Marine Biology 118, 651–661 (1994)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Trophic strategies of euphausiids in a low-latitude ecosystem

S. T. Kinsey*, **T. L. Hopkins**

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

Received: 21 August 1993 / Accepted: 24 August 1993

Abstract. Vertical distribution, diet, and morphology of adults were examined in 27 species of euphausiids occurring in the upper 1000 m in the eastern Gulf of Mexico. Vertical distribution patterns were similar to those found in the central ocean gyres and oceanic equatorial waters of the Atlantic, Indian and Pacific Oceans. Most species migrated vertically from their daytime depths of 300 to 600 m to the upper 300 m at night. Exceptions were the non-migrating species of *Stylocheiron*, which remained in the epipelagic zone day and night, and *Nematobrachion boopis*, which remained in the mesopelagic zone. Based on gut-contents analysis, the Gulf euphausiids were largely zooplanktivorous, with cyclopoid and calanoid copepods being the most common items in stomachs. Ostracods were especially common in the stomachs of *Thysanopoda* spp. and phytoplankton in the guts of *Euphausia* spp. Nearly every species' diet contained a considerable amount of olive-colored debris, which may have been marine snow generated in the epipelagic zone. Cluster analysis grouped the euphausiids into nine diet guilds. Euphausiids with a generalized morphology (i.e., spherical eyes, uniform thoracic appendages) tended to group together and demonstrated little variety in stomach contents among species. Euphausiids with a specialized morphology (i.e., bilobed eyes, elongate thoracic appendages) showed considerable variety in stomach contents among species, and several species had diets that were highly specific. Many of the species that had similar gut contents fed on prey of different sizes, as indicated by the width of the calanoid copepod mandibles found in stomachs. Principal-components analysis of seven morphological characters yielded species groups that were similar, but not identical, to those generated by cluster analysis of stomach contents data. We inferred from this that morphological characters partly determine diet, but that behavior is also important. Using the 20 most abundant species and 3 niche parameters, we attempted to identify the degree of separation among euphausiids based on the level of overlap in vertical distribution and diet composition, and on differences in mean prey size. Overlap of $<60\%$ in vertical distribution or diet composition was considered to indicate distinction of that parameter. Of 190 total species pairs, only 4 pairs did not demonstrate niche separation in at least one of these categories. We found that differences in these niche parameters were greatest among species with a specialized morphology and least among species that were morphologically generalized.

Introduction

Euphausiids are a basic component of the zooplankton in virtually all oceanic ecosystems, and they are often the principal contributors to zooplankton biomass in pelagic communities (Ponamareva 1963, Mauchline and Fisher 1969, Mauchline 1980). They are most abundant at high latitudes, frequently occurring in large swarms, but species diversity is highest in tropical-subtropical environments (Mauchline and Fisher 1969). Worldwide, there are 85 species of euphausiids in 11 genera, and many of the low-latitude species are distributed circumglobally. Euphausiids are considered to be trophic intermediates to small zooplankton and carnivorous micronekton such as midwater shrimps, fishes and cephalopods and, as such, constitute a fundamental carbon link in oceanic food webs (Pelymskiy and Arashkevich 1980).

Thirty species in five genera have been previously reported from the Gulf of Mexico (James 1970). *Thysanopoda* is considered phylogenetically to be the most ancestral genus in the Gulf assemblage and is most closely related to *Euphausia*, while *Nematoscelis*, *Nematobrachion* and *Stylocheiron* represent varying degrees of specialization (Casanova 1984). Because Gulf of Mexico water originates in the Caribbean Sea (Nowlin 1971), the Gulf euphausiid assemblage consists only of tropical-subtropical species. All of the 30 species found in the Gulf of Mexico also occur in the Atlantic, 28 in the Indian, and

---

* *Present address*: Department of Biological Science, B-157, The Florida State University, Tallahassee, Florida 32306-3050, USA

29 in the Pacific Oceans (Lewis 1954, Mauchline and Fisher 1969, Baker 1970, Youngbluth 1975, Mauchline 1980, Hirota 1987, Mikkelsen 1987).

The five genera that occur in the Gulf of Mexico show similar diel vertical distribution patterns in the Pacific (Brinton 1967, Roger 1974, Youngbluth 1975, Hirota et al. 1983, Hirota 1987), the Indian (Hirota 1987) and the Atlantic (Lewis 1954, Baker 1970, Hargreaves and James 1989) Oceans. *Thysanopoda* and *Euphausia* tend to be strong diel vertical migrators, *Nematoscelis* and *Nematobrachion* are moderate migrators, and *Stylocheiron* generally is an epipelagic non-migrator. Mauchline and Fisher (1969) reviewed stomach contents information for many species and found that most euphausiids were omnivorous or carnivorous. Nemoto (1977) reported that three bathylpelagic species of *Thysanopoda* were strict carnivores, feeding predominantly on copepods. Other investigators have shown that chlorophyll is common in euphausiids diets, although usually in trace quantities (Nemoto 1968, Ponomareva and Baulin 1987). Diel feeding rhythms have been studied, primarily to determine the role of diel vertical migration in trophic ecology (Ponomareva 1971, Roger 1975, Hu 1978, Hirota and Nemoto 1989). Numerous studies have also examined the trophic function of morphological adaptions (Mauchline 1967, 1980, Nemoto 1967, 1968, Berkes 1975, Suh and Nemoto 1988, Dalley and McClatchie 1989). Particular emphasis has been placed on the differences between euphausiids with a "generalized" body plan, characterized by uniform thoracic appendages and spherical eyes, and those with a "specialized" body plan, characterized by an elongate pair of thoracic appendages and bilobed eyes. Despite the wealth of information concerning these aspects of euphausiid ecology, no previous study has addressed vertical distribution, diet and morphology for an entire low-latitude assemblage.

Materials and methods

Description of study area

The eastern Gulf of Mexico is physically similar to other non-upwelling regions at low latitudes (McGowan 1974, Longhurst 1976). The upper 300 m of the water column in the vicinity of 27° N, 86° W can be divided into Loop Current water and resident Gulf water. The Loop Current is a seasonally variable penetration of Caribbean Subtropical Underwater which enters through the Yucatan Straits and exits via the Florida Straits, forming the Florida Current. The Loop is a warm ($\geq$ 22° C), saline ($>$ 36.5‰) current approximately 75 m thick and centered at 200 m. It can be identified by a depression of the depth of the 22° C isotherm to 150–200 m (Leipper 1970, Nowlin 1971). All the samples reported here were collected in Gulf resident water, as determined by expendable bathythermograph (XBT) and, conductivity-temperature-depth probe (CTD) casts.

Estimates of biological productivity in Gulf resident water vary from < 50 g C m^{-2} yr^{-1} (El-Sayed 1972, Hopkins unpublished data) to > 150 g C m^{-2} yr^{-1}, with the latter based on recent state-of-the-art techniques (G. Vargo personal communication). Zooplankton standing stock, 1.2 g dry wt m^{-2} (0 to 1000 m), is comparable to that in oligotrophic boundary currents (Hopkins 1982). Faunal composition and community structure of the zooplankton and micronekton communities are very similar to those of the Caribbean Sea and the tropical-subtropical Atlantic Ocean (Young and Roper 1969, Donaldson 1975, Michel and Foyo 1976, Backus et al. 1977, Heffernan and Hopkins 1981, Gartner et al. 1987, Hopkins et al. 1989, Flock and Hopkins 1992).

Table 1. Summary of plankton-tow data at 27° N, 86° W

Depth (m)	Day		Night	
	No. of tows	Vol. filtered (10^3 m^3)	No. of tows	Vol filtered (10^3 m^3)
R. V. "Columbus Iselin"				
0– 25	13	10.6	24	22.8
25– 50	8	6.5	6	5.7
50– 75	1	0.8	3	2.8
75– 100	2	1.6	6	5.7
100– 125	6	4.9	6	5.6
125– 150	7	5.7	4	3.8
150– 175	5	4.1	2	1.9
175– 200	5	4.1	2	2.0
200– 250	1	1.0	2	1.4
250– 300	5	4.4	5	3.8
300– 350	8	4.4	5	4.9
350– 400	7	5.6	2	1.8
400– 450	5	4.9	4	3.4
450– 500	7	5.1	4	3.7
500– 550	7	5.4	3	2.9
550– 600	8	8.7	4	5.0
600– 700	7	8.3	3	5.7
700– 800	2	3.1	2	4.4
800– 900	8	9.1	4	5.4
900–1000	4	6.6	1	1.8
R. V. "Suncoaster"				
0– 25	2	0.2	3	0.6
25– 50	2	0.2	3	0.6
50– 75	2	0.4	5	0.8
75– 100	2	0.4	6	1.1
100– 125	2	0.5	6	1.2
125– 150	2	0.5	6	1.3
150– 175	2	0.4	6	0.9
175– 200	2	0.4	0	0.0

Collection and analyses

Adult euphausiids were collected from the eastern Gulf of Mexico, within a circle of 18 km radius centered at 27° N 86° W. Day and night collections were taken aboard the R. V. "Columbus Iselin" during the summers of 1975–1977 and aboard the R. V. "Suncoaster" during the summer of 1990 (Table 1). The nets used on the "Columbus Iselin" were 5.3 and 2.8 m^2 opening–closing Tucker trawls and on the "Suncoaster", a 4 m^2 MOCNESS (multiple opening–closing net and environmental sensing system; Wiebe et al. 1976). The Tucker trawls had 4 mm bar-mesh bodies with 333 µm plankton cod-end nets, and the MOCNESS nets had 4 mm bar-mesh bodies with no cod-end nets. All trawl nets were equipped with 162 µm-mesh plankton nets that were nested in the mouth of the trawl. The plankton nets in the Tucker trawls and the MOCNESS were 0.2 and 0.8 m^2, respectively. The volume of water filtered was determined using dial-type flowmeters mounted both on the trawl frame and suspended in the mouth of the plankton nets. Depth was monitored using a pressure transducer, and was either traced with a time-depth recorder (Tucker trawls) or relayed via conducting cable to an on-deck computer (MOCNESS). All samples were fixed initially in 5% buffered formalin and later transferred to 50% isopropanol. Postlarval euphausiids were sorted from the raw samples, identified, and total length (TL) was measured from the posteriormost portion of the eye orbit to the tip of the telson.

The plankton nets were more effective samplers of all size classes of euphausiids than were the trawl nets (Kinsey unpublished data) and were used to estimate total abundance and to obtain quantitative vertical-distribution profiles. The total abundance for each species was estimated using the night tows to minimize bias from net avoidance, and was calculated as the total number of individuals under a square meter based on the volume of water filtered. For the purpose of defining vertical distribution, we divided the upper 1000 m of the water column into depth zones of 25 m increments from 0 to 200 m, 50 m increments from 200 to 600 m, and 100 m increments from 600 to 1000 m. Day and night abundances for each species were calculated as the number of individuals in each depth zone under a square meter in the upper 1000 m. The absolute abundance for each species was then standardized by converting to the percentage of the total population of that species occurring in each depth zone, and these data were used to generate a Bray–Curtis dissimilarity matrix (Bray and Curtis 1957) which was classified using the UPGMA cluster analysis (unweighted pair-group method using arithmetic averages; see Romesburg 1990). Species were considered to have distinct vertical distributions at $\geq 40\%$ dissimilarity ($< 60\%$ similarity).

Euphausiids used for gut-contents analysis were taken from the coarser-mesh trawl nets to prevent bias from post-capture net-feeding (Hirota 1984). The Tucker trawls were fitted with a 4 mm-mesh "fish catcher" inserted ahead of the cod-end plankton net which allowed small, potential prey items to pass through while retaining the larger euphausiids. The MOCNESS trawl nets did not need a fish catcher because they had only 4 mm mesh (no plankton cod-end net).

Euphausiid stomachs were removed and the contents were mounted in a 2:1 mixture of glycerol:water and acid fuchsin stain. Diet items were identified to the lowest taxonomic level possible and 20 diet categories were erected that encompassed all diet items. The data were recorded as the presence or absence of each diet category in each individual stomach. The total occurrences in each category for each species were then summed and the percentage occurrence of each diet category was calculated. Stomach contents were examined to identify diet guilds within the euphausiid assemblage in the eastern Gulf. The percentage composition diet data were used to create a Bray–Curtis dissimilarity matrix which was clustered using the UPGMA. Diet dissimilarity $\geq 40\%$ was considered to indicate unique diet composition (see also Zaret and Rand 1971, Berkes 1976). Diet diversity indices (D) were calculated for each species following Travers (1971).

The use of gut-contents analysis to examine diet is inherently biased by differential rates of digestion of different types of food. This bias precludes quantification of diet components (e.g. weighing each diet item). However, gut-contents analysis is the only method that allows the examination of the entire range of diet items available to an organism. By classifying each stomach content as present or absent we have circumvented the problem of quantifying gut material. Presence/absence data is also biased (e.g. 1 calanoid copepod is equal to 5 harpacticoid copepods in an individual gut), but it is a more conservative approach for making species comparisons than would be obtained by using inaccurately quantified gut material. Another potential caveat to gut-contents analysis is that some diet items may not be identifiable due to rapid digestion. To avoid missing prey items, we sacrificed taxonomic resolution (which was much greater in the raw data) and have presented coarser diet categories that could be confidently identified in every instance. For example, even diet items that rapidly degrade, such as gelatinous organisms or polychaete worms, leave traces of their existence behind in the guts (nematocysts and acicula, respectively). The categories of prey items found in euphausiid stomachs encompass every major group of zooplankton that occurs at our sample station, and the overall percentage diet composition data showed that zooplankton in euphausiid stomachs occurs in roughly the same order of dominance as found in situ (Hopkins 1982). Therefore, we believe our methodology was equally sensitive to all prey taxa and our gut-content information accurately reflects diet composition.

Calanoid copepods were the most common diet component in euphausiid stomachs. Calanoid copepod mandibles, which persist in guts and can be easily measured, were used as an indicator of prey size for each species of euphausiid. Analysis of variance (ANOVA) was used to determine if differences existed in copepod mandible widths among species of euphausiids that occurred in the same diet cluster (therefore having similar stomach contents). Mandible widths were $\log_{10}$-transformed and tested for normality using the Wilkes–Shapiro test. Homogeneity of variances was tested using Bartlett's test. Within clusters that contained significant differences in copepod mandible widths among species, the Tukey–Kramer paired-comparisons test was employed to identify which species pairs within a diet cluster differed. Because the body size of a euphausiid is probably an important parameter in its feeding ecology, we did not correct for euphausiid size when making these comparisons.

Several morphological characters were measured in each species to examine the potential role of these characters in determining diet composition. Measurements were made on five individuals of each species. Following in part the work of Nemoto (1967), we measured total length, thoracic leg intersetule distance, stomach height, stomach length, mandible pars molaris width, pars incisiva width of the cutting edge, and pars incisiva width of the spine. These measurements were $\log_{10}$-transformed to reduce the correlation of the measurement means and variances (Winans 1984). The transformed data were ordinated using principal-components analysis (PCA) of the covariance matrix. The resulting scatterplot revealed that the five points for each species were grouped tightly, so group centroids (calculated as the mean PC scores for each species) were used to simplify the plot.

Table 2. Abundance of euphausiids in upper 1000 m of eastern Gulf of Mexico estimated from night plankton tows. Abbreviations are used to describe each species in other tables and figures

Species	Abbreviation (Code)	No. m^{-2}
Thysanopoda aequalis	*Taeq*	2.0
T. monacantha	*Tmon*	0.4
T. tricuspida	*Ttri*	0.1
T. orientalis	*Tori*	0.1
T. obtusifrons	*Tobt*	<0.1
T. pectinata	*Tpec*	<0.1
Euphausia americana	*Eamr*	26.5
E. brevis	*Ebre*	8.3
E. tenera	*Eten*	81.1
E. hemigibba	*Ehem*	23.0
E. pseudogibba	*Epse*	<0.1
E. mutica	*Emut*	2.9
E. gibboides	*Egib*	1.2
Nematoscelis microps	*Nmic*	16.0
N. atlantica	*Natl*	3.5
N. tenella	*Nten*	1.5
Nematobrachion flexipes	*Nflx*	0.4
N. sexspinosus	*Nsex*	<0.1
N. boopis	*Nboo*	0.3
Stylocheiron abbreviatum	*Sabb*	6.5
S. affine	*Saff*	6.5
S. suhmii	*Ssuh*	3.0
S. carinatum	*Scar*	28.0
S. longicorne	*Slon*	10.7
S. elongatum	*Selo*	13.7
S. robustum	*Srob*	0.5
S. maximum	*Smax*	<0.1
Total		237

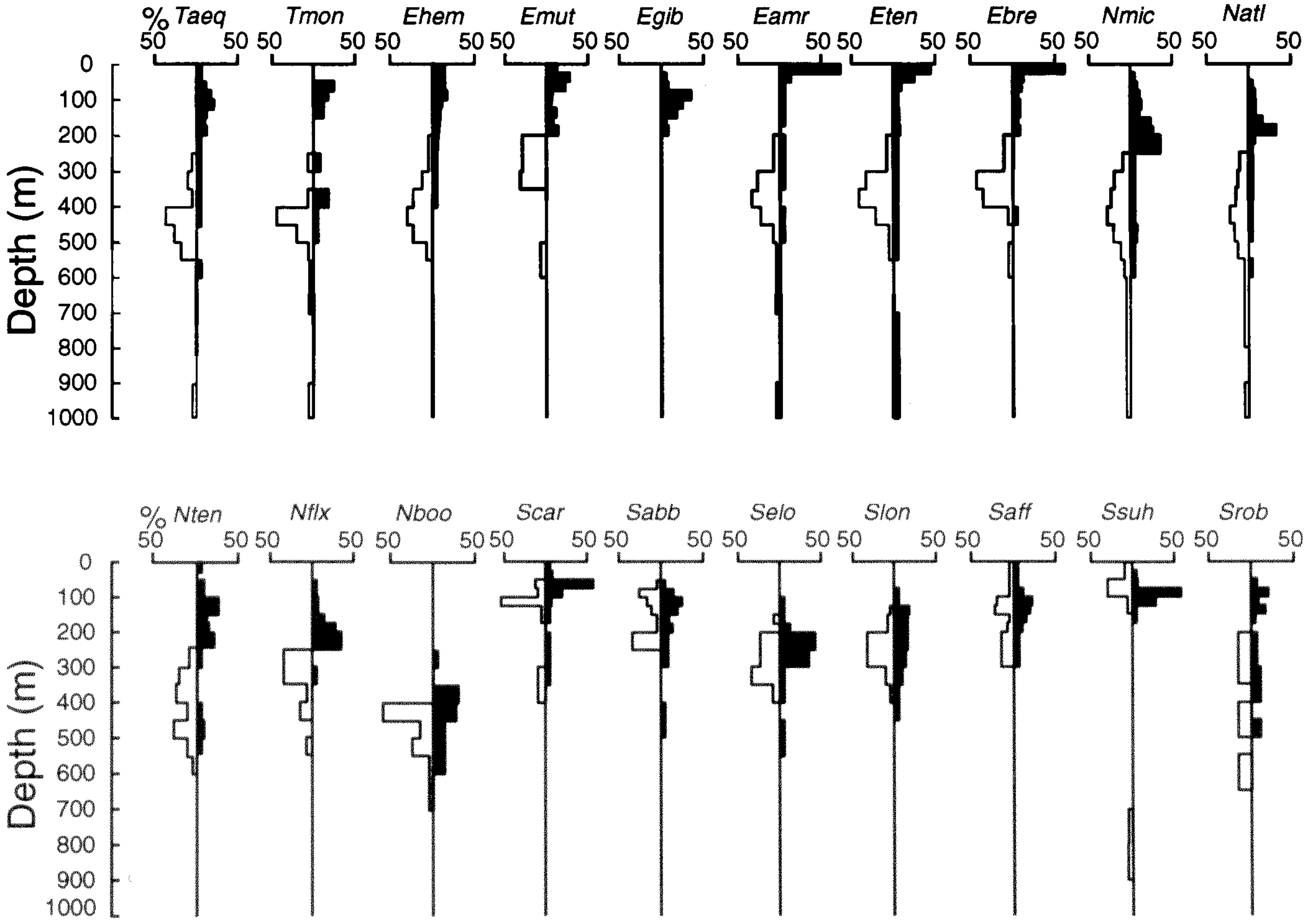

Fig. 1. Vertical distribution profiles of 20 species of euphausiids in eastern Gulf of Mexico. Species codes as in Table 2. Data are percen of total population occurring in each depth zone. Unshaded regions = day, shaded regions = night

Results

Abundance and vertical distribution

We collected 28 species of euphausiids in the Gulf of Mexico, 27 of which were abundant enough to include in this study (*Thysanopoda cristata* was not included). Two species, *T. egregia* and *T. cornuta*, have been reported for the Gulf at depths > 1000 m and consequently were not collected in our nets (James 1970). The total abundance of euphausiids was estimated at 237 m^{-2} in the upper 1000 m (Table 2). Dominant species in order of abundance were *Euphausia tenera*, *Stylocheiron carinatum*, *E. americana*, *E. hemigibba*, *Nematoscelis microps*, *S. elongatum* and *S. longicorne*, all of which had populations exceeding 10 m^{-2}. These seven species comprised 83% of the total euphausiid population in the eastern Gulf.

Twenty species of euphausiids were common enough in plankton nets to reveal their vertical distributions (Fig. 1). All species examined were diel vertical migrators, except for members of the genus *Stylocheiron* and *Nematobrachion boopis* (no daytime information was obtained for *Euphausia gibboides*). The migrating species were generally distributed in the mesopelagic zone during the day, rarely exceeding a depth of 600 m, and in the epipelagic zone at night. Only three species, *E. americana*, *E. brevis* and *E. tenera*, contributed a substantial percentage of their population to the surface waters (0 to 25 m). Most species of *Stylocheiron* were epipelagic day and night; *S. longicorne* and *S. elongatum* occurred in the lower epipelagic–upper mesopelagic zones (150 to 400 m), and *S. robustum* occurred scattered throughout the upper 600 m. *N. boopis* occurred below the permanent thermocline day and night at 350 to 600 m. Cluster analysis of the vertical distribution data revealed 10 groups of species with similar distributions during the day, and 9 at night (Fig. 2; Table 3). Only *S. carinatum* had a unique vertical distribution (< 60% overlap with all other species) both day and night.

Diet

The stomach contents of 27 species of euphausiids are presented in Table 4. As a group, the Gulf of Mexico euphausiids were largely carnivorous, with cyclopoid and calanoid copepods being the most common prey. Phytoplankton, protozoans and gelatinous prey were also common in stomachs, particularly among species of *Euphausia*, and ostracods were an important component of the

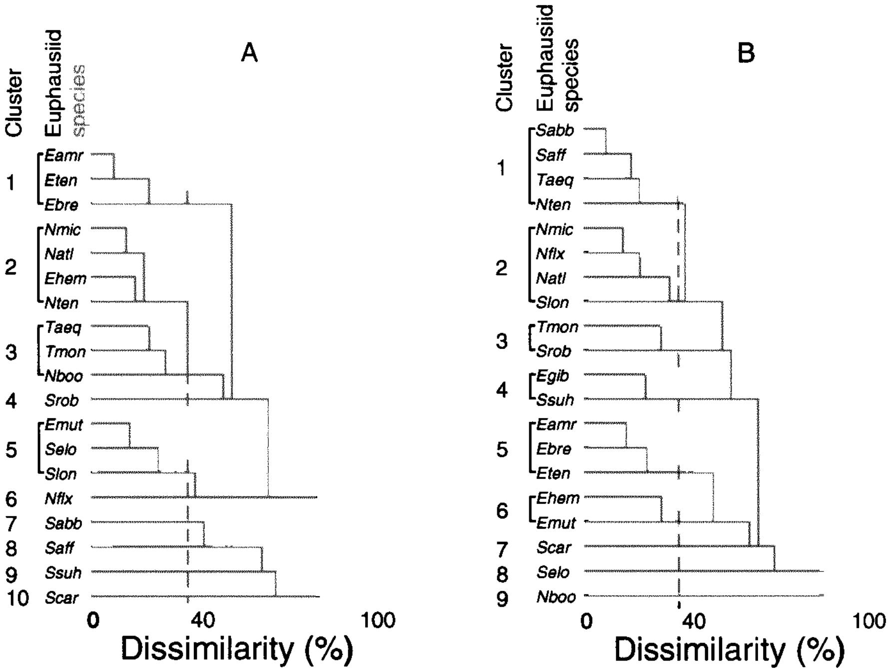

Fig. 2. Results of cluster analyses of vertical distribution data. Species codes as in Table 2. Dashed vertical line indicates 40% dissimilarity and was used to discriminate clusters. (A) day; (B) night

Table 3. Vertical distribution zones of maximum abundance and percent of euphausiid population occurring in each zone for clusters presented in Fig. 2. Values in parentheses are percentage range

Cluster	Zone of abundance (m)	% of population
Day		
1	300–450	83 (80–88)
2	300–500	75 (64–81)
3	400–550	83 (74–96)
4	200–700	100
5	200–350	83 (76–91)
6	250–350	71
7	75–125	42
	200–250	34
8	100–150	41
	200–300	29
9	50–100	60
10	100–125	55
Night		
1	75–200	75 (68–81)
2	125–250	70 (62–83)
3	50–150	59 (51–67)
4	75–150	86 (79–92)
5	0– 50	77 (69–89)
6	0–150	80 (79–81)
7	50–100	78
8	175–300	89
9	350–600	95

diet for *Thysanopoda*. Olive-colored debris was a frequent constituent of the stomach contents of nearly every species.

Cluster analysis revealed 9 groups of species with similar gut contents (Fig. 3; Table 5). Congeners tended to have similar diets, particularly among genera with a generalized morphology (*Thysanopoda* and *Euphausia*). All *Euphausia* species occurred in a single cluster (Cluster 1) and fed predominantly on non-crustacean prey. *Thysanopoda* species also clustered together (Cluster 3) and were characterized by having the greatest diet diversity (*D*) of all groups, feeding evenly on most diet items. In contrast, *Stylocheiron* had the greatest variety of trophic strategies of any genus, with 3 species having unique diet compositions ($< 60\%$ overlap) and no more than 2 members of the genus occurring in the same cluster.

Comparison of calanoid copepod mandible widths revealed that, within diet clusters, several species fed on prey of different sizes. In Clusters 1, 2, 3, and 7 of Fig. 3, the data were normally distributed and variances were homogenous. The ANOVAs detected significant differences among species within Clusters 1, 2, and 3 and the Tukey–Kramer paired-comparisons tests revealed that of 39 pairs of species that co-occurred in one of these clusters, 14 fed on copepods of different sizes (*Thysanopoda obtusifrons*, *T. pectinata*, and *Euphausia pseudogibba* were not included in the prey size analysis due to small sample size; Table 6). Twenty-five species pairs had mean prey mandible widths that were not significantly different, indicating that these pairs of species ate the same type of food and fed on prey of the same size. Differences in prey size among species that differ in morphology were also apparent. Species with a generalized body plan (*Thysanopoda* and *Euphausia*) fed on copepods that were proportionally smaller (relative to TL) than did species with a specialized body plan (*Nematoscelis*, *Nematobrachion* and *Stylocheiron*; Fig. 4).

Morphology

The scatterplot generated from the PCA of the seven morphological characters is presented with polygons that encompass the diet composition groupings generated by

Table 4. Percentage occurrence of each diet category in stomachs of 27 species of euphausiids. Species codes as in Table 2. "Other Calanoida A" category contains calanoid copepods of morphologically general *Calanus*-type, "Other Calanoida B" category contains morphologically specialized calanoid copepods such as *Heterorhabdus* spp. Values in parentheses are total number of non-empty guts examined for each species.

Diet category	*Taeq* (61)	*Tmon* (59)	*Ttri* (50)	*Tori* (31)	*Tobt* (9)	*Tpec* (25)	*Eamr* (50)	*Ebre* (25)	*Eten* (50)	*Ehem* (48)	*Epse* (25)	*Emut* (49)	*Egib* (50)
Phytoplankton	1.7	2.1	4.5			0.7	19.4	23.1	24.9	20.3	19.8	19.8	14.2
Protozoa	4.3	7.6	10.3	3.2	6.4	9.7	19.8	21.3	22.0	20.3	17.2	17.7	14.2
Gelatinous prey	2.3	8.6	11.6	6.4	6.4	12.4	14.6	13.0	10.2	13.6	8.6	11.7	13.0
Polychaeta	1.7	3.7	9.4	8.9	4.3	9.0	1.2	1.9		0.4	2.6	1.6	2.8
Mollusca	0.7	6.7	4.5	1.9	4.3	4.1	0.4			1.7	3.4	0.4	2.3
Corycaeus spp.	7.0	4.0	3.6	1.3	6.4	2.1	0.4					0.4	2.5
Oithona spp.	12.4	2.8	2.7	2.5	6.4	3.4	2.0	1.9	2.8	4.2	2.6	4.0	2.0
Oncaea spp.	12.0	5.2	4.9	14.6	12.8	8.3	2.0	1.9	0.6	3.4	0.9	1.6	2.0
Other Cyclopoida	2.0	1.2	3.1	0.6	4.3	0.7	2.4	0.9	1.1	1.3		1.2	2.0
Harpacticoida	5.0	5.8	4.5	5.1	4.3	2.8	1.2	2.8	0.6	3.4	3.4	4.0	6.8
Pleuromamma spp.	0.3	4.0	0.9	8.9	2.1	6.2							
Euchaetidae		1.8	0.9	0.6	2.1	1.4							
Candaciidae	0.7	0.9	0.4	3.2		4.1							
Other Calanoida A	12.0	9.2	8.9	4.5	8.5	1.4	9.9	8.3	6.2	6.8	10.3	11.7	9.9
Other Calanoida B	4.7	2.1	0.9	5.7		1.4							
Ostracoda	14.0	13.1	6.3	13.4	17.0	11.7	0.4			2.1		0.4	2.8
Euphausiidae	1.0	6.4	1.3	5.1		8.3	5.5	1.9	2.3	0.4	8.6	3.2	7.6
Crustacean molts	0.3	0.3				0.7			0.6	0.4	0.9		0.3
Chaetognatha	12.4	8.6	7.1	5.7	4.3	4.8	1.2		0.6	0.4		2.0	3.4
Olive-colored debris	5.4	5.8	14.3	8.3	10.6	6.9	19.8	23.1	28.2	21.2	21.6	20.2	14.2

Diet category	*Nmic* (52)	*Natl* (25)	*Nten* (37)	*Nflx* (25)	*Nsex* (25)	*Nboo* (25)	*Sabb* (50)	*Saff* (50)	*Ssuh* (26)	*Scar* (50)	*Slon* (50)	*Selo* (50)	*Srob* (30)	*Smax* (7)
Phytoplankton			1.9	2.3	4.0			6.1		3.9	14.2	19.5		
Protozoa	6.2	2.1	15.2	10.3	15.8	10.4		6.1		2.6	14.2	20.5		
Gelatinous prey	1.1		3.8	3.4	3.0	2.1		0.9	3.7	9.2	0.7	1.8	2.4	3.7
Polychaeta	3.4	6.3	4.8	4.6	2.0	2.1	0.6				0.7	0.5		
Mollusca	0.6		1.0	1.1	1.0		0.6				0.7			
Corycaeus spp.	6.2	4.2	1.0		2.0		6.7	9.6		6.6	2.1	2.3		
Oithona spp.					1.0		1.8	1.7	48.1	13.2	2.8	0.5		48.1
Oncaea spp.	6.2	8.3	4.8	3.4	2.0	4.2	15.8	27.0	14.8	11.8	9.9	13.6	4.8	14.8
Other Cyclopoida	1.7	6.3	1.9	2.3	1.0		3.6	0.9	11.1			0.5		11.1
Harpacticoida	6.2	2.1	7.6	2.3	5.0	6.3		0.9			0.7	4.5		
Pleuromamma spp.	3.4	4.2	4.8	17.2	20.8	27.1	7.9	7.0			9.9	3.2	2.4	
Euchaetidae	13.6	16.7	11.4	5.7		25.0	9.7				2.1	0.9	4.8	
Candaciidae	6.2	4.2	2.9	4.6	3.0	2.1	5.5	2.6			0.7		2.4	
Other Calanoida A	26.6	22.9	12.4	10.3	4.0	8.3	22.4	23.5	22.2	30.3	14.9	7.3	9.5	22.2
Other Calanoida B	1.7	6.3	1.0		2.0	8.3	3.6			10.5	0.7		11.9	
Ostracoda	2.8		2.9	3.4	5.0		4.8	1.7			2.1	2.7		
Euphausiidae	2.8		1.9	8.0	6.9		7.9	3.5		5.3	8.5	1.8	57.1	
Crustacean molts	0.6	4.2	1.0										2.4	
Chaetognatha	1.7		1.0	1.1	3.0		9.1	0.9		2.6			2.4	
Olive-colored debris	9.0	12.5	19.0	19.5	18.8	4.2		7.8		3.9	14.9	20.5		

cluster analysis (Fig. 5). Principal Component 1 (PC1) is well established as an overall size component in morphological data (Humphries et al. 1991), and accounted for 82% of the total variation. PC2 accounted for nearly 8% of the total variation and appeared to be a general indicator of morphological specialization; species of *Thysanopoda* and *Euphausia* (morphologically generalized) had PC2 scores > 0 and, with the exception of *Nematobrachion sexspinosus*, species of *Nematoscelis, Nematobrachion* and *Stylocheiron* (morphologically specialized) had PC2 scores < 0.

The polygons that encompass the diet guilds in Fig. 5 do not necessarily best describe morphological groupings, although the PCA also grouped the species largely by genus. *Euphausia* species are tightly clustered, except for *E. gibboides*, a comparatively large species, and *E. pseudogibba*. *Thysanopoda* species formed a reasonably coherent group, despite having a considerable range in total length. *Nematoscelis* and *Nematobrachion* species formed congeneric groups as did *Stylocheiron*, with the exception of *S. robustum* and *S. maximum*, which are morphologically distinct from the rest of their genus.

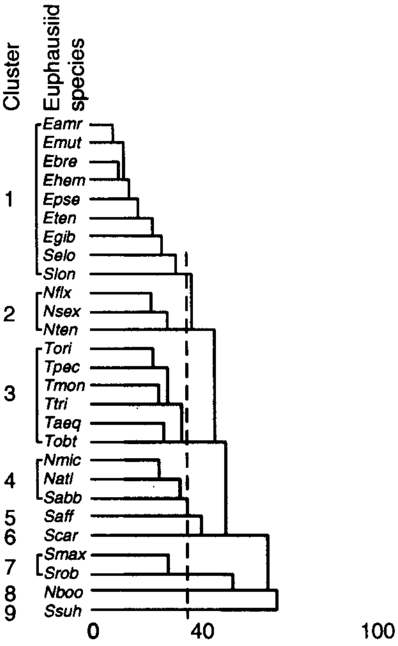

Fig. 3. Results of cluster analysis of diet compostion data. Species codes as in Table 2. Dashed vertical line indicates 40% dissimilarity and was used to discriminate clusters

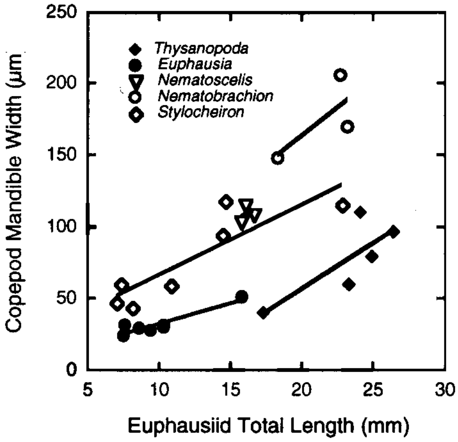

Fig. 4. Width of copepod mandibles found in stomachs as a function of euphausiid total length. Each data point represents mean total length and mean mandible width for a single euphausiid species. Open symbols are morphologically specialized species, filled symbols morphologically generalized species. r^2 values for the fitted lines = *Thysanopoda*, 0.64; *Euphausia*, 0.85; *Nematoscelis*, 0.06; *Nematobrachion*, 0.50; *Stylocheiron*, 0.76

Table 5. Characteristics of diet clusters presented in Fig. 3. Values in parentheses are ranges. Non-crustaceans: phytoplankton, protozoans, gelatinous prey, polychaetes, molluscs, chaetognaths, and olive-colored debris

Cluster	Diet diversity (*D*)	Percent diet composition		
		Copepods	Other crustaceans	Non-crustaceans
	3.1 (2.6–3.5)	23 (11–44)	6 (2–11)	71 (46–86)
2	3.5 (3.5–3.6)	46 (41–48)	10 (6–12)	44 (34–47)
3	3.8 (3.7–4.0)	42 (31–56)	17 (8–21)	41 (29–49)
4	3.4 (3.3–3.5)	75 (72–77)	8 (6–13)	17 (10–22)
5	3.1	73	5	22
6	3.1	73	5	22
7	2.1 (2.0–2.2)	45 (35–55)	53 (46–60)[a]	2 (0–5)
8	2.9	81	0	19
9	1.9	96[b]	0	4

[a] >50% euphausiids

[b] 74% cyclopoid copepods

Table 6. Euphausiid species pairs with significant differences in mean width of copepod mandibles found in euphausiid stomachs. Species codes as in Table 2. Means are presented ± standard deviations.

Species 1 × Species 2	No. of mandibles (Species 1, Species 2)	Mean width of mandibles (Species 1, Species 2)
Cluster 1		
Egib × *Ebre*	25, 13	47.1 ± 38.4, 23.8 ± 10.0
Egib × *Emut*	25, 25	47.1 ± 38.4, 27.2 ± 11.9
Selo × *Eamr*	17, 25	59.1 ± 31.1, 29.8 ± 11.1
Selo × *Ebre*	17, 13	59.1 ± 31.1, 23.8 ± 10.0
Selo × *Ehem*	17, 18	59.1 ± 31.1, 30.2 ± 19.2
Selo × *Emut*	17, 25	59.1 ± 31.1, 27.2 ± 11.9
Slon × *Eamr*	25, 25	61.9 ± 22.0, 29.8 ± 11.1
Slon × *Ebre*	25, 13	61.9 ± 22.0, 23.8 ± 10.0
Slon × *Ehem*	25, 18	61.9 ± 22.0, 30.2 ± 19.2
Slon × *Emut*	25, 25	61.9 ± 22.0, 27.2 ± 11.9
Slon × *Eten*	25, 11	61.9 ± 22,0, 31.5 ± 8.6
Cluster 2		
Nten × *Nsex*	17, 11	103.8 ± 51.2, 169.3 69.5
Cluster 3		
Taeq × *Tmon*	25, 25	43.0 ± 26.4, 85.9 78.7
Taeq × *Tori*	25, 20	43.0 ± 26.4, 96.1 69.7

Discussion

Abundance and vertical distribution

The euphausiid assemblage in the Gulf of Mexico appears to be an extension of the tropical Atlantic fauna (Lewis 1954, Baker 1970, Mikkelsen 1987, Hargreaves and James 1989). Mixed assemblages of tropical and temperate euphausiids have been reported from water-mass transition zones (Brinton 1967, Baker 1970, Youngbluth 1976) and upwelling regions (Sameoto et al. 1987), while central oceanic and equatorial water masses tend to contain relatively "pure", tropical-subtropical faunas (Youngbluth 1975, Hirota 1987). The euphausiid population in the Gulf of Mexico is therefore typical of the temporally stable central oceanic gyres and equatorial waters. The relative abundance of species in the Gulf of Mexico also parallels other low-latitude, oligotrophic areas. The dominance orders reported by Baker (1970) among the tropical species in the eastern Atlantic and Roger (1971) in south Pacific equatorial waters are similar to the dominance structure in the Gulf of Mexico. Overall, euphausiids con-

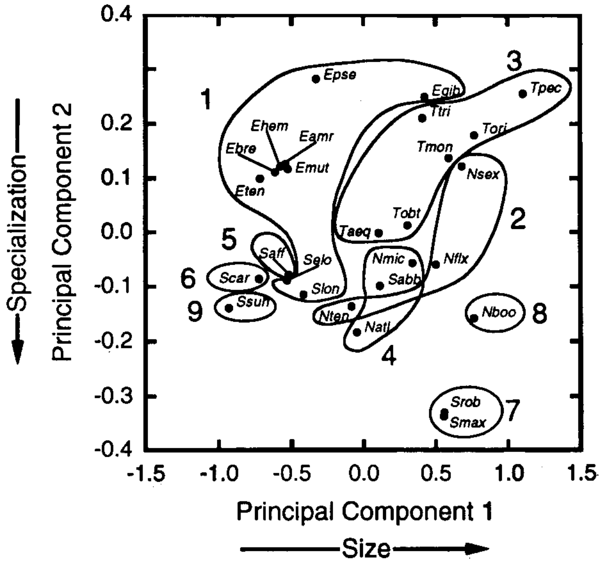

Fig. 5. Plot of Principal Component (PC) 1 on PC2 for 7 morphological measurements made on euphausiids. Euphausiid species codes as in Table 2. Each data point represents mean PC1 and PC2 score for 5 individuals measured for each species. Polygons encompass 9 feeding guilds generated using cluster analysis of diet composition data

stitute $< 1\%$ of the total zooplankton abundance in the Gulf of Mexico (Hopkins unpublished data), but comprise 17% of the total zooplankton biomass, second to copepods (Hopkins 1982).

The diel vertical distribution patterns observed in the Gulf of Mexico were remarkably similar to those found in the Florida Current (Lewis 1954), the eastern Atlantic (Baker 1970, Hargreaves and James 1989), and the central Indian and western Pacific (Hirota 1987). However, vertical distributions of most species in the eastern Pacific (Roger 1974, Youngbluth 1975) were generally deeper than those in the Gulf of Mexico. The thermocline in the eastern Pacific was at depths of 100 to 300 m (Roger 1974) and 200 to 400 m (Youngbluth 1975), whereas in the Gulf of Mexico the thermocline was at 50 to 150 m. Thermocline depth and related biological and physical parameters may at least partially explain the variation in euphausiid vertical distribution. Despite the deeper distributions of species in the eastern Pacific, the relative distributional pattern of each species appears to be consistent throughout the tropical oceans.

Diet and functional morphology

Considered as a group, euphausiids are primarily carnivorous and trophically intermediate to small micronekton and large zooplankton. Our detailed examination, however, revealed a wide variety of trophic strategies within the group. Many of the larger species had diets similar to micronektonic shrimps in the Gulf of Mexico, and fed largely on copepods and other crustacean zooplankton (Heffernan and Hopkins 1981, Flock and Hopkins 1992). The smaller euphausiids fed on small crustaceans, phytoplankton, protozoans, and gelatinous prey, allying them trophically with large copepods (Shuert and Hopkins 1987, Bennett and Hopkins 1989). Olive-colored debris was a frequent diet component of nearly every species ($> 10\%$ of the diet in 15 species), regardless of the species' size and trophic pattern. Based on the microplanktonic composition of the debris, it may be marine snow generated in the epipelagic zone (Alldredge and Gotschalk 1988).

Euphausiid trophic strategies can be broken down at the coarsest level into species with a generalized morphology and those with a specialized morphology. Among euphausiids with a generalized body plan, *Thysanopoda* species are clearly trophic generalists, which feed nearly equally on every type of food. *Euphausia* species are also generalists, but their small size precludes them from ingesting the largest diet items. With respect to diet composition, there was little variety in trophic strategies among species within these genera. In contrast, the euphausiids with a specialized morphology showed considerable variation in diet composition among congeners, and several species had highly specific diets (e.g. *Nematobrachion boopis*, *Stylocheiron suhmii*, *S. robustum* and *S. maximum*.

The fact that the morphological data only partially agrees with the diet composition data (Fig. 5) indicates that the morphological characters we measured are important in determining trophic strategy, but that other factors such as behavior and prey availability in a particular depth zone are probably also important. While this is almost certainly true, shortcomings in our morphological database probably underestimate the importance of morphology in determining diet. Firstly, we did not include basic genus and species-level meristic characters (e.g. uniform thoracic legs vs an elongate pair, spherical vs bilobed eyes, chelate vs simple appendages) in our morphological database because these characters would not have been evenly weighted with the measurement data. Secondly, general differences in body shape among species that are subjectively obvious, such as body slenderness or relative length of feeding appendages, would require a considerably greater number of measurements to be adequately described. In addition, morphology is probably important in determining vertical distribution (Brinton 1967), which could place species in different prey assemblages.

In the light of these limitations, several aspects of Fig. 5 warrant further discussion. The basic distinction between species with generalized and specialized morphologies was seen in both diet composition data and morphological data, an exception being the inclusion of *Stylocheiron longicorne* and *S. elongatum* in the *Euphausia* feeding cluster (Cluster 1). Both of these species are extremely elongate and slender, and have overall body proportions similar to species of *Euphausia*. Similarly, *Nematoscelis tenella* has a long, slender body and a lower eye lobe that is much smaller than the upper lobe, causing it to look superficially more similar to *Nematobrachion flexipes* and *N. sexspinosus* than to other members of its own genus. This resemblance may be reflected in the diet composition data which clustered these species together.

The greater variety of trophic strategies in the morphologically specialized species may indicate that their body plans provide a wider range of trophic options than is available to the morphologically generalized species. This increased trophic spectrum may simply be a result of the greater size range of prey that is available to a euphausiid with a specialized morphology. By increasing prey size relative to its own body size (Fig. 4), a species can afford to feed less often and in a more specific manner. In contrast, species of the generalized genus *Thysanopoda* are able to feed on copepods of the same size as many of the morphologically specialized species, but they must invest the cost of having a very large body size to do so. Nemoto (1967) hypothesized that *Thysanopoda* feeds continuously, whereas morphologically specialized genera process discrete meals. If species of *Thysanopoda* require continuous feeding on a wide variety of prey to meet their energy needs, fine-scale trophic specialization within the genus may be impossible.

While it is probable that morphology is extremely important in dictating trophic strategy (Mauchline 1967, 1989, Nemoto 1967), within the morphological constraints placed on each species, behavioral modification is also important. For example, those species that occurred alone in a feeding cluster may possess strong behavioral as well as morphological adaptions that distinguish them. *Stylocheiron affini*, *S. suhmii* and *S. carinatum* are similar in body form, but these three species had different diets. *Nematobrachion boopis* has a powerful pair of elongate thoracic legs and is clearly morphologically adapted to its carnivorous lifestyle. But this species also demonstrates a distinct behavioral pattern by remaining in deep water day and night, perhaps as an ambush predator on vertically migrating zooplankton.

Niche differentiation

We examined both vertical distribution and diet information for 20 of the 30 species in the Gulf of Mexico. Of 190 possible species pairs, all but four were distinct with respect to either vertical distribution or diet (Table 7). Three of the species pairs that were not distinct were composed of abundant members of the genus *Euphausia*. *E. americana*, *E. brevis*, and *E. tenera* all shared the same space and food. *Nematoscelis microps* and *N. atlantica* also demonstrated no differences in these two niche parameters. Examining species pairs within a genus demonstrated that the morphologically specialized species were more distinct from each another than the morphologically generalized species. Of 25 intrageneric species pairs among the specialized species, 23 pairs were distinct in both vertical distribution and diet, whereas only 3 of 16 (2 of 15 for *Euphausia*) pairs of the generalized species differed in both categories.

One interpretation of the differences observed among species in the space and food niche parameters is that resources are partitioned to reduce competition between species and maintain the high species diversity characteristic of low-latitude oceans. The documentation of niche differences alone, however, does not prove that species diversity is maintained by resource partitioning (Schoener 1974). McGowan and Walker (1979) concluded that resource partitioning was not important in maintaining copepod species diversity in the North Pacific Central Gyre based on the co-occurrence of species believed to utilize the same resources. In a later paper, McGowan and Walker (1985) implicated predation pressure on copepods, which keeps their abundance below the carrying capacity of the ecosystem, as the primary mechanism

Table 7. Differences in niche parameters among 20 species of euphausiids in eastern Gulf of Mexico. Species codes as in Table 2. F: differences in feeding, i.e., diet composition overlap < 60% as determined in Fig. 3; S: differences in prey size as determined by significant differences among species in mean width of copepod mandibles found in stomachs and listed in Table 4; D, N: differences in vertical distribution during day and night, respectively, based on < 60% overlap in distribution as determined in Fig. 2. 0: no differences detected in diet composition, prey size, or vertical distribution

	Tmon	*Eamr*	*Ebre*	*Eten*	*Ehem*	*Emut*	*Egib*	*Nmic*	*Natl*	*Nten*	*Nflx*	*Nboo*	*Sabb*	*Saff*	*Ssuh*	*Scar*	*Slon*	*Selo*	*Srob*
Taeq	SN	FDN	FDN	FDN	FDN	FDN	FN	FDN	FDN	FD	FDN	FN	FD	FDN	FDN	FDN	FDN	FDN	FDN
Tmon	.	FDN	FDN	FDN	FDN	FDN	FN	FDN	FDN	FDN	FDN	FN	FDN	FDN	FDN	FDN	FDN	FDN	FD
Eamr	.	.	0	0	DN	DN	N	FDN	FDN	FDN	FDN	FDN	FDN	FDN	FDN	FDN	SDN	SDN	FDN
Ebre	.	.	.	0	DN	DN	SN	FDN	FDN	FDN	FDN	FDN	FDN	FDN	FDN	FDN	SDN	SDN	FDN
Eten	.	.	.	.	DN	DN	N	FDN	FDN	FDN	FDN	FDN	FDN	FDN	FDN	FDN	SDN	DN	FDN
Ehem	.	.	.	.	.	D	N	FN	FN	FN	FDN	FDN	FDN	FDN	FDN	FDN	SDN	SDN	FDN
Emut	.	.	.	.	.	.	SN	FDN	FDN	FDN	FDN	FDN	FDN	FDN	FDN	FDN	SDN	SDN	FDN
Egib	.	.	.	.	.	.	.	FN	FN	FN	FN	FN	FN	FN	F	FN	N	N	FN
Nmic	.	.	.	.	.	.	.	.	0	FN	FD	FDN	DN	FDN	FDN	FDN	FD	FDN	FDN
Natl	.	.	.	.	.	.	.	.	.	FN	FD	FDN	DN	FDN	FDN	FDN	FD	FDN	FDN
Nten	.	.	.	.	.	.	.	.	.	.	DN	FDN	FD	FD	FDN	FDN	FDN	FDN	FDN
Nflx	.	.	.	.	.	.	.	.	.	.	.	FDN	FDN	FDN	FDN	FDN	FD	FDN	FDN
Nboo	.	.	.	.	.	.	.	.	.	.	.	.	FDN	FDN	FDN	FDN	FDN	FDN	FDN
Sabb	.	.	.	.	.	.	.	.	.	.	.	.	.	FD	FDN	FDN	FDN	FDN	FDN
Saff	.	.	.	.	.	.	.	.	.	.	.	.	.	.	FDN	FDN	FDN	FDN	FDN
Ssuh	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	FDN	FDN	FDN	FDN
Scar	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	FDN	FDN	FDN
Slon	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	N	FDN
Selo	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	FDN

of diversity maintenance. The apparent lack of niche separation among copepods in the Pacific contrasts with the considerable differentiation we have found in euphausiids, particularly among the morphologically specialized species, and several micronektonic groups in the Gulf of Mexico (Heffernan and Hopkins 1981, Hopkins and Baird 1985, Passarella and Hopkins 1991, Flock and Hopkins 1992, Hopkins and Gartner 1992). This contrast may point to a transition in the mechanism of diversity maintenance from lower trophic levels controlled by predation, to higher trophic levels controlled by resource partitioning. Like many copepod species, members of *Euphausia* are small, abundant, and reside in the epipelagic zone at night in the eastern Gulf, where predators are most concentrated (Hopkins 1982, Hopkins and Gartner 1992). *Euphausia* demonstrated the least amount of intrageneric niche separation of any genus, while the larger, morphologically specialized species were well separated (Table 7). Our data may indicate that euphausiids are near a transition from a predation-controlled system to one where resources are partitioned.

Acknowledgements. We thank A. Rodriguez for his assistance with the vertical distribution data. This study was funded by NSF Grants DES75-03845, OCE75-03845 and OCE84-10787.

References

Alldredge, A. L., Gotschalk, C. C. (1988). The contribution of marine snow of different origins to biological processes in the water column. EOS Trans., Am. geophys. Un. 69: p. 1092. (Abstr.)

Backus, R. H., Craddock, J. E., Haedrich, R. L., Robison, B. H. (1977). Atlantic mesopelagic zoogeography. Mem. Sears Fdn mar. Res. 1: 266–287

Baker, A., de C. (1970). The vertical distribution of euphausiids near Fuerteventura, Canary Islands ('Discovery' SOND cruise, 1965). J. mar. biol. Ass. U.K. 50: 301–342

Bennett, J. L., Hopkins, T. L. (1989). Aspects of the ecology of the calanoid copepod genus *Pleuromamma* in the eastern Gulf of Mexico. Contr. mar. Sci. Univ. Tex. 31: 119–136

Berkes, F. (1975). Some aspects of feeding mechanisms of euphausiid crustaceans. Crustaceana 29: 266–270

Berkes, F. (1976). Ecology of euphausiids in the Gulf of St. Lawrence. J. Fish. Res. Bd Can. 33: 1894–1905

Bray, J. R., Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325–349

Brinton, E. (1967). Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12: 451–483

Casanova, B. (1984). Phylogenie des Euphausiaces (Crustaces Eucarides). Bull. Mus. natn. Hist. nat., Paris 6: 1077–1089

Dalley, D. E., McClatchie, S. (1989). Functional feeding morphology of the euphausiid *Nyctiphanes australis*. Mar. Biol. 101: 195–203

Donaldson, H. A. (1975). Vertical distribution and feeding of sergestid shrimps (Decapoda: Natantia) collected near Bermuda. Mar. Biol. 31: 37–50

El-Sayed, S. Z. (1972). Primary production and standing crop of phytoplankton. In: Bushnell, V. C. (ed.) Chemistry, primary productivity, and benthic algae of the Gulf of Mexico. Serial Atlas, Folio 22. American Geophysical Society, New York, p. 8–13

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. Crustacean Biol. 12: 210–223

Gartner, J. V., Jr., Hopkins, T. L., Baird, R. C., Milliken, D. M. (1987). The lanternfishes (Pisces: Myctophidae) of the eastern Gulf of Mexico. Fish. Bull. U.S. 85: 81–98

Hargreaves, P. M., James, P. T. (1989). Geographic and vertical distribution of euphausiid species in the warm waters of the North Atlantic. J. mar. biol. Ass. India 31: 150–163

Heffernan, J. J., Hopkins, T. L. (1981). Vertical distribution and feeding of the shrimps genera *Gennadas* and *Bentheogennema* (Decapoda: Panaeidea) in the eastern Gulf of Mexico. J. Crustacean Biol. 1: 461–474

Hirota, Y. (1984). Feeding of euphausiids in the plankton net after capture. Bull. Plankton Soc. Japan 31: 53–60

Hirota, Y. (1987). Vertical distribution of euphausiids in the western Pacific Ocean and the eastern Indian Ocean. Bull. Japan Sea reg. Fish. Res. Lab. 37: 175–224

Hirota, Y., Nemoto, T. (1989). Relationship between feeding and vertical distribution of euphausiids in the western Pacific Ocean. Bull. Plankton Soc. Japan 36: 127–135

Hirota, Y., Nemoto, T., Marumo, R. (1983). Vertical distribution of euphausiids in Sagami Bay, central Japan. La Mer 21: 151–163. (Bull. Soc. franco-jap. Océanogr., Tokyo)

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. (1985). Feeding ecology of four hatchetfishes (Sternoptychidae) in the eastern Gulf of Mexico. Bull. mar. Sci. 36: 260–277

Hopkins, T. L., Gartner, J. V., Jr. (1992). Resource-partitioning and predation impact of a low-latitude myctophid community. Mar. Biol. 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

Humphries, J. M., Bookstein, F. L., Chernoff, B., Smith, G. R., Elder, R. L., Poss, S. G. (1981). Multivariante discrimination by shape in relation to size. Syst. Zool. 30: 291–308

Hu, V. J. H. (1978). Relationships between vertical migration and diet in four species of euphausiids. Limnol. Oceanogr. 23: 296–306

James, B. M. (1970). Euphausiacean Crustacea. In: Pequegnat, W. E., Chace, F. A. (eds.) Contribution to the biology of the Gulf of Mexico. Tex. A&M Univ. oceanogr. Stud. 1: 205–229

Leipper, D. F. (1970). A sequence of current patterns in the Gulf of Mexico. J. geophys. Res. 75: 637–657

Lewis, J. B. (1954). The occurrence and vertical distribution of the Euphausiacea of the Florida Current. Bull. mar. Sci. Gulf Caribb. 4: 265–301

Longhurst, A. R. (1976). Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. Deep-Sea Res. 23: 729–754

Mauchline, J. (1967). Feeding appendages of the Euphausiacea (Crustacea). J. Zool., Lond. 153: 1–43

Mauchline, J. (1980). The biology of mysids and euphausiids. In: Blaxter, J. H. S., Russel, F. S., Yonge, M. (eds.) Advances in marine biology. Vol. 18. Academic Press, London, p. 373–623

Mauchline, J. (1989). Functional morphology and feeding of euphausiids. In: Felgenhauer, B. E., Watling, L., Thistle, A. B. (eds.) Functional morphology of feeding and grooming in Crustacea. A. A. Balkema, Rotterdam

Mauchline, J., Fisher, L. R. (1969). The biology of euphausiids. In: Russel, F. S., Yonge, M. (eds.) Advances in marine biology. Vol. 7. Academic Press, London, p. 1–454

McGowan, J. A. (1974). The nature of oceanic ecosystems. In: Miller, C. B. (ed.) The biology of the oceanic Pacific. Oregon State University Press, Corvallis, p. 9–28

McGowan, J. A. (1979). Structure in the copepod community of the North Pacific Central Gyre. Ecol. Monogr. 49: 195–226

McGowan, J. A., Walker, P. W. (1985). Dominance and diversity maintenance in an oceanic ecosystem. Ecol. Monogr. 55: 103–118

Michel, H. B., Foyo, M. (1976). Caribbean zooplankton. Pt 1. Siphonophora, Heteropoda, Copepoda, Euphausiacea, Chaetognatha and Salpidae. Office of Naval Research, Department of the Navy, Washington (Rep. Off. nav. Res. Stock No. 008-051-00066-6)

Mikkelsen, P. M. (1987). The Euphausiacea of eastern Florida (Crustacea: Malocostraca). Proc. biol. Soc. Wash. 100: 275–295

Nemoto, T. (1967). Feeding pattern of euphausiids and differentiations in their body characters. Inf. Bull. Planktol. Japan 61: 157–170

Nemoto, T. (1968). Chlorophyll pigments in the stomachs of euphausiids. J. oceanogr. Soc. Japan 24: 253–260

Nemoto, T. (1977). Food and feeding structures of deep-sea *Thysanopoda* euphausiids. In: Andersen, N. R., Zahuranec, B. J. (eds.) Oceanic sound scattering prediction. Plenum Press, New York, p. 457–480

Nowlin, W. D. (1971). Water masses and general circulation of the Gulf of Mexico. Oceanol. int. 6: 28–33

Passarella, K. C., Hopkins, T. L. (1991). Species composition and food habits of the micronektonic cephalopod assemblages in the eastern Gulf of Mexico. Bull. mar. Sci. 49: 638–659

Pelymskiy, A. G., Arashkevich, Y. G. (1980). Quantitative characteristics of the feeding of euphausiids in the tropical part of the Pacific Ocean. Oceanology, Wash. 20: 199–203

Ponomareva, L. A. (1963). Euphausiids of the North Pacific, their distribution and ecology. Dokl. Akad. Nauk. SSSR. 1–142. [Israel Program for Scientific Translation 1966; IPST No. 1368]

Ponomareva, L. A. (1971). Circadian migrations and feeding rhythm of some Indian Ocean euphausiid species. Oceanology, Wash. 11: 226–231

Ponomareva, L. A., Baulin, Y. V. (1987). Laser fluorescence study of gut chlorophyll content of tropical euphausiids. Oceanology Wash. 27: 640–642

Roger, C. (1971). Distribution verticale des euphausiacés (crustacés) dans les courants équatoriaux de l'Océan Pacifique. Mar. Biol. 10: 134–144

Roger, C. (1974). Repartitions bathymetriques et migrations verticales des euphausiaces (Crustaces) dans les zones de peche au thon du Pacifique sud-tropical. Cah. O.R.S.T.O.M. Sér. Océanogr. 12: 221–239

Roger, C. (1975). Rhythmes nutritionnels et organisation trophique d'une population de crustacés pélagiques (Euphausiacea). Mar. Biol. 32: 365–378

Romesburg, H. C. (1990). Cluster analysis for researchers. Robert E. Krieger Publishing Co., Malabar, Florida

Sameoto, D., Guglielmo, L., Lewis, M. K. (1987). Day/night vertical distribution of euphausiids in the eastern tropical Pacific. Mar. Biol. 96: 235–245

Schoener, T. W. (1974). Resource partitioning in ecological communities. Science, N. Y. 185: 27–39

Shuert, P. G., Hopkins, T. L. (1987). The vertical distribution and feeding ecology of *Euchaeta marina* in the eastern Gulf of Mexico. Contr. mar. Sci. Univ. Tex. 30: 49–61

Suh, H.-L., Nemoto T. (1988). Morphology of the gastric mill in ten species of euphausiids. Mar. Biol. 97: 79–85

Travers, M. (1971). Diversite du microplancton du Golfe de Marseille in 1964. Mar. Biol. 8: 308–343

Wiebe, P. H., Burt, K. H., Boyd, S. H., Morton, A. W. (1976). A multiple opening–closing net and environmental sensing system for sampling zooplankton. J. mar. Res. 34: 313–326

Winans, G. A. (1984). Multivariate morphometric variability in pacific salmon: technical demonstration. Can. J. Fish. aquat. Sciences 41: 1150–1159

Young, R. E., Roper, C. F. E. (1969). A monograph of the Cephalopoda of the North Atlantic: the family Cycloteuthidae. Smithson. Contr. Zool. 5: 1–24

Youngbluth, M. J. (1975). The vertical distribution and diel migration of euphausiids in the central waters of the eastern South Pacific. Deep-Sea Res. 22: 519–536

Youngbluth, M. J. (1976). Vertical distribution and diel migration of euphausiids in the central region of the California Current. Fish. Bull. U.S. 74: 925–936

Zaret, T. M., Rand, A. S. (1971). Competition in tropical stream fishes: support for the competitive exclusion principal. Ecology 52: 336–342

Communicated by N. H. Marcus, Tallahassee