CHAPTER 4

Food habits of numerically dominant decapods and mysids in the subarctic Pacific and Bering Sea

INTRODUCTION

While the diets of euphausiids in the SAP and BS have been well studied since the 1960's (e.g. Ponomareva, 1963), the decapods have been less intensely studied (Aizawa 1974, Donaldson 1976, Nishida *et al.*, 1988), including shrimp feeding in the ESA (Nishida *et al.* 1988) and in the WSA (Aizawa 1974), but not in the CSA or BS. Presently there are no feeding studies available of mysids in the SAP.

Hopkins, *et al.*, (1984) discussed midwater micronektonic decapods in the Gulf of Mexico and found their feeding impact as equivalent to that of myctophids in the same region. Since the feeding impact of the MNC in the subarctic Pacific is still unknown, this Chapter examines feeding of three dominant decapod and one mysid species via gut fullness and gut digestion indices and qualitative gut content analysis to test for the differences between: 1) day and night; 2) depth distribution; 3) regions of the subarctic Pacific; 4) sex; and 5) species.

Daily ration estimates of shrimp and mysids are available in the literature, and these previous reports will be presented and compared to results for the decapods and mysids given here. Estimates of the daily ration by percent body weight of biomass production consumed by the micronektonic crustaceans, as well as changes in gut content composition and feeding periodicity by region and time of day should help clarify day and night feeding patterns and any changes in feeding by time of day and by region.

METHODS

Samples were collected with an RMT 8 (See Chapter 3, Fig. 3-1) at 4 stations during the summer, 1997 cruise of the RV Hakuho-Maru (see Nishikawa *et al.*, 2001). These data included samples from 0 - 1000 m, in 12 discrete sampled layers at each station. CTD data was collected at each station during the cruise (Ocean Research Institute, University of Tokyo, 1998).

Gut Content analysis

As many as 10 intact individuals (when available) of *Sergestes similis, Bentheogennema borealis, Hymenodora frontalis* and *Eucopia grimaldii* were randomly sorted from collections from each depth layer sampled during each RMT-8 haul and were dissected. Each individual was sexed, wet weight (to the nearest 0.1 mg) and carapace length (from the occipital to the mid-dorsal posterior margin of the carapace, to the nearest 0.05 mm) measured. The foregut was removed from each organism and wet weight recorded before staining with methylene blue. After staining for 45 minutes, 2-3 drops of glycerine were applied to each gut to ease gut content identification. Gut fullness was estimated on a 1 - 5 scale (0 being empty and 4 being full), as well as gut content digestion status (0 being completely digested, and 4 being freshly ingested). The highest values of gut wet weight and fullness were used to represent maxima of gut fullness. A dissection microscope was used for qualitative assessment of gut contents, each class of which was assigned a code (Table 4-I) to be used in the analysis. Gut contents for each species were examined on the basis of identifiable remains assigned codes in Table 4-1.

Data analysis

Significance of feeding differences between depth layers, day and night, sex and regions was mainly evaluated by F and t tests. Feeding patterns were examined via PCA on correlations for each species per discrete depth layer, and the results displayed in a cluster analysis (Ward's minimum variance) to determine groups of similarly feeding species. Clusters were ordered by the 1st principal component derived from the PCA analysis. In Ward's minimum variance method, the distance between two clusters is the ANOVA sum of squares between the two clusters added up over all the variables. Ward's method analyzes the distance between two clusters is the analysis of variance sum of squares between the clusters summed over all variables. For interpretation, the sum of squares are converted to R^2 values. Ward's Minimum Variance method tends to join clusters with small numbers of observations and is biased toward producing clusters with roughly the same number of observations. The analysis was performed with JMP (JMP, version 5: SAS Institute, Cary NC, 1989 - 2002), a statistical software package and analysis tool for Mac OSX.

Four-factor ANOVA was performed to identify significant differences in gut fullness, individual wet weight and carapace length for each of the four species examined here against: day/night, region, depth and sex. Single-factor ANOVA was performed to examine gut content composition by species among the 4 regions of the SAP and BS. Mean gut content composition was determined by analyzing the occurrence of each gut content item identified within guts averaged over the total number of individuals recovered with any gut contents. Single factor ANOVA analysis of gut content composition was performed to examine differences in feeding (as determined by gut contents) among the 4 regions: the WSA, CSA, ESA and BS, when samples allowed. In the case of an insufficient number of individuals within any region, that region was then excluded from the ANOVA analysis. Multivariate analysis comparing diet composition among the 4 MNC species was performed via correlation analysis while between species diets were examined both by PCA cluster analysis and by Spearman's r (rho).

Daily ration, or biomass consumed, was estimated according the method described in Moku *et al.* (2000). A stomach content index (SCI) was calculated on the basis of gut content wet weight (g) divided by individual body weight and multiplied by 100. The resultant SCI was multiplied by 24 (h) and divided by egestion time. Egestion times from published literature rates (Teal 1971; Omori 1974; Mincks *et al.*, 2000) were used to estimate egestion times in water temperatures found in the SAP and BS (Table 4-II). The resultant estimates were used in combination with biomass estimates obtained from RMT 1 nets, which collected zooplankton concurrently with the RMT 8 nets.

RESULTS

Hydrography

In terms of temperature and salinity, there was remarkable similarity in stability of water masses below 200 m (see Chapter 2, Results). The main exception was dissolved oxygen, which exhibited the sharpest cline at 100 m in the BS, and to an increasingly deeper depths and shallower gradient from the WSA to ESA. The largest concentration of Chlorophyll-a was in the WSA at 50 m. A large El Nino event in 1997 (Huyer *et al.*, 2002) resulted in warmer (2-5 °C) than average sea surface temperature (SST) in the ESA and BS and cooler (1-4 °C) than average SST in the WSA (satellite data NOAA, 1997). Salinity was highest (>33.5 psu) in the upper 100 m of the northern part of the study area (BS and northern ESA). The CSA and BS had warmer SST than the ESA (9 °C and 7 °C, respectively). Water temperature in the CSA dropped to ca. 3 °C at ca. 125 m and remained steady to 1000 m.

Gut Contents

Gut contents were classified according to the morphology of the individual components of the gut (Table 4-I). Gut contents of mysids and decapods are difficult to study because of maceration of food by the mandibles and the gastric mill (Fig. 4-1). Therefore, identification of gut contents is limited to objects that resist maceration. The items found in the guts of the MNC are listed and codes described in relative gut content abundance tables for each species. Debris was unformed aggregations of unidentifiable items. Detritus and green detritus are aggregates of masses and greenish masses. Oily globs were typically reddish, immiscible liquids found inside the guts, often associated with crustacean fragments. Hairs were hair-like masses possibly muscle tissue. Crustacean fragments were classed into many categories, mainly because of the extreme

Table 4-I. Gut content codes, shorthand, and description of items found in MNC guts collected via RMT-8 during cruise KH 97-2.

Gut content codes		Description
010	debris	formless matter or particles
020	detritus	clumps of matter or particles
021	green detritus	green clumps of matter
030	oily globs	oil in balls or clumps
040	hairs	long hair-like matter
050	chaetognath hook(s)	self-expl.
051	chaetognath head(s)	self-expl.
060	crustacean fragments	legs or other parts of crustaceans
061	crustacean larvae	self-expl.
062	crustacean mandibles	parts of mandibles
063	crustacean antennal scale	self-expl.
064	crustacean eye(s)	lenses, fragments of lenses, etc.
065	crutacean legs	legs or leg fragments
070	carapace fragments	square or rectangular pieces of chitin-like material
080	copepod fragments	arms, legs, carapace of copepods
081	Metridia spp.	copepods of metridia
082	copepod antenna	antenna fragments
083	copepod furca	self-expl.
090	spicules	short rods or needles
100	eggs	eggs
110	pteropod	pteropod shell
120	unknown	unknown form
130	hooks	hollow, curved hooks
140	fish bone(s)	self-expl.
141	fish scale(s)	self-expl.
150	gelatinous mass	formless, clear, cohesive mass
160	bucky ball	diatomaceous sphere
170	mysid furca	Eucopia sp.
180	mysids fragments	Eucopia sp., legs, antenna scales, oostegites
190	fish eye	self-expl.

Table 4-II. Reported egestion values for pelagic crustaceans (Teal 1971, Omori 1974, Mincks et al. 2000).

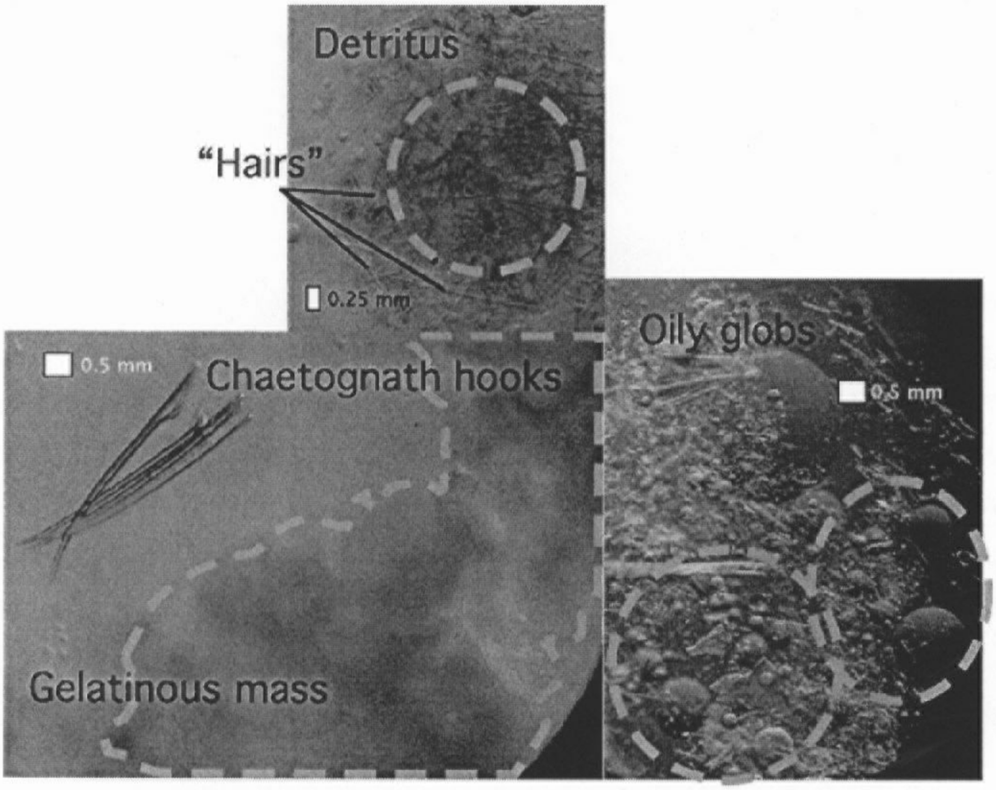

Fig. 4-1. Gut content item microphotographs. Scales as shown for each image, and each image as labeled.

fragmentary nature in which they were recovered. Most crustacean remains were fragments of carapaces, legs and mandibles. Crustacean eyes were recognized mainly as disarticulated cones, although some more complete eye fragments were also found. Copepod fragments were more easily recognizable, comprising antenna fragments and fragments of carapaces and legs. Spicules were small (< 0.05 mm) spines, disarticulated in the gut. Pteropods were recognized by the presence of shells inside the gut. Some diatomaceous spheres were also found, identified as "buckyballs" due to the geodesic shape of their skeletons. Gelatinous masses were often associated with chaetognath remains, but not always. Some mysid remains (i.e. furca and other fragments) were also identified. Examination of gut contents showed that levels of maceration differed between species. *Sergestes similis* had the most intact gut contents of all 4 species investigated while *Eucopia grimaldii* had no easily recognizable gut contents.

Species-specific gut contents

A gut content comparison of the 4 species examined here is shown in Fig. 4-2. Overall total composition of gut contents among decapods was similar, but they significantly differed from gut contents of the mysid *Eucopia grimaldii* (ANOVA; $P < 0.05$). The main differences among the decapods were that *Bentheogennema borealis* and *Hymenodora frontalis* contained mysid remains (4 and 2 %, respectively), but *Sergestes similis* did not. In addition, *S. similis* had a lower portion of fish (2%) in total gut contents compared to *B. borealis* and *H. frontalis* (7 and 3%, respectively). Copepod remains comprised a larger portion of diet in *H. frontalis* (19%), when compared to the other shrimps (<17%). *Eucopia grimaldii* had much larger proportions of debris (36.5%), oily globs (31.5%) and gelatinous masses (21.9%) than any of the 3 shrimp species. *E. grimaldii* had the least proportion of recognizable gut content items of all 4 MNC species, despite having a stomach that is less scleroterized than the shrimps with fewer gastric teeth (personal observation). Correlation analysis of gut content item composition among the 4 MNC species is shown in Table 4-III. The diets of *Hymenodora frontalis* and *Bentheogennema borealis* were the most closely correlated, followed by *H. frontalis* and *Sergestes similis*, (Spearman's rho, $P<0.0001$). The diet of *Eucopia grimaldii* had the lowest correlation with any of the other MNC diets, and only had a slight correlation with *B. borealis* (0.44) supported by the results of gut content examination.

Gut fullness - species differences between day/night, region, depth and sex

There were no differences among any of the MNC examined in this Chapter in feeding, as defined by gut fullness, either between day and night or males and females within the WSA, CSA or ESA

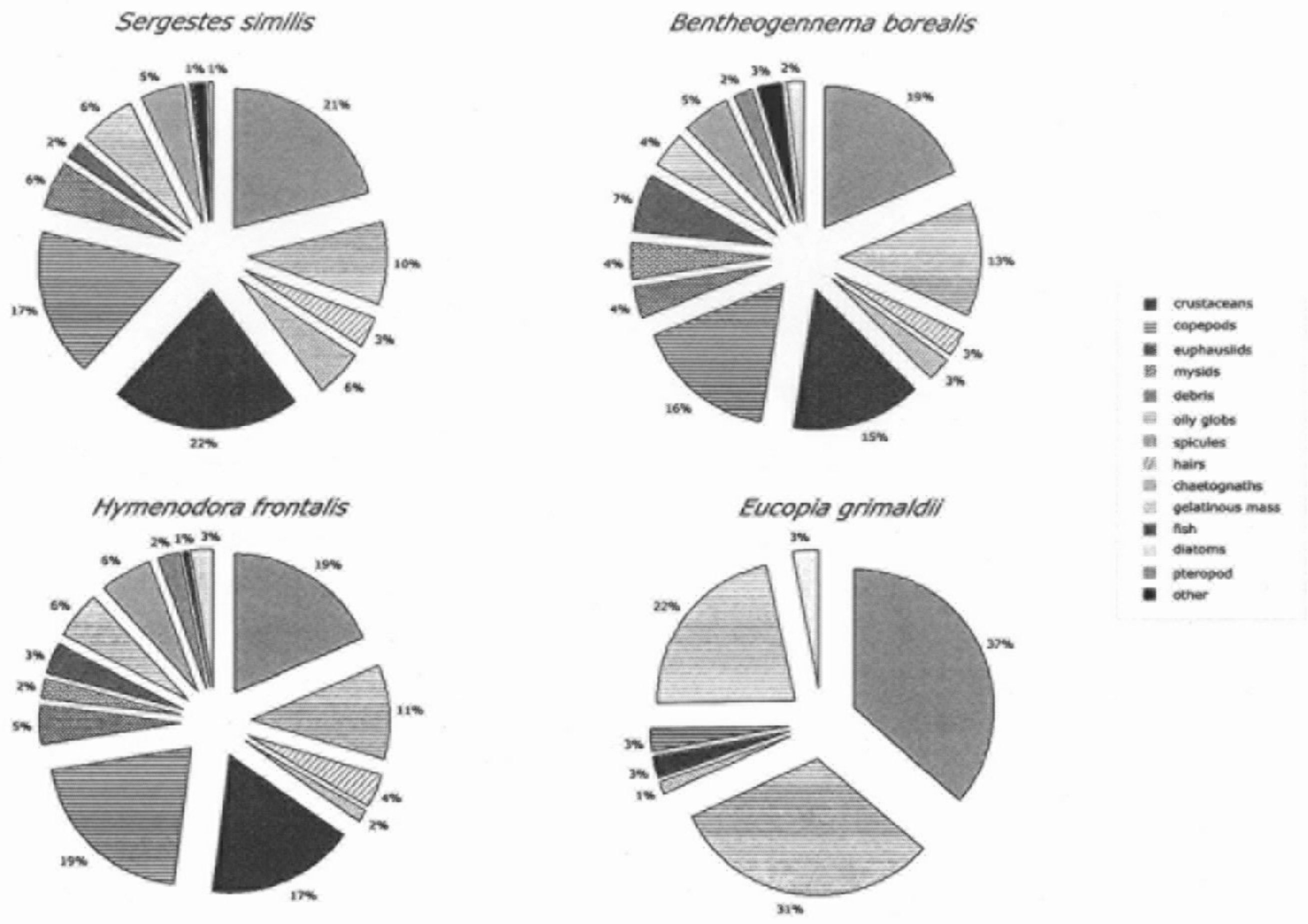

Fig. 4-2. Composition of MNC gut contents for the 4 dominant species examined in this chapter. Gut contents are classified according to Table 4-I. Fraction values of recovered gut content items recovered from MNC stomachs are indicated. Legend lists gut content items by major groups.

Table 4-III. Correlations and Spearman's Rho values comparing gut contents of dominant MNC species in the SAP and BS. Correlations are along the top diagonal while Rho values are along the bottom diagonal.

	Sergestes similis	*Bentheogennema borealis*	*Hymenodora frontalis*	*Eucopia grimaldii*
Sergestes similis	**	0.9160	0.9541	0.3289
Bentheogennema borealis	*0.8007*	**	0.9646	0.4428
Hymenodora frontalis	*0.8643*	*0.8901*	**	0.3571
Eucopia grimaldii	*0.6480*	*0.3391*	*0.5317*	**

($p = 2.04$; $P > 0.05$). Single-factor ANOVA showed no significant difference in mean gut content composition among the WSA, CSA, ESA ($P > 0.05$).

Sergestes similis

There were 200 individuals of this shrimp collected in the SAP (Table 4-IV), and the sole individual from the BS was excluded from this analysis. Ratios of males to females differed only at night in the ESA (39 to 19 respectively). Females were larger than males in the WSA and ESA, but not in the CSA ($P>0.01$). Less than 20% of the foreguts were empty, regardless of area or time of day. Over 50% of the foreguts contained detritus and crustacean fragments. Chaetognath hooks, euphausiid mandibles and euphausiid compound eye cones were the most easily recognizable gut contents. Green detritus was only abundant in guts from the ESA. This was also true of gelatinous masses, present in over 80% and 30% of guts from night and day hauls respectively in the ESA. Unidentified intact crustacean larvae were recovered from guts from the CSA (night) and WSA (day). Oily globs were a constant feature of *S. similis* guts, except in the day WSA hauls.

The 4-way ANOVA for gut fullness (Table 4-V) showed a significant region depth and day/night effect, indicating that the degree of gut fullness was not equally spread throughout the day or night water column, or among regions. There were no significant effects for sex. Gut fullness with depth, both day and night, along with the relative percentage of gut fullness for each depth layer is shown in Fig. 4-3. There was less feeding evident in the WSA and CSA during the day. The most feeding was evident in the ESA, both day and night. The number of guts that were full or nearly full (3 – 4) decreased from all guts in depth layer 120 - 200 m to 60% or less in depth layers 400 - 600 m. There were more empty guts at night in the ESA when compared to the daytime. Empty guts peaked at 500 - 600 m (> 50%) before dropping off again. In the WSA at night, gut fullness was highest in the 20 - 200 m depth layers. In the CSA, maximal feeding seemed to move from the 400 - 500 m layer in the daytime to the 100 - 150 m layer at night. The trend of fuller guts in deeper depths in the daytime compared to nighttime was also evident in the WSA and ESA. However, in the ESA, feeding was evident throughout the water column, day or night.

Bentheogennema borealis

This was the second most abundant of the 3 shrimp species examined ($n = 262$) for gut content analysis (Table 4-VI). Ratios of males to females differed most at night in all regions, greatest in the CSA (0 to 39, respectively), and also showed a trend of larger females than males in the WSA and ESA, but not the CSA. Very few individuals were recovered from the BS ($n=5$). Gut contents were

Table 4-IV. Sergestes similis: foregut and hindgut analysis by region, day and night. Frequency of occurrence of each class of gut content item in examined stomachs is expressed as a fraction of guts containing that item. The 3 top items (by percentage) by region and time of day are shaded.

	WSA				CSA				ESA			
	Day		Night		Day		Night		Day		Night	
Males to Females	8	9	25	23	19	15	5	7	13	17	39	19
No. ind. examined	17		48		34		12		30		58	
No. ind. with food	15		44		29		11		29		47	
% with food	0.88		0.92		0.85		0.92		0.97		0.81	
mean size (mm)	7.31		7.79		7.43		7.85		9.37		9.50	
mean wt. (mg)	0.24		0.27		0.27		0.28		0.42		0.45	
Food Items	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %
debris	4	6.5	6	3.8	7	8.6	0	0.0	3	1.4	15	4.2
detritus	8	12.9	10	6.3	16	19.8	7	18.9	23	10.6	37	10.3
green detritus	6	9.7	4	2.5	1	1.2	0	0.0	18	8.3	26	7.3
oily globs	0	0.0	17	10.6	13	16.0	8	21.6	13	6.0	38	10.6
hairs	2	3.2	10	6.3	3	3.7	5	13.5	6	2.8	6	1.7
chaetognath hook(s)	3	4.8	5	3.1	4	4.9	4	10.8	5	2.3	13	3.6
chaetognath head(s)	0	0.0	6	3.8	0	0.0	0	0.0	1	0.5	5	1.4
crustacean fragments	9	14.5	24	15.0	4	4.9	2	5.4	12	5.5	15	4.2
crustacean larvae	2	3.2	0	0.0	0	0.0	3	8.1	0	0.0	0	0.0
crustacean mandibles	2	3.2	5	3.1	0	0.0	0	0.0	12	5.5	11	3.1
crustacean antennal scale	1	1.6	2	1.3	0	0.0	0	0.0	3	1.4	3	0.8
crustacean eye(s)	0	0.0	5	3.1	0	0.0	0	0.0	8	3.7	8	2.2
crutacean legs	0	0.0	0	0.0	0	0.0	0	0.0	16	7.3	5	1.4
carapace fragments	10	16.1	21	13.1	11	13.6	2	5.4	21	9.6	35	9.8
copepod fragments	2	3.2	18	11.3	8	9.9	4	10.8	19	8.7	31	8.7
metridia spp.	0	0.0	0	0.0	0	0.0	1	2.7	0	0.0	0	0.0
copepod antenna	0	0.0	0	0.0	0	0.0	0	0.0	19	8.7	27	7.5
copepod furca	0	0.0	0	0.0	0	0.0	0	0.0	10	4.6	19	5.3
spicules	11	17.7	9	5.6	14	17.3	1	2.7	6	2.8	11	3.1
eggs	0	0.0	3	1.9	0	0.0	0	0.0	2	0.9	3	0.8
pteropod	1	1.6	0	0.0	0	0.0	0	0.0	0	0.0	2	0.6
unknown	0	0.0	2	1.3	0	0.0	0	0.0	0	0.0	0	0.0
hooks	1	1.6	0	0.0	0	0.0	0	0.0	0	0.0	1	0.3
fish bone(s)	0	0.0	1	0.6	0	0.0	0	0.0	0	0.0	2	0.6
fish scale(s)	0	0.0	2	1.3	0	0.0	0	0.0	6	2.8	5	1.4
gelatinous mass	0	0.0	10	6.3	0	0.0	0	0.0	9	4.1	40	11.2
bucky ball	0	0.0	0	0.0	0	0.0	0	0.0	5	2.3	0	0.0
mysid furca	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
mysids fragments	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
fish eye	0	0.0	0	0.0	0	0.0	0	0.0	1	0.5	0	0.0

Table 4-V. Summary of four-factor ANOVA for gut fullness.

Gut fullness	d.f.	*F*	*P*
Hymenodora frontalis			
Day/Night	1	0.194	0.6598
Region	3	1.4998	0.2139
Depth	9	0.8789	0.544
Sex	1	0.0676	0.7949
Bentheogennema borealis			
Day/Night	1	0.3982	0.5286
Region	3	1.7291	0.1616
Depth	7	2.8789	0.0066
Sex	2	0.652	0.5219
Sergestes similis			
Day/Night	1	11.0805	0.0011
Region	2	14.9921	<0.0001
Depth	14	3.4815	<0.0001
Sex	1	1.2594	0.2633
Eucopia grimaldii			
Day/Night	1	2.2392	0.1354
Region	3	1.3949	0.2439
Depth	8	3.2747	0.0013
Sex	1	0.4847	0.4867

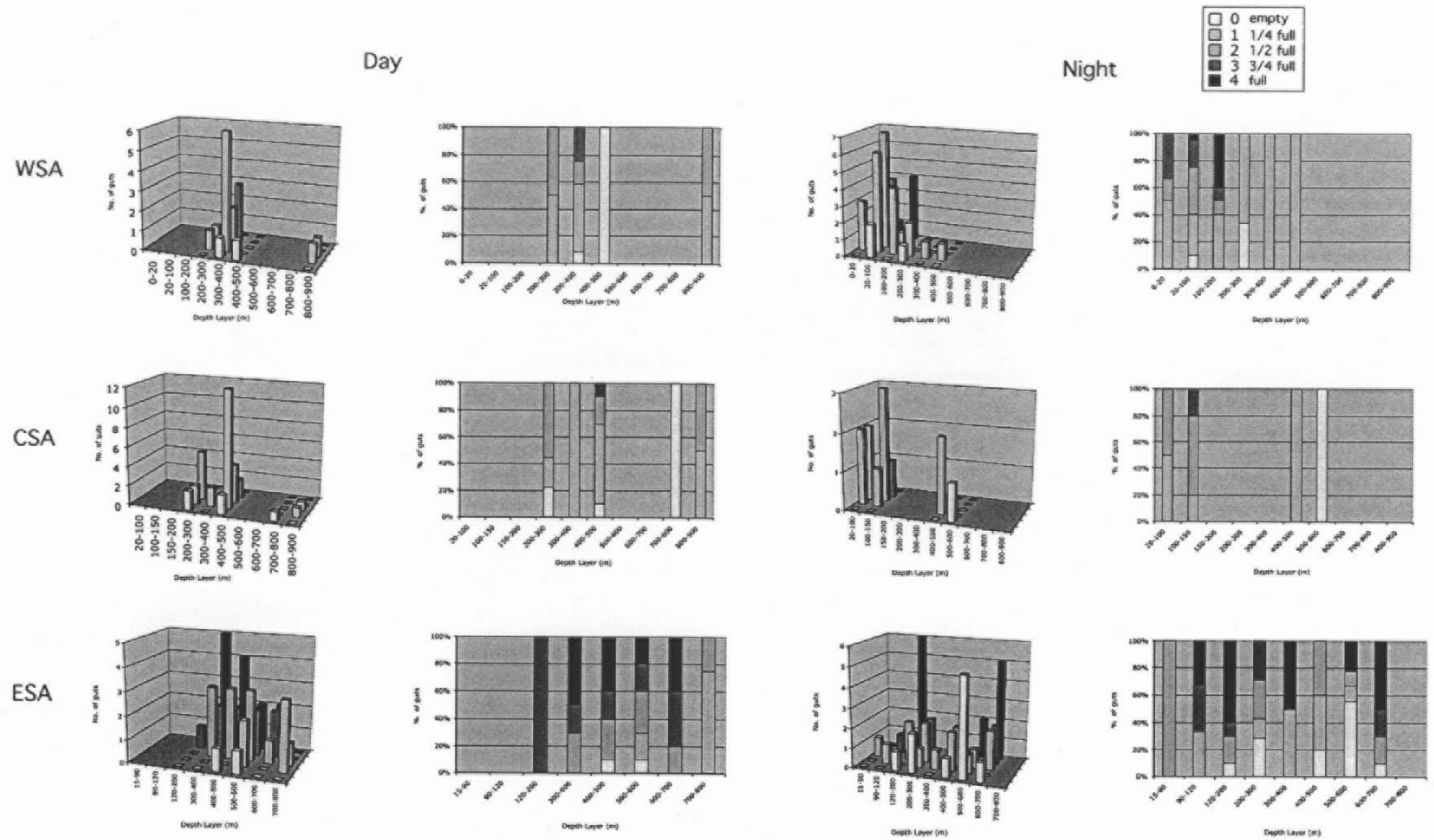

Fig. 4-3. *Sergestes similis* gut fullness and proportional abundance by depth layer (as described in text). Day on the left side, night on the right. Regions indicated along the left-most column.

Table 4-VI. Bentheogennema borealis: foregut and hindgut analysis by region, day and night. Frequency of occurrence of each class of gut content item in examined stomachs is expressed as a fraction of guts containing that item. The 3 top items (by percentage) by region and time of day are shaded.

	WSA				CSA				ESA				BS	
	Day		Night		Day		Night		Day		Night		Total	
Males to Females	15	29	2	18	14	27	0	39	4	23	2	18	1	4
No. ind. examined	44		20		41		39		27		20		5	
No. ind. with food	41		16		32		31		26		20		5	
% with food	0.93		0.80		0.78		0.79		0.96		1.00		1.00	
mean size (mm)	8.50		6.41		7.04		7.94		9.25		8.39		11.26	
mean wt. (mg)	0.81		0.39		0.56		0.69		0.96		0.75		1.52	
Food Items	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %
debris	7	3.5	0	0.0	26	14.61	3	1.7	14	8.6	0	0.0	0	0.0
detritus	20	10.0	5	4.7	12	6.74	17	9.5	18	11.0	5	5.1	5	16.7
green detritus	3	1.5	3	2.8	9	5.06	10	5.6	8	4.9	7	7.1	5	16.7
oily globs	24	12.0	15	14.0	27	15.17	25	14.0	21	12.9	16	16.2	0	0.0
hairs	6	3.0	4	3.7	4	2.25	5	2.8	2	1.2	3	3.0	4	13.3
chaetognath hook(s)	10	5.0	9	8.4	4	2.25	7	3.9	8	4.9	2	2.0	0	0.0
chaetognath head(s)	3	1.5	6	5.6	0	0.00	3	1.7	0	0.0	0	0.0	0	0.0
crustacean fragments	17	8.5	3	2.8	4	2.25	8	4.5	7	4.3	3	3.0	3	10.0
crustacean larvae	0	0.0	0	0.0	0	0.00	0	0.0	0	0.0	0	0.0	0	0.0
crustacean mandibles	11	5.5	6	5.6	2	1.12	7	3.9	2	1.2	1	1.0	0	0.0
crustacean antennal scale	3	1.5	1	0.9	1	0.56	1	0.6	0	0.0	0	0.0	0	0.0
crustacean eye(s)	2	1.0	1	0.9	1	0.56	0	0.0	1	0.6	1	1.0	0	0.0
crutacean legs	0	0.0	5	4.7	13	7.30	8	4.5	0	0.0	0	0.0	0	0.0
carapace fragments	23	11.5	7	6.5	14	7.87	18	10.1	0	0.0	0	0.0	3	10.0
copepod fragments	14	7.0	6	5.6	15	8.43	17	9.5	18	11.0	12	12.1	3	10.0
metridia spp.	1	0.5	2	1.9	1	0.56	1	0.6	19	11.7	11	11.1	0	0.0
copepod antenna	6	3.0	5	4.7	8	4.49	10	5.6	0	0.0	0	0.0	0	0.0
copepod furca	1	0.5	3	2.8	1	0.56	2	1.1	0	0.0	0	0.0	1	3.3
spicules	14	7.0	6	5.6	2	1.12	3	1.7	0	0.0	0	0.0	1	3.3
eggs	0	0.0	0	0.0	0	0.00	0	0.0	15	9.2	7	7.1	0	0.0
pteropod	0	0.0	2	1.9	7	3.93	0	0.0	2	1.2	12	12.1	0	0.0
unknown	0	0.0	0	0.0	0	0.00	0	0.0	1	0.6	2	2.0	0	0.0
hooks	0	0.0	0	0.0	0	0.00	0	0.0	0	0.0	0	0.0	0	0.0
fish bone(s)	4	2.0	4	3.7	0	0.00	2	1.1	0	0.0	0	0.0	0	0.0
fish scale(s)	21	10.5	6	5.6	12	6.74	12	6.7	0	0.0	0	0.0	3	10.0
gelatinous mass	8	4.0	8	7.5	8	4.49	15	8.4	0	0.0	0	0.0	1	3.3
bucky ball	2	1.0	0	0.0	6	3.37	3	1.7	7	4.3	1	1.0	0	0.0
mysid furca	0	0.0	0	0.0	0	0.00	0	0.0	4	2.5	3	3.0	1	3.3
mysids fragments	0	0.0	0	0.0	1	0.56	2	1.1	16	9.8	13	13.1	0	0.0
fish eye	0	0.0	0	0.0	0	0.00	0	0.0	0	0.0	0	0.0	0	0.0

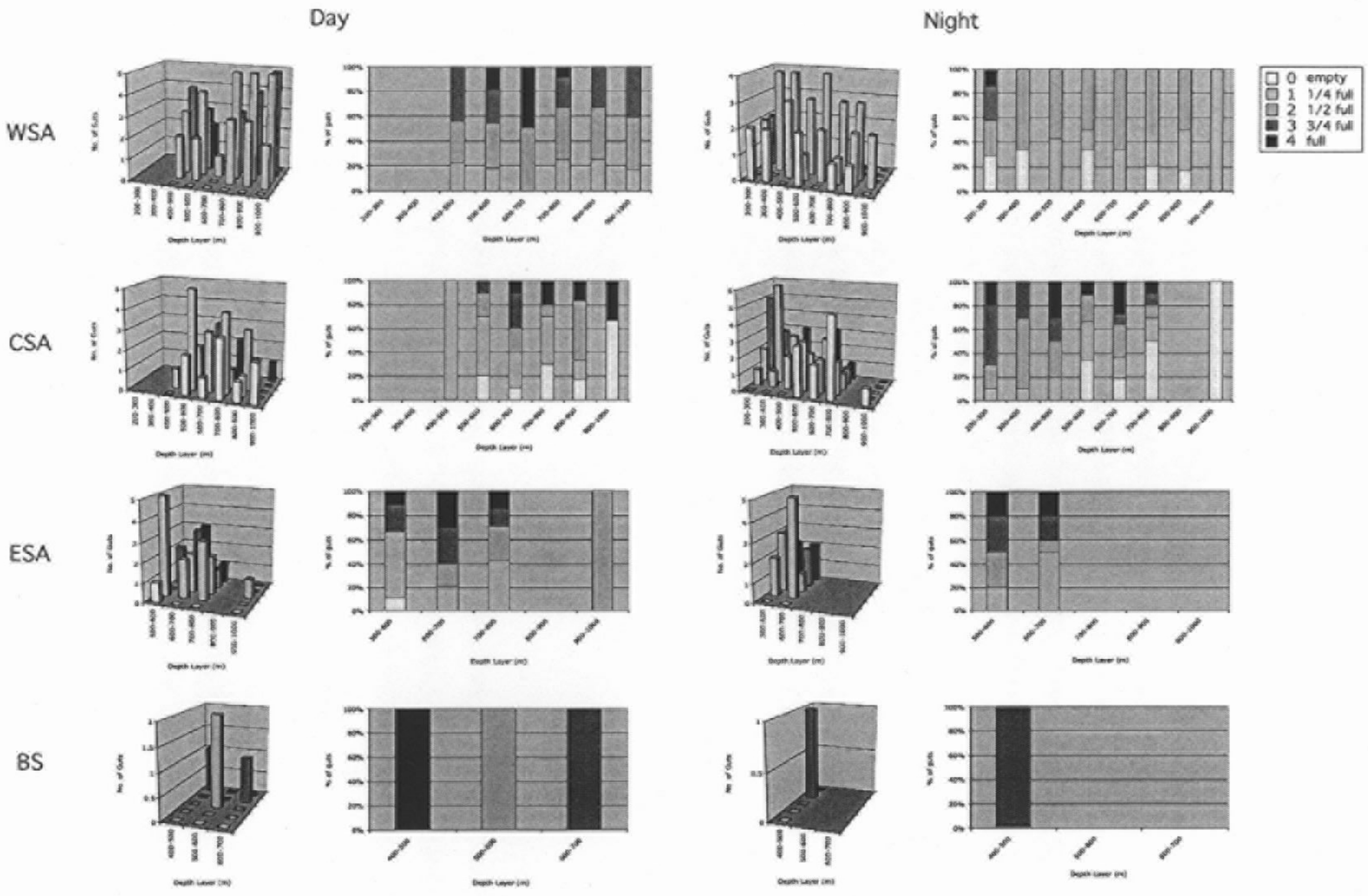

Fig. 4-4. *Bentheogennema borealis:* gut fullness and proportional abundance by depth layer (as described in text). Day on the left side, night on the right. Regions indicated along the left-most column.

heavily macerated, regardless of digestion status, with few structures larger than copepod legs surviving. Carapace and copepod fragments were also very common (> 35% of guts) in the WSA (day and night) and CSA day. Fish bones were more common in *B. borealis* compared to *S. similis* (9 - 25% to 2 - 4%, respectively). Unlike *S. similis*, over 50% of guts contained oily globs, and they were the most common of all food items in the subarctic Pacific (SAP). There seemed to be less feeding in the CSA compared to the WSA or ESA (ca. 79%), but was not significantly different. The 4-way ANOVA for gut fullness (Table 4-V) showed no significant effects of day/night, region and sex, and only a slight effect for depth. This indicates that gut fullness levels were not evenly distributed throughout the water column. Gut fullness with depth, both day and night, along with the relative percentage of gut fullness for each depth layer is shown in Fig. 4-4. Gut fullness levels throughout the daytime vertical range in the WSA were relatively consistent, there were no empty guts in any of the daytime shrimps, and at least 75% of the guts were half full. Empty guts were more common at night. Shrimps with full or nearly full guts were most common (>40%) in the daytime 600 - 700 m depth layer, and in the 200 - 300 m layer at night. Empty guts in the CSA were more common, comprising >60% of guts in the daytime 900 - 1000 m layer. Nighttime distribution patterns of empty guts were similar to daytime distributions, except that the incidence of full or nearly full guts was highest (70%) in the upper reaches of the vertical range (200 - 300 m layer) compared to the daytime. Daytime gut fullness distribution patterns in the ESA were not as clear as those of either the WSA of CSA.

Hymenodora frontalis

This was the most abundant of all the animals examined (n=467; Table 4-VII), and the only decapod present in the BS in large numbers (n=105). Feeding patterns were similar to those of *Bentheogennema borealis*; with debris and detritus composing more than 55% of gut contents in the ESA, and to lesser extents in the remaining regions. The other main gut content items included copepod, crustacean and carapace fragments, and gelatinous masses. Chaetognath hooks and fish bones and scales were among the minor gut content constituents.

The 4-way ANOVA for gut fullness (Table 4-IV) showed no significant effects of day/night, region and sex, or depth. Gut fullness with depth, both day and night, along with the relative percentage of gut fullness for each depth layer is shown in Fig. 4-5, and shows a slight trend towards increasing gut fullness with depth.

Table 4-VII. Hymenodora frontalis: foregut and hindgut analysis by region, day and night. Frequency of occurrence of each class of gut content item in examined stomachs is expressed as a fraction of guts containing that item. The 3 top items (by percentage) by region and time of day are shaded.

	WSA				CSA				ESA				BS			
	Day		Night		Day		Night		Day		Night		Day		Night	
Males to Females	10	39	29	51	21	33	26	52	16	39	12	26	22	53	12	18
No. ind. examined	49		80		54		78		55		38		75		30	
No. ind. with food	40		53		23		59		35		29		43		14	
% with food	0.82		0.66		0.43		0.76		0.64		0.76		0.57		0.47	
mean size (mm)	6.51		6.47		7.20		7.21		6.88		5.83		6.81		4.59	
mean wt. (mg)	0.38		0.41		0.46		0.48		0.41		0.31		0.44		0.22	
Food Items	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %
debris	23	7.9	9	3	5	3.0	29	6.7	13	4.8	0	0	22	7.7	6	6.7
detritus	32	11.0	27	9	17	10.1	30	6.9	18	6.7	5	5.1	30	10.6	9	10.1
green detritus	17	5.8	10	3.3	9	5.4	18	4.1	6	2.2	7	7.1	18	6.3	2	2.2
oily globs	39	13.4	22	7.3	15	8.9	46	10.6	22	8.1	16	16.2	37	13.0	11	12.4
hairs	8	2.7	17	5.7	9	5.4	18	4.1	13	4.8	3	3.0	4	1.4	1	1.1
chaetognath hook(s)	9	3.1	18	6	13	7.7	19	4.4	11	4.1	2	2.0	15	5.3	5	5.6
chaetognath head(s)	0	0	5	1.7	6	3.6	7	1.6	5	1.9	0	0	5	1.8	0	0
crustacean fragments	25	8.6	5	1.7	2	1.2	3	0.7	5	1.9	3	3.0	11	3.9	5	5.6
crustacean larvae	0	0	0	0	0	0	1	0.2	0	0	0	0	0	0	0	0
crustacean mandibles	7	2.4	15	5	9	5.4	19	4.4	14	5.2	1	1.0	3	1.1	1	1.1
crustacean antennal scale	0	0	0	0	0	0	1	0.2	0	0	0	0	0	0	0	0
crustacean eye(s)	0	0	4	1.3	2	1.2	4	0.9	5	1.9	1	1.0	3	1.1	1	1.1
crutacean legs	7	2.4	24	8	9	5.4	27	6.2	16	5.9	0	0	1	0.4	0	0
carapace fragments	35	12.0	30	10	17	10.1	42	9.7	27	10	0	0	27	9.5	11	12.4
copepod fragments	24	8.2	32	10.7	15	8.9	50	11.5	29	10.7	12	12.1	25	8.8	10	11.2
metridia spp.	0	0	2	0.7	1	0.6	2	0.5	1	0.4	11	11.1	0	0	0	0
copepod antenna	16	5.5	25	8.3	12	7.1	38	8.7	23	8.5	0	0	21	7.4	8	9.0
copepod furca	7	2.4	4	1.3	4	2.4	10	2.3	7	2.6	0	0	4	1.4	2	2.2
spicules	0	0	6	2	2	1.2	13	3.0	8	3.0	0	0	2	0.7	0	0
eggs	0	0	0	0	0	0	1	0.2	0	0	7	7.1	0	0	0	0
pteropod	1	0.3	7	2.3	3	1.8	16	3.7	8	3.0	12	12.1	0	0	0	0
unknown	0	0	0	0	0	0	0	0	0	0	2	2.0	0	0	0	0
hooks	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
fish bone(s)	14	4.8	1	0.3	1	0.6	1	0.2	4	1.5	0	0	9	3.2	5	5.6
fish scale(s)	5	1.7	1	0.3	2	1.2	7	1.6	3	1.1	0	0	7	2.5	3	3.4
gelatinous mass	21	7.2	18	6	9	5.4	13	3.0	12	4.4	0	0	29	10.2	8	9.0
bucky ball	1	0.3	13	4.3	5	3.0	16	3.7	12	4.4	1	1.0	1	0.4	0	0
mysid furca	0	0	0	0	0	0	0	0	1	0.4	3	3.0	4	1.4	1	1.1
mysids fragments	0	0	5	1.7	1	0.6	4	0.9	7	2.6	13	13.1	4	1.4	0	0
fish eye	0	0	0	0	0	0	0	0	0	0	0	0	2	0.7	0	0

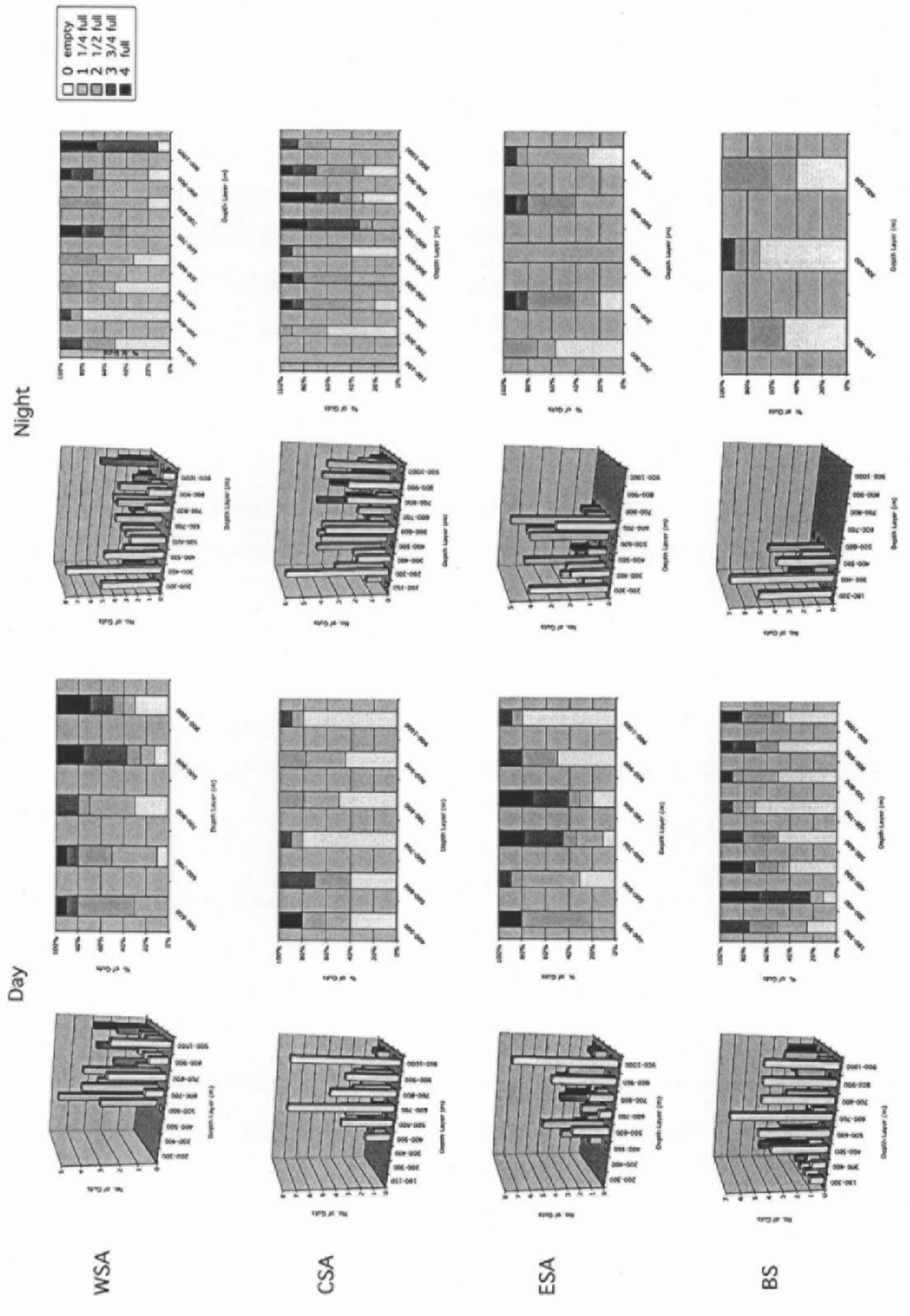

Fig. 4-5. *Hymenodora frontalis*: gut fullness and proportional abundance by depth layer (as described in text). Day on the left side, night on the right. Regions indicated along the left-most column.

Eucopia grimaldii

This mysid was the 2nd most abundant of the 4 species described here, with 307 individuals used in this analysis (Table 4-VIII). Ratios between males and females were different only in the ESA between day and night (18:32 and 17:43, males vs. females, respectively). Gut contents from this individual mainly consisted of bola located in the hindgut, however 99% of foreguts were empty. Bola were primarily plastic, well-digested translucent masses, and were impossible to resolve into any recognizable animal parts. Over 50% of all guts from the SAP contained oily globs and debris. Other recognizable remains included crustacean fragments, spicules, and carapace fragments.

The 4-way ANOVA for gut fullness (Table 4-IV) showed only a slight relation between gut fullness and depth, indicating that feeding was not uniform at all depths. This is demonstrated by the high incidence of guts only 25% full at all stations and depths. In the WSA, empty guts were more common (70%) at the uppermost limit of daytime vertical distribution (400 - 500 m), while nearly full guts were restricted to the deepest layers (800 - 1000 m) (Fig. 4-6). At night the percentage of empty guts gradually increased with increasing depth, peaking at 40% in the 900 - 1000 m depth layer. These patterns were not evident in other regions of the SAP, nor the BS. In the CSA, the maximum percentage of empty guts either in the daytime or nighttime (70 and 50%, respectively) was observed in the middle of the vertical range, and there were more empty guts in the daytime compared to the nighttime. There were fewer empty guts in the ESA compared to the other regions. The occurrence of empty guts in the daytime ESA were mainly in the uppermost limit of the daytime vertical range (400 - 500 m). At night, the highest percentage of empty guts (40%) was in the 300 - 400 m depth layer. Patterns of gut fullness in the BS were opposite of those seen in the WSA.

Clustering and total gut contents

The clusters resulting from analysis of vertical distribution patterns of the 4 MNC species examined in this chapter and relative frequency of gut content items are plotted for each MNC species for the SAP & BS, day and night combined. All regions showed 2 clusters of associations between gut contents (diet items) and depth. The data are organized by using two classification dendrograms: one with horizontal orientation (x-axis) and the other with vertical orientation (y-axis). Positive associations are marked deep red, deep green marks negative associations, white represents least significant associations and black represents no association. The heat map colors are arranged as follows: deep red shows the most common gut content items, deep green shows the least common items. White represents items that are in between. Within the SAP and BS as a whole, clustering

Table 4-VIII. Eucopia grimaldii: foregut and hindgut analysis by region, day and night. Frequency of occurrence of each class of gut content item in examined stomachs is expressed as a fraction of guts containing that item. The 3 top items (by percentage) by region and time of day are shaded.

	WSA				CSA				ESA				BS			
	Day		Night		Day		Night		Day		Night		Day		Night	
Males to Females	18	32	17	43	23	27	27	43	41	19	10	7	42	35	10	21
No. ind. examined	50		60		50		70		60		17		77		31	
No. ind. with food	32		47		30		56		52		12		62		23	
% with food	0.64		0.78		0.60		0.80		0.87		0.71		0.81		0.74	
mean size (mm)	4.91		4.88		4.59		4.66		3.91		3.30		4.18		4.99	
mean wt. (mg)	0.17		0.15		0.16		0.16		0.11		0.08		0.12		0.19	
Food Items	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %	No. guts with item	Freq of Occ. %
debris	8	13.8	32	26.7	24	35.3	51	32.9	48	32.7	12	33.3	52	32.3	10	20.4
detritus	0	0.0	0	0.0	0	0.0	9	5.8	23	15.6	0	0.0	21	13.0	0	0.0
green detritus	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
oily globs	29	50.0	44	36.7	28	41.2	47	30.3	28	19.0	12	33.3	39	24.2	23	46.9
hairs	0	0.0	0	0.0	0	0.0	2	1.3	0	0.0	0	0.0	1	0.6	0	0.0
chaetognath hook(s)	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
chaetognath head(s)	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
crustacean fragments	2	3.4	2	1.7	0	0.0	4	2.6	0	0.0	0	0.0	0	0.0	2	4.1
crustacean larvae	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
crustacean mandibles	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
crustacean antennal scale	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
crustacean eye(s)	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
crutacean legs	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
carapace fragments	0	0.0	0	0.0	2	2.9	7	4.5	0	0.0	0	0.0	0	0.0	1	2.0
copepod fragments	2	3.4	5	4.2	1	1.5	3	1.9	0	0.0	0	0.0	0	0.0	1	2.0
metridia spp.	1	1.7	4	3.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	2.0
copepod antenna	0	0.0	0	0.0	0	0.0	1	0.6	0	0.0	0	0.0	0	0.0	0	0.0
copepod furca	0	0.0	1	0.8	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
spicules	0	0.0	0	0.0	3	4.4	8	5.2	0	0.0	0	0.0	0	0.0	0	0.0
eggs	1	1.7	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
pteropod	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
unknown	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
hooks	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
fish bone(s)	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
fish scale(s)	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
gelatinous mass	0	0.0	22	18.3	10	14.7	23	14.8	48	32.7	12	33.3	48	29.8	11	22.4
bucky ball	15	25.9	10	8.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
mysid furca	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
mysid fragments	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
fish eye	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0

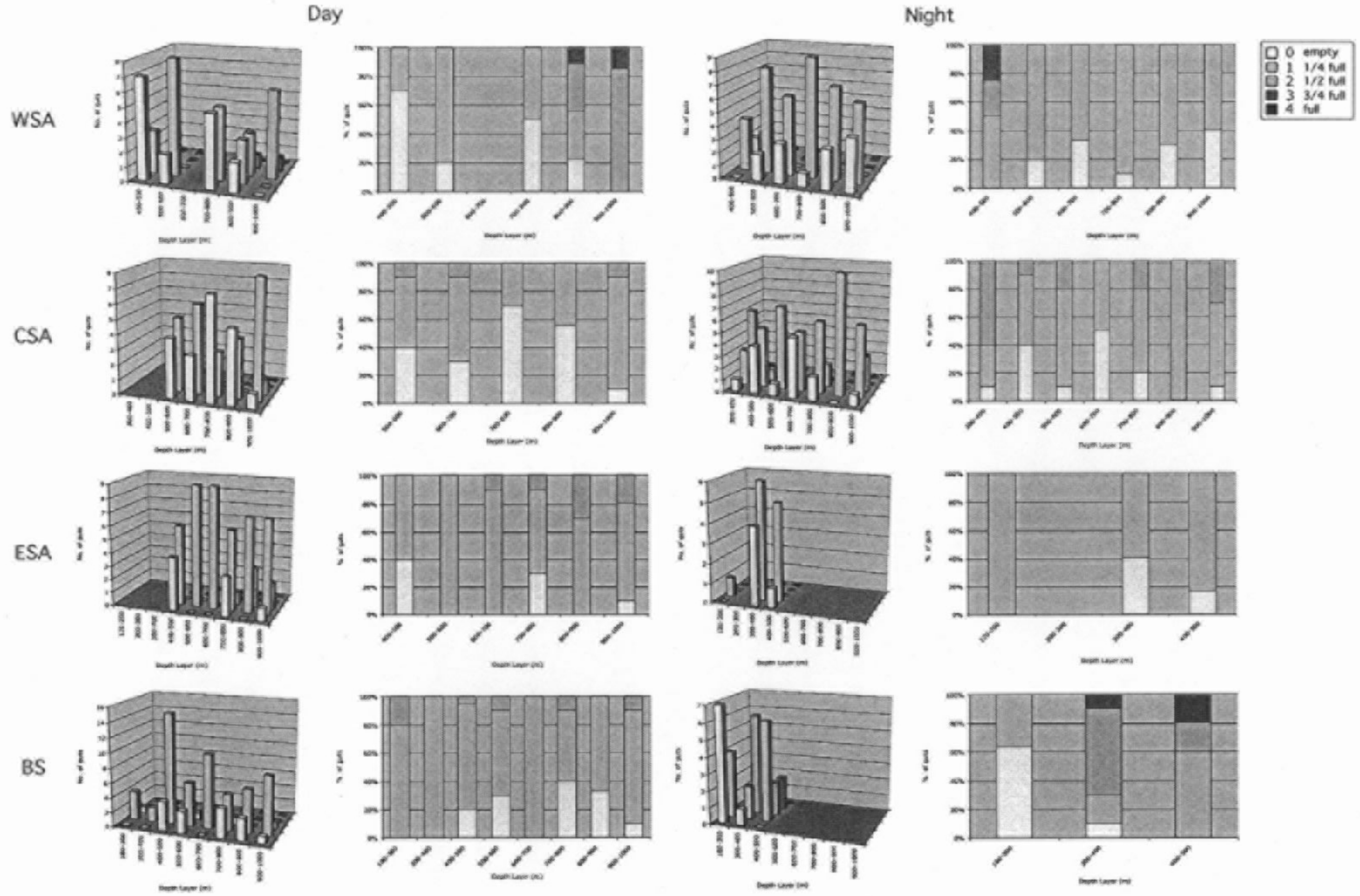

Fig. 4-6. *Eucopia grimaldii:* gut fullness and proportional abundance by depth layer (as described in text). Day on the left side, night on the right. Regions indicated along the left-most column.

revealed that of the 4 species examined here, *Sergestes similis* and *Hymenodora frontalis* were most similar in terms of gut content composition, and *Eucopia grimaldii* differed from all the others (Fig. 4-7). When each region was examined separately, there were differences in gut content composition between species. Within the WSA, *S. similis* and *B. borealis* were most similar, whereas in the CSA, ESA and BS *B. borealis* and *H. frontalis* were most similar. As noted above, *E. grimaldii* had different gut content composition than all other species. The distribution of gut content items in the WSA and CSA differed from all other areas in that mysid fragments and fish eyes and eggs were clustered independently from the majority of gut content items, symbolizing their overall rarity in MNC guts in those regions.

Diet preferences of *S. similis* as revealed by gut contents showed that feeding in the daytime WSA (Fig. 4-8) was least diverse and mainly concentrated within the 300 – 400 m depth layer. At night, it was narrowly concentrated within the 20 – 200 depth layer. Diets within the CSA were not as diverse as those seen in the WSA. However, the majority of gut content items were concentrated within narrow vertical distributions, the 400 – 500 m layer during the daytime and within the 20 – 150 m layer at night. Diets within the ESA differed from the previous two regions in two ways: diets were more diverse, and gut content items were distributed across a greater vertical range. While the numbers of diet items were roughly similar (daytime n=23, nighttime n=22) as well as the composition of diet items between day and night, there were some minor differences in the constituent diet items between day and night. These included fish bones and pteropods at night, while bucky balls and hooks were found during the daytime.

Diets of *Bentheogennema borealis* tended to be more diverse when compared to *S. similis*, for all regions except in the ESA (Fig. 4-9). Unlike the situation with *S. similis*, the variation of diets was not confined to narrow vertical distributions. There was a general upward movement of the depth of occurrence of diverse diets between day and night. In the daytime WSA, most diet items were found in individuals from the 500 – 600 m layer and rose to the 200 – 400 m layers at night. In the daytime CSA, the 600 – 700 m layer was where most diet items were recovered, while at night the CSA more closely resembled the nighttime WSA. The ESA was where the diversity of diet items was much less than either the CSA or WSA, and the vertical distribution of recovered diet items was more concentrated. In the daytime ESA, the 600 – 700 m depth layer was where diet items were most concentrated, while at the distribution at night was evenly split between the two layers where individuals were examined.

The diets of *Hymenodora frontalis* were more consistent in diversity than any other MNC

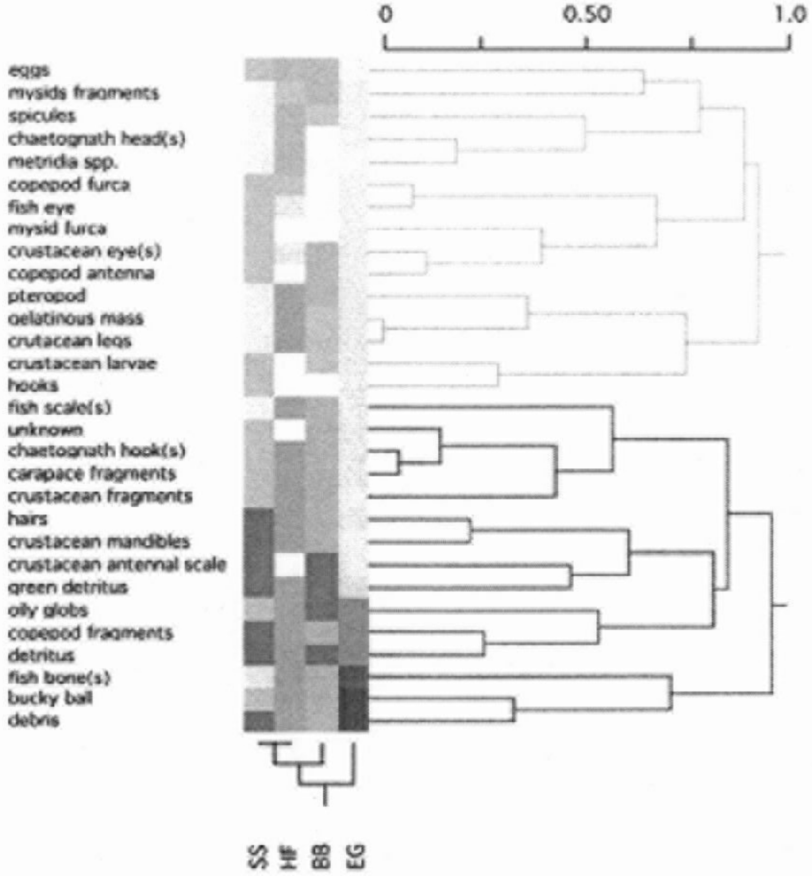

Fig. 4-7. SAP & BS combined hierarchical clustering of 4 MNC species examined in this chapter, by frequency of gut contents (as described in text). Species are listed along the bottom, gut content items along the left column.

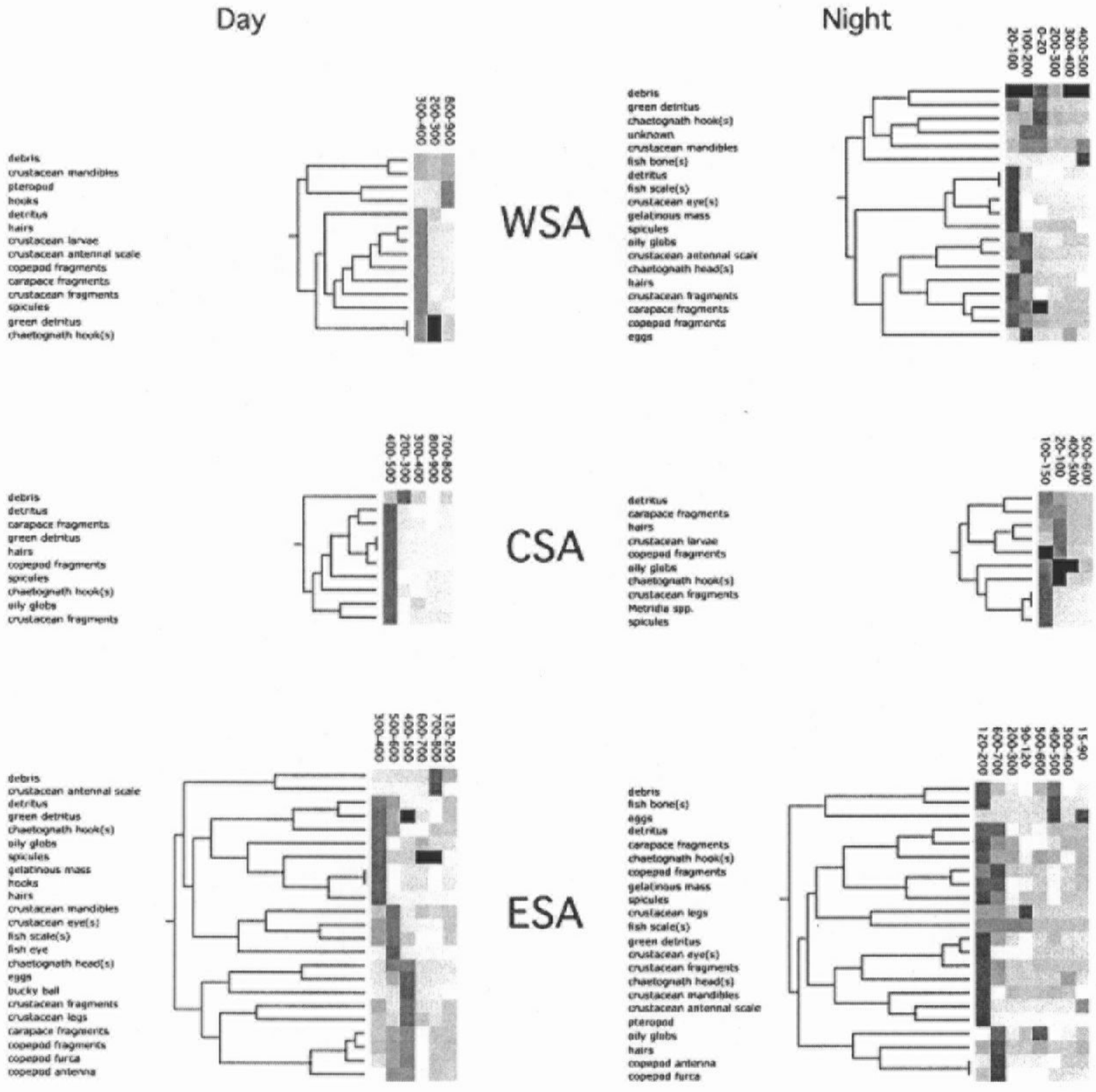

Fig. 4-8. *Sergestes similis* 2-way cluster diagram of depth and gut content items. Day is on the left column, night on the right. Regions are as in text. Gut content items listed along the left of each cluster.

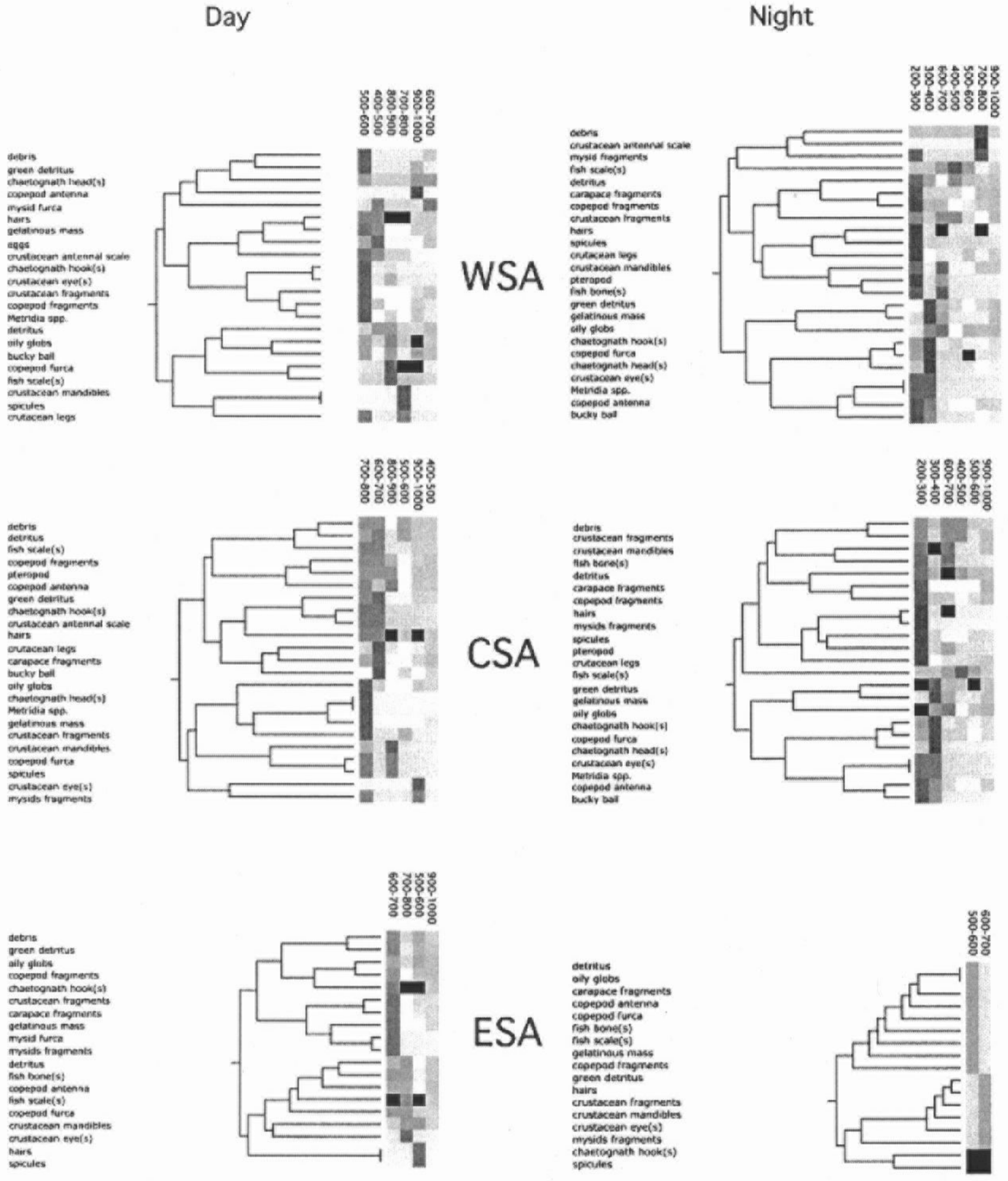

Fig. 4-9. *Bentheogennema borealis* 2-way cluster diagram of depth and gut content items. Day is on the left column, night on the right. Regions are as in text. Gut content items listed along the left of each cluster.

species examined (Fig. 4-10). In the WSA and CSA, diets seemed to be more diverse at night when compared to the daytime. However, the daytime diets in the ESA and BS were apparently more diverse than those same regions at night. The distribution of diet items throughout the water column is also greater than that seen in either *S. similis* or *B. borealis*. In the daytime WSA, there seemed to be two clusters of diet item concentration: one in the 500 – 700 m depth layer, and another in the 700 – 900 m depth layers. However, there were no clear patterns in diet items between the two clusters. Although the nighttime also showed that most diet items were either in the 600 – 700 m or 800 – 900 m depth layers, they were not as clearly delineated when compared to the daytime clusters. In the daytime CSA, the majority of diet items were found within the 800 – 900 m depth layer, with another concentration within the 700 – 800 m depth layer. In the nighttime CSA, the main concentrations of diet items were in shallower waters, mainly the 400 – 500 m and 600 – 700 m depth layers. In comparison, the shallower and deeper layers seemed to be relatively poor in diet items. There was a similar "belt" of diet items concentrated within the 500 – 800 m depth layers of the daytime ESA, comprising the majority of diet items. Although some diet items were more heavily represented in the 200 – 400 m depth layers at night, most were still located within the same 500 – 600 m depth layer as in the daytime. Of all the regions, the daytime BS had the greatest dispersion of diet items with depth, with no patterns evident. This trend was also apparent in the nighttime BS, but in this case, the number of layers was limited to three. However, the main concentration of diet items appeared to be within the 400 – 500 m depth layer.

Of all the MNC species considered here, *Eucopia grimaldii* had the lowest number of diet items (Fig. 4-11). Nevertheless, the WSA and nighttime CSA were all regions with a greater diversity of diet items than the daytime CSA, ESA and BS. The daytime and nighttime WSA were similar in that they both exhibited a concentration of diet items in a narrow distributional band in the daytime 900 – 1000 m depth layer and in the nighttime 500 – 600 m depth layer. In both cases, these indicated copepod fragments. While the daytime CSA diet items were dispersed throughout the water column, there was a concentration of copepod-related diet items in the nighttime 300 – 400 m depth layer. Both day and night in the ESA were characterized by a great dispersion of a small number of diet items. In the daytime BS, there was a concentration of diet items in the 500 – 600 m depth layer, which was also found in the nighttime 400 – 500 m depth layer.

DISCUSSION

Some authors have reported that net feeding can affect gut content analyses (Omori 1974), while other authors using RMT gear (Foxton and Roe 1974; Roe 1984) have suggested that net feeding is

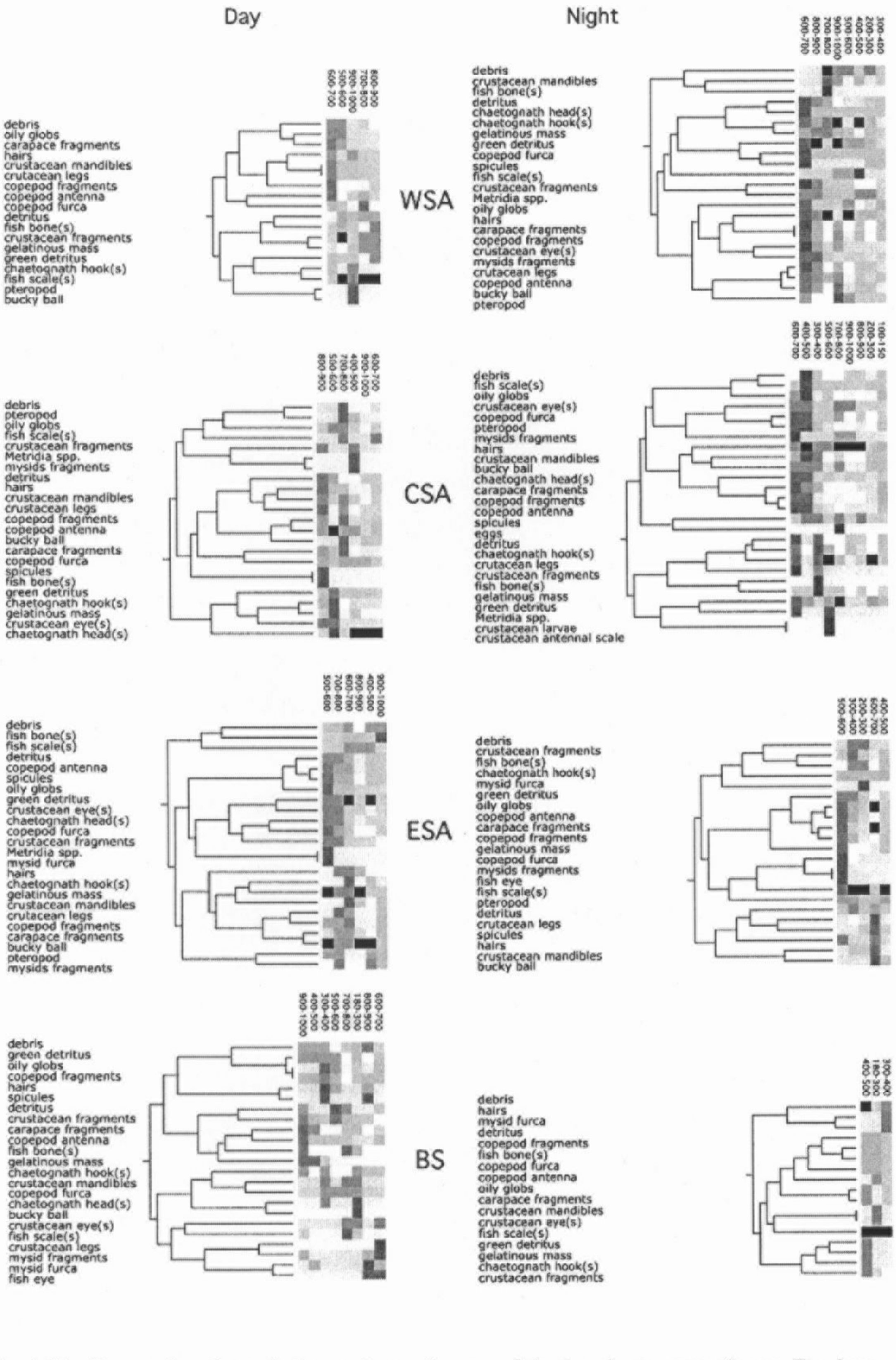

Fig. 4-10. *Hymenodora frontalis* 2-way cluster diagram of depth and gut content items. Day is on the left column, night on the right. Regions are as in text. Gut content items listed along the left of each cluster.

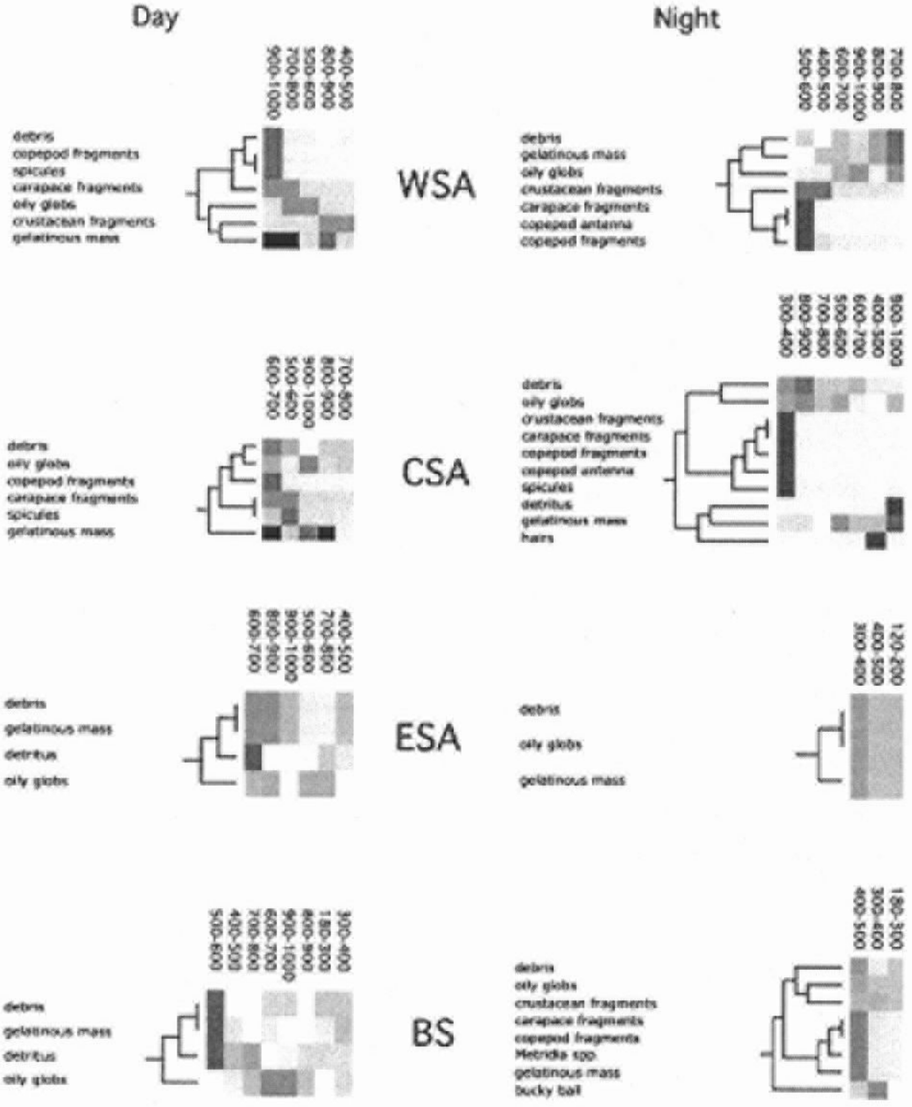

Fig. 4-11. *Eucopia grimaldii* 2-way cluster diagram of depth and gut content items. Day is on the left column, night on the right. Regions are as in text. Gut content items listed along the left of each cluster.

unimportant in decapods. An argument against net feeding in this study would rely upon the physical "delicacy" of genera like *Sergestes* and *Eucopia*, individuals of which are usually moribund in net samples. More robust species, such as *Bentheogennema borealis*, while usually more active (authors pers. observation) exhibit no swimming activity or escape response, even when prodded. Therefore, for the species studied here, net feeding may be considered negligible.

The lack of data for the night hauls in the BS and ESA due to equipment failure likely contributed to underestimating MNC feeding impact, especially for species in the mesopelagic zone. This is important for lower mesopelagic species, e.g. *Hymenodora frontalis* and *Eucopia grimaldii*, which have reported peak biomass from below 600 m (Omori 1974; Roe 1984). However, from gut content analysis, it is not likely that feeding habits are significantly different at depths below those examined here. This is partly due to the relative uniformity of the meso- and bathypelagic water column below 500 m, especially when compared to the epipelagic zone, and partly due to the absence of significant increases in gut fullness among *H. frontalis* and *B. borealis*, both mesopelagic species. While *S. similis* was the only species in this study that underwent clear diel vertical migration the relatively low incidence of empty guts demonstrated that feeding continued as *S. similis* fed opportunistically on whatever prey was available.

It was described in the Chapter 3 that *S. similis* was the only species that migrated through the oxygen minimum layer, and the significant differences in gut fullness with depth seen here indicate that this shrimp does not feed at the same rate throughout its vertical range. Since increasing temperature would imply an increase in metabolic rate, and therefore oxygen consumption, it may be that most feeding is done in the shallower and warmer waters above the thermocline and oxygen gradient, and individuals with full guts then retreat to lower, colder depths for digestion, obviating the need for constant feeding. However, while gut fullness ratios in the WSA and CSA show that the incidence of full guts were more common at shallower depths, the incidence of full or nearly full guts in the ESA clearly showed that feeding was occurring at most depths, day and night. The patterns in the WSA and CSA seem to contradict the hypothesis of Teal (1971) who suggested that decapods would feed throughout the water column regardless of the effects of decreasing temperature on decapod metabolism. This does seem to be the case for the mesopelagic species examined here which appeared to feed throughout their ranges, which, except for the CSA, were located entirely within the oxygen minimum layer.

Both *Bentheogennema borealis* and *Hymenodora frontalis* rose to, and fed at or above, the minimum oxygen gradient at night. Although upward nighttime vertical migration has been described as a function of feeding, both Donaldson (1975) and Walters (1976) disagreed, since they found relatively continuous feeding both day and night. Roe (1984) concluded that the upward movement of shrimps into richer nighttime depths, where they are surrounded by food, possibly enables shrimp to fill their guts more easily. Although the results here seem to agree with Donaldson and Walters, due to the continuous feeding represented by gut fullness, it may be that the relative abundance of food at all depth levels makes feeding a secondary motive for DVM. Prey preference may be a more important factor.

The general lack of identifiable gut contents from the mysid *Eucopia grimaldii* makes analysis of this species' dietary impact regarding specific food items difficult. Roe (1984) found that identification of food items in *Eucopia unguiculata* was equally difficult, and impossible to count food items. However, he identified small copepods (e.g. *Clausocalanus*) as the most common prey, and less commonly, coelentrates in *E. unguiculata* guts, identified by nematocysts and purplish tissue. Compared to the foreguts of the shrimp in this study, *E. grimaldii* foreguts were much smaller, similar to the findings by Roe (1984). Recovered bola were gel-like and nearly uniform in composition, with very few recognizable food items. Most were recovered from the hindgut, the explanation of which is unclear. Possibly this signifies that: a) feeding had occurred earlier, b) feeding occurred less often, or c) digestion was quicker, than that of decapod MNC. However, since data regarding digestion rates in the genus *Eucopia* are unavailable, this cannot be proven. There were no significant differences between males and females in terms of feeding patterns for any of the species examined. The fact that *Bentheogennema borealis, Hymenodora frontalis* and *Eucopia grimaldii* could coexist in relatively large numbers within similar depth ranges suggest that they do not directly compete for food. While this could be argued in the case of *E. grimaldii* on the basis of the points listed above, it may not hold for *B. borealis* and *H. frontalis*. If these species do in fact directly compete for food, there may be enough predation on them that reduce the respective populations to a level where there is enough food available to support sustained reproduction (Donaldson 1975; Flock and Hopkins 1992). However, since the abundances of both these species are above 1.2 ind/m^2 in the top 1000 m throughout the SAP, both day and night, it may be that they are preferentially feeding on either different species of copepods, or different sized copepods. Whether they are following either one of these feeding preferences or not is a subject for a future quantitative study.

Gut content and cluster analysis - feeding implications

The patterns of gut contents by depth layers showed that there were concentrations of items within fairly limited vertical ranges. There were clear differences in the vertical positioning of these ranges as shown by an upward shift at night even for the mesopelagic mysid *Eucopia grimaldii*. Peaks in biomass (Chapter 3, vertical distribution) were not always parallel with diversity of feeding as shown by gut content composition. This may be a reflection of the relative richness of different depth layers, in that the increase in gut content composition variety may reflect omnivorous feeding on a more diverse zooplankton community. This may also reveal that these layers are relatively poorer than other layers with less diverse zooplankton. Comparison with gut fullness and proportional abundance by depth layers supports this. Depth layers with greater proportional gut fullness were not always the same depth layers with greater numbers of gut content items. This needs to be examined in greater detail, preferably with a quantitative gut content analysis combined with antibody analyses to account for gelatinous zooplankton component of MNC feeding.

This Chapter shows that feeding by the MNC species investigated here continued, at various degrees of intensity, regardless of time of day or depth layer. Although not all individuals were found with gut contents, there was enough variation in digestion levels to show that feeding was a continuous activity, and not a case of night feeding followed by digestion during the day. As far as *Sergestes similis* is concerned, the data here agree with Donaldson (1975) regarding sergestiid shrimps off Hawaii, Nishida *et al.*, (1988) in the eastern subarctic Pacific, and Roe (1984) among caridean and penaeidean shrimps in the Northeast Atlantic. It is important to keep in mind the fact that a primary factor of underestimation relates to the impact of soft-tissues and body fluids in feeding, particularly from gelatinous and crustacean prey, as well as in euphausiids feeding upon copepods (Mauchline and Fisher 1969). Gelatinous prey can be inferred by the presence of nematocysts in the gut, but body fluids have no such markers. The differences between gut fullness levels, depth and gut contents reveal that feeding patterns of the epipelagic *Sergestes similis* are more discriminating than those of the mesopelagic MNC. This is supported by the high incidence of gut content items (e.g. copepods and chaetognaths) within distinct depth layers both day and night. In the mesopelagic MNC, however, these patterns were less clear, showing that feeding, as determined by gut content items and gut fullness, was spread out over a wider vertical range, both day and night. This could mean that the mesopelagic MNC feed more opportunistically than the epipelagic *Sergestes similis*. A detailed quantitative examination of food items is necessary to establish whether MNC feeding, particularly in the mesopelagic zone, reflects dietary preferences.

Chindonova (1959) reported that *Eucopia grimaldii* in the Northwestern Pacific fed mainly on crustaceans, jellyfish and radiolaria, as well as having a high incidence of empty foreguts and hindguts, supporting the results found here. Unfortunately, although the individuals examined here did not have much in the way of recognizable gut contents (mostly featureless bola in the hindgut), it is unlikely that these masses are the remnants of chaetognaths since no hooks were found in any guts. Feeding may be infrequent, since Childress (1972) described the low respiration and metabolic requirements of deep-living mysids, and may explain the highly digested state of gut contents and relatively plentiful empty guts. However, this species has been overlooked in previous studies of food webs in the SAP and it seems that the large abundances coincident with mesopelagic shrimp abundances lead to the conclusion that their feeding strategy likely differs from that of the shrimps, and do not directly compete for food.

Hopkins *et al.* (1992) and other workers have reported the presence of "greenish detritus" in the guts of mesopelagic shrimps, also found here in both the epipelagic *Sergestes similis* and mesopelagic *Hymenodora frontalis* and *Bentheogennema borealis*. This "green detritus" may be the remnants of floc or fecal matter as well as aggregations of other detritus in the water column. Although not a major portion of shrimp diets in the SAP, it has been reported as a common food item in the Gulf of Mexico by Flock and Hopkins (1992), and by Roe (1984) in the NE Atlantic. Heffernan and Hopkins (1981) commented on two possible sources of "green detritus" in shrimp guts. Firstly, the shrimp could be actively removing "green detritus" from the water, or secondly, it could be the result of secondary ingestion, or derived from the guts of ingested prey. Due to the fact that most of the metazoan prey they concurrently recovered from shrimp guts were small copepods, they concluded that the "green detritus" was not a result of secondary feeding, but had been actively removed from the water. In addition, fecal pellet debris was found to contain much the same kinds of fragments observed in shrimp foreguts (Heffernan and Hopkins, 1981).

Copepods were another main component of shrimp diets, the only species identified being *Metridia* sp. Euphausiids were also a common prey item, as evidenced by the number of crustacean mandibles and eye cones in shrimp guts. Another common item were chaetognath hooks and heads. Chaethognaths may also be the source of the "gelatinous masses" found in shrimp guts, since there did not seem to be any evidence of cnidarian predation as revealed by the presence of nematocysts. It is unlikely that chaetognaths are connected with gelatinous masses found in mysid guts, since chaetognath heads and hooks were completely lacking. Fish scales have been presented as evidence of net feeding, since several authors have listed the objections that the scales typically found in guts are from fishes not normally prey of shrimps. However, the discovery of bones and eye lenses confirms previous reports of predation on midwater fishes (e.g. *Cyclothone* spp.).

Daily Ration estimates

A general estimate of daily rations and particulate flux for the 4 species considered here can be calculated, in order to estimate their predation impact on zooplankton stocks. Decapod and mysid biomass derived daily ration estimates throughout the 0 - 1000 m water column for each of the 4 regions of the SAP are shown in Table 4-IX. Estimates of DR for dominant MNC were highest in the WSA and CSA compared to the ESA and BS. Daily ration ranged from 1.9 – 9.6% of daily zooplankton stocks in the SAP and BS. The average mesozooplankton DR for dominant MNC in the SAP and BS is estimated as 0.69 gDW/m^2, with no significant difference ($P>0.05$) in DR between day and night. Due to the qualitative nature of the investigation here, these figures should be viewed as rough estimates only. Nevertheless, the importance of the MNC, especially that of the mysid *Eucopia grimaldii* (second-most important consumer), as predators within the SAP and BS is emphasized by the results presented here. Comparing daily ration estimates for myctophid fishes, Moku *et al.* (2000) described the daily ration of myctophids on zooplankton stocks in the WSA as 0.14 - 3.3%, greater than that reported by Hopkins *et al* (1994) in the Gulf of Mexico (0.4%). Hopkins and Sutton (1998) described the resource partitioning strategies of midwater fishes and shrimps in the Gulf of Mexico as being based upon 3 niche parameter variables: food composition, food size, and (nighttime) vertical positioning of predators. They concluded that feeding spread over the 24-hour diel period would spread the impact of predation pressure and enhance resource partitioning. As seen here, the only significant differences in day/night gut fullness levels were seen in the epipelagic Sergestes similis, and not in any of the mesopelagic MNC. The data and methodology presented here do not support the kind of analysis performed by Hopkins and Sutton (1998), but does seem to support their conclusions that niche (feeding) overlap and potential for competition due to similar vertical distribution patterns can be balanced by time of feeding and size of preferred prey. While their study concerned highly speciose low-latitude oligotrophic ecosystems, the same mechanism can be used to explain trophic relations within the relatively species-poor, but high abundance and biomass conditions found in a high latitude ecosystem like the SAP and BS.

The qualitative results of this chapter set a base point for further investigation into MNC feeding in the SAP and BS. Further study, including detailed quantitative examination (to the species level) of gut content prey items, as well as attempting to evaluate the size and number of prey items, is necessary. These studies will require detailed examination of the size and shape of mandibles to estimate the size of the original euphausiids, and the size and shape of copepod legs,

Table 4-IX. Estimates (by species) of zooplankton biomass ingested (DR) and daily predation on zooplankton stocks. Regions as in text.

	WSA	CSA	ESA	BS
Estimated zooplankton biomass ingested Estimated DR (gDW/m2)				
Hymenodora frontalis	0.020	0.055	0.016	0.044
Sergestes similis	0.003	0.004	0.004	0.000
Bentheogennema borealis	0.038	0.018	0.006	0.001
Eucopia grimaldii	0.036	0.044	0.007	0.020
Total	0.096	0.122	0.033	0.065
Daily predation on zooplankton stocks (gDW/m2)				
Hymenodora frontalis	0.0004	0.007	0.003	0.006
Sergestes similis	0.0001	0.0018	0.001	0.0001
Bentheogennema borealis	0.0011	0.009	0.001	0.000
Eucopia grimaldii	0.001	0.007	0.000	0.003
Total	0.002	0.024	0.005	0.009
Daily predation on zooplankton stocks (%)				
Hymenodora frontalis	2.0	3.6	1.0	4.4
Sergestes similis	0.3	0.4	0.4	0.0
Bentheogennema borealis	3.8	1.7	0.3	0.1
Eucopia grimaldii	3.6	3.6	0.2	2.0
Total	9.6	9.3	1.9	6.5

as well as the size, shape and number of spines in the case of the chaetognaths. Since these studies ultimately rely on subjective interpretation of gut contents, gut maceration and digestion continue to make identifying and quantifying of soft-bodied items difficult to impossible. However, these studies are necessary in order to better understand the interactions in the food web of the SAP and BS, as well as determining the flow of energy from the epipelagic to mesopelagic zones via the MNC.