -2, <i>Cyclothone alba</i> -1, <i>Notolychnus valdiviae</i> -1, <i>Cyclothone braueri</i> -1, <i>Cyclothone alba</i> -2, <i>Valenciennellus tripunctulatus</i> -3, <i>Valenciennellus tripunctulatus</i> -1, <i>Valenciennellus tripunctulatus</i> -2, <i>Eucopia sculpticauda</i> , <i>Eucopia australis</i> , <i>Myctophum affine</i> -2, <i>Myctophum affine</i> -3, <i>Lampanyctus alatus</i> -1, <i>Notolychnus valdiviae</i> -2, <i>Sergestes sargassi</i> , <i>Notoscopelus resplendens</i> -2, <i>Lepidophanes guentheri</i> -1, <i>Benthoosema suborbitale</i> -1, <i>Benthoosema suborbitale</i> -2, <i>Lampanyctus alatus</i> -2, <i>Myctophum affine</i> -1, <i>Eucopia unguiculata</i> , <i>Diaphus mollis</i> -4
Cluster 2	<i>Lampanyctus alatus</i> -3, <i>Notoscopelus resplendens</i> -5, <i>Lampanyctus alatus</i> -4, <i>Lepidophanes guentheri</i> -2, <i>Lepidophanes guentheri</i> -5, <i>Lepidophanes guentheri</i> -6, <i>Lepidophanes guentheri</i> -3, <i>Sergestes atlanticus</i> , <i>Sergestes paraseminudus</i> , <i>Cyclothone pallida</i> -2/3, <i>Vinciguerria poweriae</i> -1, <i>Ceratoscopelus warmingii</i> -1, <i>Sternoptyx pseudobscura</i> -2, <i>Notoscopelus resplendens</i> -3, <i>Notoscopelus resplendens</i> -4, <i>Gonostoma elongatum</i> -1/2, <i>Gonostoma elongatum</i> -3/4, <i>Diaphus dumerilii</i> -1, <i>Diaphus dumerilii</i> -2, <i>Cyclothone acclinidens</i> -1, <i>Cyclothone pallida</i> -4
Cluster 3	<i>Diaphus mollis</i> -2, <i>Diaphus mollis</i> -3, <i>Diaphus dumerilii</i> -3, <i>Sergia robustus</i> , <i>Sergia splendens</i>
Cluster 4	<i>Sternoptyx pseudobscura</i> -1
Cluster 5	<i>Sternoptyx pseudobscura</i> -3
Cluster 6	<i>Argyropelecus aculeatus</i> -1, <i>Argyropelecus hemigymnus</i> -1, <i>Argyropelecus hemigymnus</i> -2
Cluster 7	<i>Ceratoscopelus warmingii</i> -2, <i>Ceratoscopelus warmingii</i> -3
Cluster 8	<i>Ceratoscopelus warmingii</i> -4
Cluster 9	<i>Sternoptyx diaphana</i> -2, <i>Sternoptyx diaphana</i> -3
Cluster 10	<i>Sternoptyx diaphana</i> -1
Cluster 11	<i>Gonostoma elongatum</i> -5/7, <i>Vinciguerria poweriae</i> -2, <i>Vinciguerria poweriae</i> -3, <i>Gonostoma elongatum</i> -8/9, <i>Gonostoma elongatum</i> -10/12, <i>Sergestes armatus</i> , <i>Sergestes vigilax</i> , <i>Sergestes edwardsii</i> , <i>Lepidophanes guentheri</i> -4, <i>Sergestes henseni</i>
Cluster 12	<i>Diaphus lucidus</i> -5, <i>Diaphus lucidus</i> -6, <i>Diaphus lucidus</i> -4
Cluster 13	<i>Argyropelecus aculeatus</i> -2, <i>Argyropelecus aculeatus</i> -3
Cluster 14	<i>Gennadas bouvieri</i> , <i>Gennadas capensis</i> , <i>Gennadas valens</i> , <i>Gennadas scutatus</i> , <i>Vinciguerria nimbaria</i> -3, <i>Acanthephyra purpurea</i> , <i>Systellaspis debilis</i> , <i>Acanthephyra curtirostris</i> , <i>Parapandalus richardi</i>
Cluster 15	<i>Chauliodus sloani</i> -2/20, <i>Stomias affinis</i> -2/19, <i>Sternoptyx pseudobscura</i> -4/5
Cluster 16	<i>Vinciguerria nimbaria</i> -1, <i>Vinciguerria nimbaria</i> -2
Cluster 17	<i>Argyropelecus aculeatus</i> -4/5
Cluster 18	<i>Diaphus lucidus</i> -3, <i>Photostomias guernei</i> -3/12

Table 3. Comparison of copepod composition (% biomass of copepods identified to genus) in diets of the Myctophidae and Sergestidae of the eastern Gulf of Mexico

Myctophidae		Sergestidae	
Prey genus	% diet	Prey genus	% diet
<i>Pleuromamma</i>	48.3	<i>Pleuromamma</i>	39.9
<i>Euchaeta</i>	12.3	<i>Euchaeta</i>	22.2
<i>Undeuchaeta</i>	8.2	<i>Candacia</i>	21.3
<i>Undinula</i>	5.4	<i>Undinula</i>	4.7
<i>Candacia</i>	4.5	<i>Chirundina</i>	2.6
<i>Scolecithrix</i>	4.5	<i>Euchirella</i>	2.4
<i>Nannocalanus</i>	2.9	<i>Eucalanus</i>	2.2
<i>Corycaeus</i>	2.9	<i>Scottocalanus</i>	1.1
<i>Temora</i>	2.0	<i>Nannocalanus</i>	0.8
<i>Neocalanus</i>	1.9	<i>Rhincalanus</i>	0.7
<i>Eucalanus</i>	1.5	<i>Corycaeus</i>	0.7
<i>Rhincalanus</i>	0.9	<i>Oncaea</i>	0.6
<i>Paracandacia</i>	0.8	<i>Paracandacia</i>	0.4
<i>Euchirella</i>	0.7	<i>Gaetanus</i>	0.3
<i>Scottocalanus</i>	0.7	<i>Phyllopus</i>	0.1
Other genera (8)	2.5	Other genera (1)	<0.1

the 2 *Sergia* spp. This material often constituted most of the food volume but was not successfully quantified by our methods in terms of biomass; these 2 shrimp genera perhaps belong in 1 or possibly 2 separate clusters.

Prey size

Cluster analysis of data on food size (Table 4) yielded 11 clusters, with 3 of these (Clusters 1, 5 and 7) containing 10 or more cluster units. Cluster 1, the largest, with 45 units, grouped species which fed mostly on relatively small prey (<6 mm). The percent range for this size fraction was 43 to 100% of food biomass, with an average of 70%. The species composition of this dominant cluster closely aligned (37 of 45 cluster units) with those in the large clusters (1 and 2) of the diet composition analysis (Table 2), where small- to intermediate-sized crustaceans were the principal food and copepods were the largest biomass category. Cluster 1

Table 4. Cluster analysis summary of size composition (% food biomass in each size category) of diets of Gulf of Mexico midwater fishes and shrimps. Listings are in order of occurrence in each cluster

Cluster 1	<i>Cyclothone acclinidens</i> -1, <i>Cyclothone acclinidens</i> -2, <i>Argyropelecus hemigymnus</i> -2, <i>Cyclothone alba</i> -2, <i>Cyclothone pseudopallida</i> -3, <i>Valenciennellus tripunctulatus</i> -3, <i>Cyclothone braueri</i> -2, <i>Notolychnus valdiviae</i> -2, <i>Cyclothone acclinidens</i> -3, <i>Notolychnus valdiviae</i> -1, <i>Sergestes sargassi</i> , <i>Cyclothone pseudopallida</i> -1, <i>Cyclothone pseudopallida</i> -2, <i>Cyclothone alba</i> -1, <i>Valenciennellus tripunctulatus</i> -2, <i>Cyclothone braueri</i> -1, <i>Sergestes pectinatus</i> , <i>Eucopia unguiculata</i> , <i>Sternoptyx pseudobscura</i> -1, <i>Myctophum affine</i> -2, <i>Valenciennellus tripunctulatus</i> -1, <i>Lampanyctus alatus</i> -1, <i>Myctophum affine</i> -3, <i>Benthoosema suborbitale</i> -1, <i>Lampanyctus alatus</i> -2, <i>Benthoosema suborbitale</i> -2, <i>Gonostoma elongatum</i> -3/4, <i>Notoscopelus resplendens</i> -2, <i>Lepidophanes guentheri</i> -1, <i>Gonostoma elongatum</i> -1/2, <i>Ceratoscopelus warmingii</i> -3, <i>Diaphus mollis</i> -4, <i>Ceratoscopelus warmingii</i> -2, <i>Lepidophanes guentheri</i> -2, <i>Eucopia sculpticauda</i> , <i>Ceratoscopelus warmingii</i> -1, <i>Vinciguerria poweriae</i> -1, <i>Diaphus dumerilii</i> -3, <i>Diaphus mollis</i> -2, <i>Cyclothone pallida</i> -2/3, <i>Diaphus dumerilii</i> -2, <i>Argyropelecus aculeatus</i> -1, <i>Argyropelecus hemigymnus</i> -1, <i>Diaphus dumerilii</i> -1, <i>Myctophum affine</i> -1
Cluster 2	<i>Sergestes paraseminudus</i> , <i>Sergia robustus</i> , <i>Sergia splendens</i> , <i>Sergestes atlanticus</i> , <i>Sergestes henseni</i> , <i>Sternoptyx pseudobscura</i> -2
Cluster 3	<i>Vinciguerria nimbaria</i> -2
Cluster 4	<i>Eucopia australis</i>
Cluster 5	<i>Diaphus lucidus</i> -4, <i>Sternoptyx diaphana</i> -3, <i>Lampanyctus alatus</i> -4, <i>Notoscopelus resplendens</i> -5, <i>Lepidophanes guentheri</i> -4, <i>Argyropelecus aculeatus</i> -2, <i>Lepidophanes guentheri</i> -3, <i>Lepidophanes guentheri</i> -6, <i>Lampanyctus alatus</i> -3, <i>Ceratoscopelus warmingii</i> -4, <i>Notoscopelus resplendens</i> -4, <i>Sternoptyx diaphana</i> -1, <i>Sternoptyx diaphana</i> -2, <i>Lepidophanes guentheri</i> -5, <i>Diaphus mollis</i> -3, <i>Notoscopelus resplendens</i> -3, <i>Argyropelecus aculeatus</i> -3
Cluster 6	<i>Gonostoma elongatum</i> -5/7, <i>Parapandalus richardi</i>
Cluster 7	<i>Acanthephyra curtirostris</i> , <i>Systellaspis debilis</i> , <i>Gennadas scutatus</i> , <i>Gennadas valens</i> , <i>Vinciguerria poweriae</i> -2, <i>Gennadas bouvieri</i> , <i>Gennadas capensis</i> , <i>Diaphus lucidus</i> -6, <i>Sergestes vigilax</i> , <i>Vinciguerria nimbaria</i> -3, <i>Vinciguerria poweriae</i> -3, <i>Sergestes armatus</i>
Cluster 8	<i>Cyclothone pallida</i> -4
Cluster 9	<i>Diaphus lucidus</i> -5, <i>Argyropelecus aculeatus</i> -4/5, <i>Gonostoma elongatum</i> -8/9, <i>Gonostoma elongatum</i> -10/12, <i>Sternoptyx pseudobscura</i> -3, <i>Acanthephyra purpurea</i>
Cluster 10	<i>Sternoptyx pseudobscura</i> -4/5, <i>Photostomias guernei</i> -3/12, <i>Chauliodus sloani</i> -2/20, <i>Diaphus lucidus</i> -3, <i>Stomias affinis</i> -2/19
Cluster 11	<i>Vinciguerria nimbaria</i> -1, <i>Sergestes edwardsii</i>

included both fishes and shrimps. Cluster 5, grouping 17 cluster units (all fishes), had members which also fed on small- to intermediate-sized prey, but most prey were smaller than 6 mm (range: 32 to 64%; mean: 53%). The composition of this cluster showed similarities (8 of 17 species concurrent) with diet composition Cluster 2. The third largest group, Cluster 7, was composed of 8 shrimp and 4 fish cluster units which fed on relatively large prey, most of which exceeded 10 mm (range: 41 to 74%; mean: 60%). Species composition was similar to that of diet composition Cluster 14 in which chaetognaths, euphausiids and fish averaged 74% of food biomass. Cluster 2 contained 6 cluster units, 1 fish (*Sternoptyx pseudobscura*) and 5 sergestid shrimp units, with food biomass approximately evenly split between less than 6 mm (mean: 54%) and greater than 6 mm (mean: 46%) prey. Cluster 9 also grouped 6 cluster units, including 1 shrimp, *Acanthephyra purpurea*. Most of the food biomass of members of this cluster exceeded 10 mm in size (range: 63 to 75%; mean: 67%) and consisted of chaetognaths, fish, euphausiids, and large pteropods and polychaetes. Cluster 10 aggregated 5 fish cluster units, 3 of which were the most abundant stomiid species in the EGOM,

Photostomias guernei, *Chauliodus sloani* and *Stomias affinis* (Sutton & Hopkins 1996b). Food biomass was mostly in the >10 mm size category (range: 72 to 99%; mean: 88%), with prey consisting primarily of large decapods and fishes. The remaining 5 clusters (3, 4, 6, 8 and 11) were comprised of 1 or 2 species each, and in 6 of 7 cases the major size fraction of food biomass was larger than 6 mm.

Spatial distribution

Cluster analysis of nighttime vertical distribution (Table 5) yielded the largest number of clusters, 26, of any of the 3 niche variables, with the species composition of these clusters having little apparent correlation with food type or size. Only 4 clusters contained 10 or more cluster units (Clusters 2, 4, 7 and 15). Cluster 2, the largest, had 18 cluster units, all fishes except for *Parapandalus richardi*. Fourteen of the 18 units had population centers (i.e. where half the population resides above and below a depth zone) in the middle of the epipelagic zone at 75 to 125 m, the median zone being 75 to 100 m. Cluster 4 had 11 cluster units which

Table 5. Cluster analysis summary of nighttime vertical distributions of midwater fishes and shrimps in the upper 1000 m of the eastern Gulf. Cluster units in sequence they occurred in each cluster

Cluster 1	<i>Diaphus lucidus</i> -3, <i>Diaphus lucidus</i> -4, <i>Notoscopelus resplendens</i> -3, <i>Notoscopelus resplendens</i> -5
Cluster 2	<i>Diaphus mollis</i> -3, <i>Diaphus mollis</i> -4, <i>Ceratoscopelus warmingii</i> -3, <i>Parapandalus richardi</i> , <i>Lepidophanes guentheri</i> -1-5, <i>Lepidophanes guentheri</i> -6, <i>Lepidophanes guentheri</i> -4, <i>Vinciguerria nimbaria</i> -1, <i>Vinciguerria nimbaria</i> -2, <i>Vinciguerria nimbaria</i> -3, <i>Ceratoscopelus warmingii</i> -1, <i>Ceratoscopelus warmingii</i> -2, <i>Ceratoscopelus warmingii</i> -4, <i>Diaphus dumerilii</i> -3, <i>Diaphus mollis</i> -2, <i>Lampanyctus alatus</i> -3, <i>Lampanyctus alatus</i> -4, <i>Notolychnus valdiviae</i> -2
Cluster 3	<i>Notoscopelus resplendens</i> -4
Cluster 4	<i>Diaphus lucidus</i> -5, <i>Diaphus lucidus</i> -6, <i>Vinciguerria poweriae</i> -1, <i>Vinciguerria poweriae</i> -2, <i>Vinciguerria poweriae</i> -3, <i>Sergestes henseni</i> , <i>Sergia splendens</i> , <i>Sergestes paraseminudus</i> , <i>Sergestes armatus</i> , <i>Sergestes pectinatus</i> , <i>Sergestes sargassi</i>
Cluster 5	<i>Gonostoma elongatum</i> -5/7, <i>Systellaspis debilis</i>
Cluster 6	<i>Chauliodus sloani</i> -2/20
Cluster 7	<i>Benthoosema suborbitale</i> -1, <i>Lepidophanes guentheri</i> -3, <i>Lepidophanes guentheri</i> -1, <i>Diaphus dumerilii</i> -1, <i>Lepidophanes guentheri</i> -2, <i>Benthoosema suborbitale</i> -2, <i>Diaphus dumerilii</i> -2, <i>Lampanyctus alatus</i> -1, <i>Notolychnus valdiviae</i> -1, <i>Lampanyctus alatus</i> -2
Cluster 8	<i>Gonostoma elongatum</i> -1/2
Cluster 9	<i>Gonostoma elongatum</i> -3/4
Cluster 10	<i>Notoscopelus resplendens</i> -2
Cluster 11	<i>Argyropelecus aculeatus</i> -1, <i>Argyropelecus aculeatus</i> -2, <i>Argyropelecus aculeatus</i> -3, <i>Argyropelecus aculeatus</i> -4/5, <i>Gonostoma elongatum</i> -8/9
Cluster 12	<i>Myctophum affine</i> -1, <i>Myctophum affine</i> -2, <i>Myctophum affine</i> -3
Cluster 13	<i>Sergestes atlanticus</i> , <i>Sergestes edwardsii</i> , <i>Sergestes vigilax</i>
Cluster 14	<i>Gonostoma elongatum</i> -10/12
Cluster 15	<i>Cyclothone acclinidens</i> -1, <i>Cyclothone acclinidens</i> -2, <i>Cyclothone acclinidens</i> -3, <i>Acanthephyra curtirostris</i> , <i>Eucopia unguiculata</i> , <i>Sternoptyx pseudobscura</i> -1, <i>Sternoptyx pseudobscura</i> -2, <i>Sternoptyx pseudobscura</i> -3, <i>Sternoptyx pseudobscura</i> -4/5, <i>Eucopia australis</i>
Cluster 16	<i>Sternoptyx diaphana</i> -1, <i>Sternoptyx diaphana</i> -2, <i>Sternoptyx diaphana</i> -3
Cluster 17	<i>Eucopia sculpticauda</i>
Cluster 18	<i>Photostomias guernei</i> -3/12
Cluster 19	<i>Cyclothone alba</i> -1, <i>Cyclothone alba</i> -2
Cluster 20	<i>Cyclothone pallida</i> -2/3, <i>Cyclothone pallida</i> -4
Cluster 21	<i>Cyclothone pseudopallida</i> -1, <i>Cyclothone pseudopallida</i> -2, <i>Cyclothone pseudopallida</i> -3
Cluster 22	<i>Argyropelecus hemigymnus</i> -1, <i>Argyropelecus hemigymnus</i> -2, <i>Gennadas scutatus</i> , <i>Valenciennellus tripunctulatus</i> -1, <i>Valenciennellus tripunctulatus</i> -2, <i>Valenciennellus tripunctulatus</i> -3, <i>Acanthephyra purpurea</i>
Cluster 23	<i>Gennadas bouvieri</i> , <i>Gennadas capensis</i>
Cluster 24	<i>Sergia robustus</i> , <i>Gennadas valens</i>
Cluster 25	<i>Stomias affinis</i> -2/19
Cluster 26	<i>Cyclothone braueri</i> -1, <i>Cyclothone braueri</i> -2

included several size classes each of the myctophid *Diaphus lucidus*, the phosichthyid *Vinciguerria poweriae*, and 6 species of sergestids. All of these units were centered in the lower half of the epipelagic zone at 125 to 175 m (median zone 125 to 150 m). Cluster 7 grouped 10 cluster units of myctophids which centered shallow in the epipelagic zone at 25 to 50 m. Cluster 15, also of 10 units, had an array of non-migrators including representatives of the fish genera *Cyclothone* and *Sternoptyx* and the shrimp genera *Eucopia* and *Acanthephyra*. These occurred deep in the mesopelagic zone at night (825 to 925 m; median zone 900 to 925 m). Three clusters, 1, 11 and 22, had 4 to 7 units. Cluster 22, a mixture of sternoptychid fish and aristeid and caridean shrimp species, occurred in the upper mesopelagic zone, the median depth being

300 to 325 m. Cluster 11 grouped 4 size classes of *Argyropelecus aculeatus* and one unit of *Gonostoma elongatum*, with their populations centering in the lower epipelagic zone at 150 to 175 m. Cluster 1 contained several size classes each of 2 myctophids, *Diaphus lucidus* and *Notoscopelus resplendens*, which also centered in the lower epipelagic zone, between 75 and 150 m.

The remaining 19 clusters, each with 1 to 3 units, can be assigned to 3 broad depth zones: epipelagic (0 to 250 m), upper mesopelagic (250 to 650 m) and deep mesopelagic (>650 m). The shallow depth group included 9 clusters (3, 5, 6, 8, 9, 10, 12, 13 and 14) consisting of strongly migrating myctophids, sergestids, stomiids and *Gonostoma elongatum*. The intermediate depth group had 7 clusters (18, 19, 21, 23, 24, 25 and

Table 6. Results of multiple niche parameter cluster analyses for resource partitioning among the midwater fishes and shrimps of the eastern Gulf of Mexico. The 3 niche parameters considered were diet composition, food size and predator nighttime vertical distribution

	Number of pairings	% of total pairings
Species pair concurrences for all 3 parameters (i.e. no niche separation)	48 ^a	1.0
Species niche separation based on a single parameter	531	11.2
Niche separation based on 2 parameters	1064	22.4
Niche separation based on all 3 parameters	3110	65.4
Total pairings in analysis	4753	

^a23 of the concurrences were pairings of different size classes of the same species

26) and included shallow *Sergia* and *Gennadas* shrimps, *Cyclothone* and the stomiids. This group had portions of or entire populations which did not migrate or, if migrating, did not reach the epipelagic zone at night. The deepest group (Clusters 16, 17 and 20) included deep mesopelagic *Cyclothone* and *Sternop-tyx* and the mysid shrimp genus *Eucopeia*.

It should be noted that defining depth centers for the Stomiidae was especially problematic as a significant fraction of their populations do not migrate on a daily basis but remain at depth, thereby generating a strongly polymodal vertical distribution pattern (Sutton & Hopkins 1996b). Our feeding data, however, suggest that most stomiid predation is in the epipelagic zone at night, with little feeding occurring in the non-migratory components of the populations (Sutton & Hopkins 1996a). Also note that a number of species were distributed over more than 1 depth cluster, examples being *Gonostoma elongatum* and *Notoscopelus resplendens*, which occur, respectively, in 5 and 3 different clusters. This results from changes in species migration patterns which occur with ontogeny (e.g. Badcock 1970, Gibbs et al. 1971, Badcock & Merrett 1976, Clarke 1978, Willis & Percy 1980, Hulley 1981, Gartner et al. 1987, Lancraft et al. 1988), with larger, older individuals of a species more often found deeper in the water column.

Trellis matrix results for species pairs

Using the species pairs trellis diagram we were able to estimate the degree of niche overlap or, conversely, niche differentiation, with the 3 niche parameters combined. Trellis analysis yielded a total of 4753 combinations of cluster pairings of 77 fish and 21 shrimp units. The data summary in Table 6 shows that in only 48 cases (i.e. 1% of all pairings) was there no niche differentiation. Approximately half this number (23) were pairings of different size classes of the same fish species. The pairings involving different species included:

combinations of 8 myctophid species; *Cyclothone acclinidens* and *Eucopeia unguiculata*; *Vinciguerria poweriae* and *Sergestes armatus*; *Sergestes pectinatus* and *Sergestes sargassi*; and *Gennadas capensis* and *Gennadas bouvieri*. In 2 instances there was no apparent niche differentiation between a fish and a shrimp species (*Eucopeia unguiculata* and *Cyclothone acclinidens* 2,3, *Sergestes armatus* and *Vinciguerria poweriae* 2,3). The remainder of the 4753 pairings yielded niche differentiation by a single parameter, 2 parameters or all 3 parameters. Thus, 99% of the pairings demonstrated some degree of niche separation. Only 11% of the pairings showed single parameter differentiation, whereas 88% were differentiated by 2 or more parameters, with 65% of all pairings being differentiated by all 3 niche variables.

DISCUSSION

The 3 variables considered as important niche parameters were food composition, food size and nighttime predator vertical distribution. Two of the parameters were based on nutrition and one on space. In the mesopelagic ecosystem, spatial separation or concurrence at night is a valid estimator of potential competition for vertically distributed resources as vertically migrating species generally feed at night (e.g. Omori 1969, Foxton & Roe 1974, Merrett & Roe 1974, Donaldson 1975, Hopkins & Baird 1975, Walters 1976, Gorelova 1977, Kinzer & Schulz 1985, Kawamura & Fujii 1988). Animals feeding at different horizons, even on the same prey species, at night in the epi/mesopelagic zone are partitioning the common resource and thus minimizing competition. Our data suggest that diffuse competition exists as MacArthur (1972) and Pianka (1974) predicted and that species niches in the ecosystem show considerable overlap (e.g. consider the large multispecies clusters in Tables 2 & 4). The latter enables dense species packing, especially in the epipelagic zone at night, the apparent period of most

active feeding. Not all of the species considered here, however, forage exclusively at night. Hopkins & Baird (1973) and Baird & Hopkins (1981) have shown that there is active feeding during the daytime by the non-migratory sternoptychids (*Valenciennellus*, *Sternoptyx*) and Lancraft (pers. comm.) has made similar observations on *Cyclothone*, and there is evidence that, while EGOM aristeids feed primarily at night, foraging continues throughout the diel period (Heffernan & Hopkins 1981). Others have reported daytime or acyclic feeding in myctophids (Samyshev & Shetinkin 1971, Clarke 1978), sternoptychids (Merrett & Roe 1974, Clarke 1978), gonostomatids (DeWitt & Cailliet 1972), and aristeid, sergestid, caridean and mysid shrimps (Roe 1984, Nishida et al. 1988). Spreading predation pressure over the 24 h diel period would enhance resource partitioning and not be in conflict with the concept of niche separation being discussed here.

In summary, our analysis supports the concept of diffuse competition, where individual species are impacted by many other species in the ecosystem, including intergroup competitive pressure. The present results have demonstrated much niche coherence between representatives of the 2 dominant micronektonic taxa, the midwater fishes and shrimps. Despite considerable niche overlap and thus the potential for competition, it appears that when a spectrum of niche parameters is considered, resource partitioning exists at the species level and in many instances, intraspecifically, at the size cohort level as well. This enables the high species diversity observed in warm water oligotrophic regimes which so characterizes the epi/mesopelagic zone of a large fraction of the world ocean.

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