Feeding Relationships of Dominant Fish Species in the Visayan Sea

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ABSTRACT

This study examines the diet composition of 15 fish species belonging to 11 families in the Visayan Sea. A total of 50 prey items were identified from 323 stomachs examined. Cluster analysis was used to assess similarities in the composition of prey items in individuals of similar sizes but of different species, and in individuals of the same species but of different size categories. The results showed high similarity among individuals of the same species and low similarity between different species of similar size categories. Two major clusters were formed, showing generalist feeding (high niche widths) and trophic segregation (low food niche overlap). These suggest that food resources in the Visayan Sea are not limited and that a wide range of habitats is available to the fish community.

Keywords: Stomach analysis, food niche overlap, food niche width, diet composition

INTRODUCTION

Studies on diet composition are important in community ecology because the use of resources by organisms has a major influence on population interactions within a community. Studies of species resource requirements have been used in attempts to understand factors controlling the distribution and abundance of organisms (Ross, 1986). Information about the food habits of fishes is useful in defining predator-prey relationships because predator pressure has a pervasive influence on the evolution of a population. Data on different food items consumed by fish may eventually result in identification of stable food preference and in creation of trophic models as a tool to understand complex ecosystems (Lopez-Peralta and Arcila, 2002; Bachok, 2004).

The Visayan Sea is considered as one of the country's most productive fishing grounds, with an average annual catch of about 200,000mt (BFAR, 2002). However, recent reports show that there has been a decline in small scale and commercial fish production in the area due to increased fishing pressure (Hermes et al., 2004). Most of the studies that have been conducted in the Visayan Sea deal with stock assessment of commercially important species. Non-commercially important species have received less attention and their biology is, to a large extent, poorly documented.This study provides empirical information on gut contents of the more abundant fish species caught by trawls in the Visayan Sea and examines the extent of feeding relationships among them.

METHODS

Sampling Area and Field Collection

Visayan Sea is located in central Philippines between 11^o and 12^o N and 123^o and 124^o E, and covers a total area of 5,184 km^2 (BFAR, 2002). It is bounded by

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coastal areas of northeastern Panay, northern Negros Occidental, Bantayan Island, and Masbate (Fig. 1).

Samples were collected during a research cruise in the Visayan Sea in July 2003 on board the RV DA-BFAR. A major activity of the cruise was a trawl survey covering 10 stations distributed within the study area. At each station, a single 1-hour tow was conducted during the daytime with the use of a two-seam trawl with a cod end mesh size of 5.08 cm. A cover net with a mesh size of 1 cm was attached to the cod end to examine gear selectivity (another study). The trawl was towed at an average speed of 4.5 knots. Specimens representing the entire size range of the more abundant fish species caught in 5 of the 10 stations were collected for stomach content analysis and preserved on board in 10% buffered seawater-formalin solution. For larger fish, an incision was made along the belly to allow the formalin to penetrate the stomach to minimize possible post mortem digestion.

Laboratory Processing

In the laboratory, fish were sorted and identified to species level. Prior to dissection, total length, standard length, and fork length of each individual were measured to the nearest 1mm using a ruler and total wet weight was measured to the nearest 0.01 g using an electronic balance. Stomachs were removed from the digestive tract and weighed to the nearest 0.01 g. The contents were removed and preserved in 10% buffered formalin for later analysis. After the removal of its contents, the stomach sac was weighed. Total stomach content was then calculated as the difference of stomach weight with contents minus the stomach sac. Stomach contents were examined under the dissecting microscope and identified to the lowest taxonomic level possible. Prey items were identified and grouped into major categories including: (a) microcrustaceans (amphipods, caperellids, cladocerans, cumaceans, euphausids, halocarids, isopods, mysids, *Lucifer*, and ostracods), (b) larval crustaceans (crab

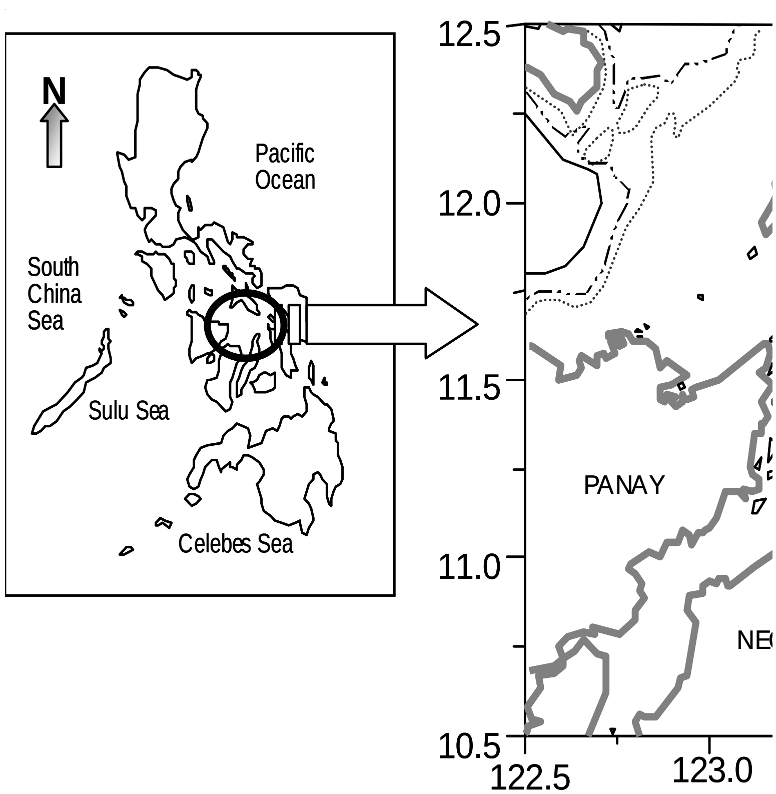

Figure 1. Map of the Visayan Sea showing the 5 sampling stations where samples for stomach content analysis were collected during the Visayan Sea Project cruise in June 2003.

megalopa and zoea, shrimp mysis, and Cypris larvae), (c) benthic worms (annelid worms, ribbon worms, flatworms, gnathostomulids, and sipunculids), (d) echinoderms (brittle star, bipinnaria, and pentactula), and (e) urochordates (ascidians and larvaceans).

Data Analysis

Feeding intensity was determined by calculating the fullness index (FI) using the formula of Hureau (1969) (as given in del Norte-Campos, 1995):

$$FI\ (\%) = \frac{\text{weight of stomach contents (g)}}{\text{body weight (g)}} \times 100$$

Examination of stomach contents employed numerical analysis described by Windell and Bowen (1978), wherein food items present were identified and counted. The frequency of occurrence (FOC) of identified food items was calculated using the formula,

$$FOC = \frac{\text{no. of food item } i}{\text{total no. of food items}} \times \%\ \text{identified}$$

where % identified = 100 - % unidentified. Unidentified materials were visually estimated as percentage of the total stomach content.

The narrow size range of each fish species did not allow the categorization of size classes prior to the stomach content analysis. With the premise that prey differs with growth, sizing was done after prey identification using a mathematical tool. A two-step cluster analysis (using the program COMM, Piepenburg and Piatkowski, 1992) was done on FOC data, first, to determine if size categories (e.g. small, medium, and large) for each fish species could be identified on the basis of prey similarity. For example, "small" *Selaroides leptolepis, Neopomacentrus filamentosus,* and *Leiognathus bindus* were assigned with the same sizes (<100mm) although "small" *N. filamentosus* and *L. bindus* were of shorter lengths. The second step was done on the various size categories of the different species to determine similarities in gut contents with respect to size.

Food niche overlap across length classes was computed using Schoener's Index (as given in Salgado,et.al, 2004),

$$SI_{xy} = 1- 0.5\ (\sum | P_{xi} - P_{yi} |)$$

where P_{xi} = relative frequency of food type i in the stomach of species x and P_{yi} = relative frequency of food type i in the stomach of species y. The index ranges from 0, for entirely dissimilar diets, to 1 when the composition of the diets is identical but values >0.6 can be considered biologically significant (Wallace, 1981; Wallace and Ramey , 1983; Salgado, et al., 2004). Food niche width was also computed for each species using the Shannon-Wiener Index on data across all length classes using the formula,

$$H' = - \sum (P_i) \log (P_i)$$

where P_i = proportion of prey item i in the stomach of the predator.

RESULTS AND DISCUSSION

Fifteen species belonging to 11 families were examined in the study and their respective size groupings resulting from the initial cluster analysis are listed in Table 1. Some species did not form size classes due to their narrow length range. Out of 323 stomachs examined, only 8 were empty.

A total of 50 prey items were identified excluding chyme (unidentified foods), rubble, sediment, and fish scales and bones (counted in the absence of fish in the sample). Shrimps were the most abundant prey in the stomachs of *Pentapodus setosus*, *Upeneus asymmetricus*, *Plotosus lineatus*, *Saurida undusquamis*, *Parapercis alboguttata*, and *Lagocephalus. lunaris*. Calanoids were abundant in *N. filamentosus*, *Apogon notatus*, and *L. bindus*; fish larvae for *S. leptolepis*, fish for *Synodus variegatus*, polychaetes for *Leiognathus rivulatus*, nematodes for *Arothron manillensis*, amphipods for *Scolopsis affinis*, and pelagic harpacticoids (mostly *Microsetella*) for *Rastrelliger kanagurta*.

The assessment of possible dietary shifts in the different species showed that there was a general absence of variation in the pattern of prey preference with increase in size in all 15 of them. For example, *L. bindus* (Fig. 2a) showed overlapping size groupings while clear groupings were observed in *S. variegatus* (Fig. 2b).

Species	N	No. of non-empty Stomachs	Size Range (TL in mm)	Size Classes (TL in mm)		
				Small	Medium	Large
DEMERSAL						
F. Leiognathidae						
Leiognathus bindus	38	37	56 - 122	<100	101-110	>110
Leiognathus rivulatus	19	19	76 - 132		<100	>100
F. Mullidae						
Upeneus asymmetricus	28	27	95 - 142	<110	110-120	>120
F. Nemipteridae						
Pentapodus setosus	15	15	111 - 162		no size class	
Scolopsis affinis	16	16	128 - 213	<155	155-175	>175
F. Plotosidae						
Plotosus lineatus	24	21	99 - 264	<120	120-200	>200
F. Penguipeidae						
Parapercis alboguttata	7	7	126 - 215		no size class	
F. Synodontidae						
Saurida undosquamis	18	18	144 - 268		<200	>200
Synodus variegatus	16	16	124 - 245	<150	150-200	>200
F. Tetraodontidae						
Arothron manillensis	16	15	86 -119		<100	>100
Lagocephalus lunaris	18	18	79 - 227		<200	>200
PELAGIC						
F. Carangidae						
Selaroides leptolepis	34	33	78 - 153	<100	100-130	>130
F. Scombridae						
Rastrelliger kanagurta	26	26	142 - 208		no size class	
REEF ASSOCIATED						
F. Gobiidae						
Apogon notatus	15	14	71 - 85		no size class	
F. Pomacentridae						
Neopomacentrus filamentosus	33	33	66 - 139	<100	101-110	>110
Total	**323**	**315**				

Table 1. List of fish species used for stomach content analysis from Visayan Sea.

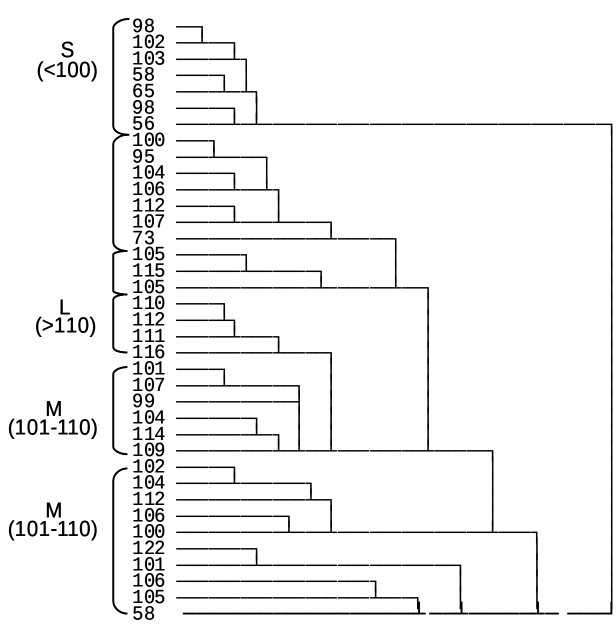

Figure 2a. Results of cluster analysis of *L. bindus* based on prey similarity by size class.

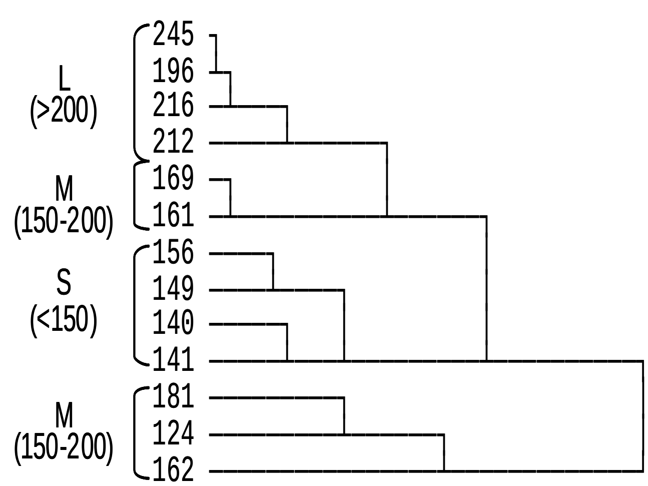

Figure 2b. Result of cluster analysis of *S. variegatus* based on prey similarity by size class.

In spite of differences in the clarity of clustering, there was a general similarity in prey items across all size classes within a given species (Figs. 3a and 3b), thus showing the absence of a shift in diet. Furthermore, when prey similarities between size classes of the various species were examined, the second step of the cluster analysis showed low similarities (Fig. 4). Hence, the results show that similarity in apparent prey preference is higher among different sizes of the same species, than between similar size classes of different species.

The general absence of a dietary shift is attributed to the narrow range of lengths of specimens available to the study. This may not necessarily be an artifact of size selectivity of the trawl, since the sizes of fish retained in the cover net were no different from those retained in the main net (unpublished information). Furthermore close to ¼ of the typical catch in the trawl was made up of relatively fast-swimming scombrids (*Rastrelliger* spp) (unpublished report). Hence, if there were larger, generally faster-swimming fish in the surveyed areas, a representative portion of them would

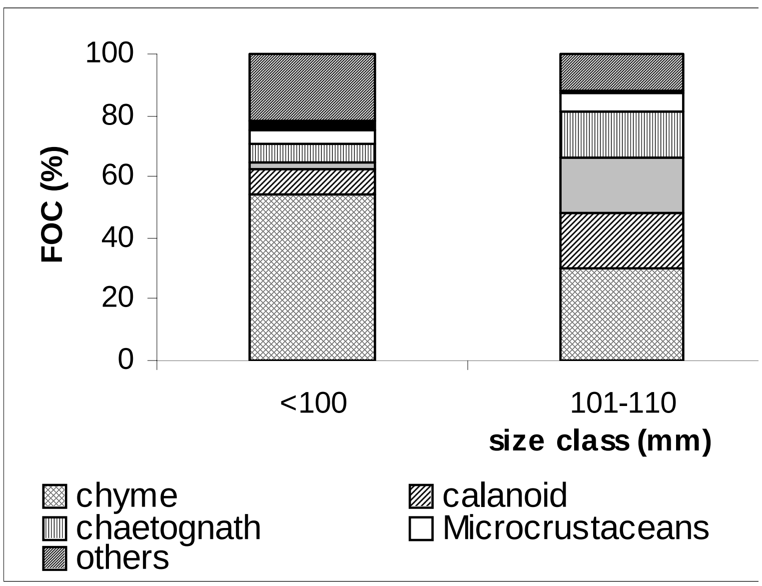

Figure 3a. Diet composition of *L. bindus* according to size class.

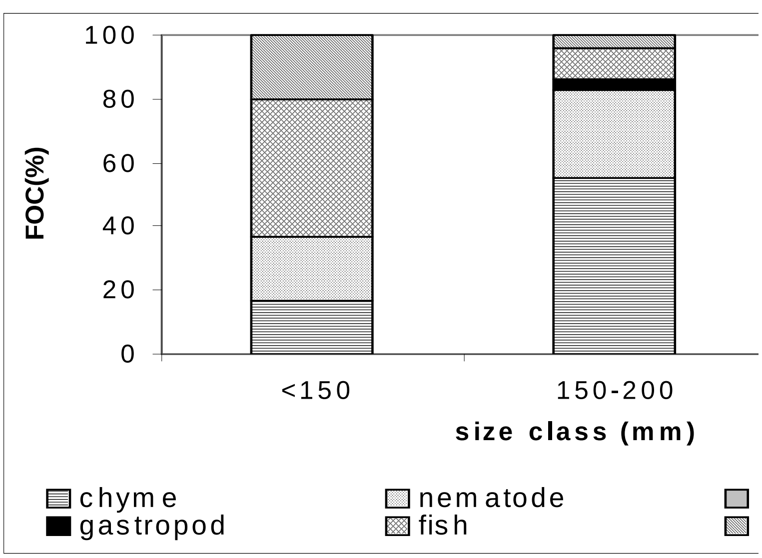

Figure 3b. Diet composition of *S. variegatus* according to size class.

have been caught by the net. Their absence in the catches thus reflects the predominance of small and younger fish in the Visayan Sea. In most cases, the largest specimens observed from the catches were much smaller compared to their maximum reported sizes in the literature (Table 4). This is a common observation in heavily-fished waters.

Fish are generally opportunistic feeders and show a relatively high degree of variability in prey preference either within or among species. The shift in feeding mode from larvae to early juveniles shows that they feed at different levels of the food chain during different stages of their life cycle. However, ontogenetic changes in feeding habits of fish as they grow do not depend on body size per se, rather these are correlated with changes in key aspects of feeding mechanisms (Wainwright and Richard, 1995). Several factors affect feeding in fish and can be categorized into intrinsic and extrinsic factors (Hourston et al., 2004). Intrinsic factors include mode of feeding, differences in swimming ability, and location in the water column, while extrinsic factors include variation in prey composition among habitat types and susceptibility of prey to predation.

The assemblages formed by the cluster analysis (Fig.4) can also be related to their overall habits. The two major clusters formed clearly separate the strictly demersal species (assemblage 2) from the overlapping occurrence of pelagic, reef associated, and some demersal species (assemblage 1). Assemblage 1 can be further separated into 3 sub-groups: 1_A, 1_B, and 1_C. The first sub-group (1_A) is formed by the pelagic carnivores *S. leptolepis* and *R. kangurta*. A reef-associated species *A. notatus*, was grouped together with demersal species *P. lineatus* and *L. rivulatus* in the second sub-group (1_B) while *N. filamentosus* and *L. bindus* formed the third subcluster (1_C). Sub-groups 1_A and 1_B had guts which typically contained large amounts of partially digested material (chyme), although planktonic prey such as fish larvae (1_A) and calanoids (1_B) were also common (Table 2). For sub-group 1_C, other plankton groups like larvaceans and

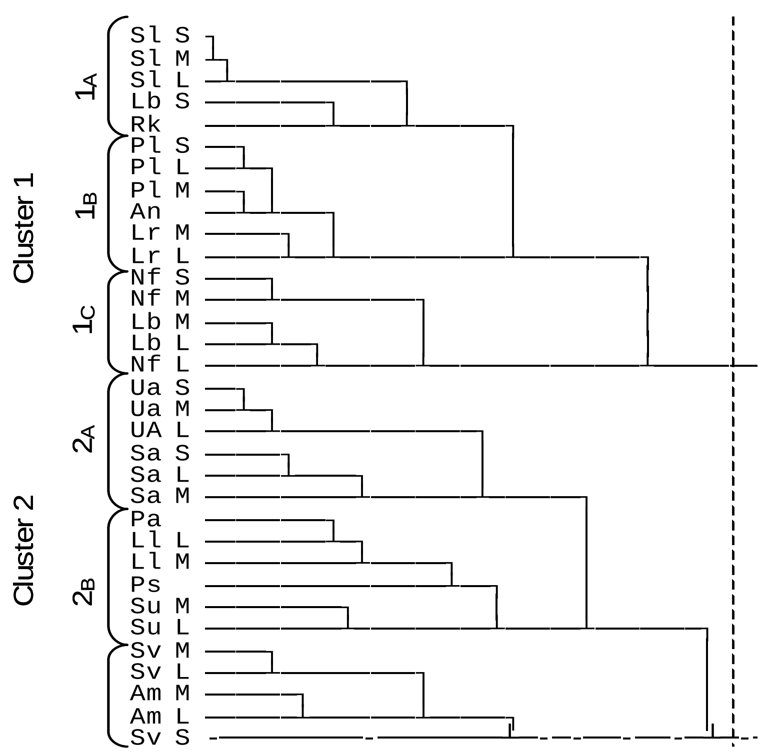

Figure 4. Cluster analysis of size classes of 15 fish species based on prey similarity. S denotes small, M for medium, and L for large.

		1_A					1_B						1_C				
	prey items	Sl (S)	Sl (M)	Sl (L)	Lb (S)	Rk	Pl (S)	Pl (L)	Pl (M)	An	Lr (M)	Lr (L)	Nf (S)	Nf (M)	Lb (M)	Lb (L)	Nf (L)
**	Polychaete larvae	-	-	-	-	0.13	-	-	-	-	-	-	-	-	-	-	-
	Silicoflagellates	-	-	-	-	0.08	-	-	-	-	-	-	-	-	-	-	-
A_1	Urochordates	-	-	-	2.22	-	-	-	-	-	5.34	-	9.63	0.64	18.03	15.17	2.61
	chaetognath	0.07	0.14	-	5.77	0.02	-	-	-	-	1.67	0.33	0.04	-	15.03	12.32	7.69
	fisheggs	-	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-	6.46
	Pteropod	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.22	-
	salps	-	-	-	-	-	-	-	-	-	-	-	-	-	3.41	3.14	-
	Cnidarians	-	-	-	-	-	-	-	-	-	-	-	-	-	0.39	-	-
	cop. Nauplius	-	-	-	0.79	0.03	-	-	-	-	-	-	-	-	-	-	-
	fishbones	-	-	-	-	-	-	0.78	1.55	-	-	-	-	-	-	-	-
A_2	cyclopoid	-	-	-	1.74	5.14	1.04	-	0.10	-	0.18	0.33	0.98	1.58	0.21	0.79	1.03
	harpacticoid	-	-	-	1.20	14.22	3.44	-	-	-	0.54	4.00	1.57	1.11	0.21	-	0.48
	Dinoflagellates	0.07	0.13	-	0.44	8.70	-	-	-	-	-	-	-	-	-	2.50	-
	Diatoms	0.53	1.06	-	8.61	5.22	-	-	-	0.71	-	-	-	-	-	-	-
$B_{2\text{-}1}$	algae	-	-	-	0.44	-	-	-	-	-	-	-	-	-	3.07	2.50	-
	copepod	-	-	-	3.54	-	-	-	-	-	-	-	-	-	-	2.50	-
	Benthicworms	-	-	-	-	-	-	0.20	0.25	-	0.87	6.50	-	-	-	-	-
	fishscale	-	-	-	0.20	-	-	-	4.23	-	-	-	-	-	-	-	-
	squid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
$B_{2\text{-}2}$	Larva crustaceans	1.28	1.33	1.22	1.78	0.79	1.56	-	-	-	-	-	2.80	0.07	-	0.19	0.34
	polychaete	0.02	-	0.05	2.08	0.17	-	0.07	0.69	-	-	-	0.12	0.31	0.95	0.34	0.18
	bivalve	0.09	0.17	-	-	0.87	0.18	-	0.06	-	-	-	-	-	1.17	-	-
	gastropod	0.16	0.17	0.14	-	0.27	-	-	-	-	0.87	-	-	-	0.36	-	-
$B_{2\text{-}3}$	forams	-	-	-	0.12	-	-	-	-	-	-	-	-	-	-	-	-
	rubble	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	crab	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	sediment	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B_1	Microcrustaceans	14.80	11.35	18.25	4.46	1.36	-	0.07	0.28	3.33	6.24	7.61	5.06	3.17	6.22	9.48	16.63
	shrimp	1.05	0.77	1.32	3.05	0.02	2.69	3.58	8.19	6.36	-	0.70	-	0.21	0.95	5.38	-
	Chyme	47.50	49.00	46.00	53.78	51.92	86.88	94.40	82.88	82.14	71.63	64.13	18.64	30.56	29.89	28.67	32.62
	Calanoid	14.60	16.42	12.78	8.67	10.99	3.38	0.37	0.88	4.60	4.02	2.15	61.04	62.26	17.97	15.02	31.96
	FILA	18.10	17.63	18.58	-	0.01	-	-	-	-	-	-	-	-	-	-	-
	Echinoderm larva	-	-	-	0.87	-	-	-	-	-	8.34	9.75	-	-	-	0.15	-
	Fish	-	-	-	-	0.00	-	-	-	2.86	-	-	-	0.08	0.42	-	-
	Nematode	1.74	1.81	1.66	0.24	0.02	0.83	0.54	0.89	-	0.31	4.51	0.14	-	1.70	0.63	-

**depauperate

Table 2. Two way coincidence table showing variation in gut contents of the different fish species examined from the Visayan Sea.
***Note:* Table rows are arranged according to prey item assemblages and columns are arranged according to species-size clusters**

		2_A					2_B							2_C				
	prey items	Ua (S)	Ua (M)	Ua (L)	Sa (S)	Sa (M)	Sa (L)	Pa	Ll (L)	Ll (M)	Ps	Su (M)	Su (L)	Sv (M)	Sv (L)	Am (M)	Am (L)	Sv (S)
**	Polychaete larvae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Silicoflagellates	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Urochordates	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	chaetognath	-	-	-	-	0.91	-	-	-	-	-	-	0.78	-	-	-	-	-
	fisheggs	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A_1	Pteropod	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	salps	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Cnidarians	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	cop. Nauplius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	fishbones	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	cyclopoid	-	1.30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A_2	harpacticoid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Dinoflagellates	-	-	-	-	1.46	-	-	-	-	-	-	0.32	-	-	-	-	-
	Diatoms	-	-	-	-	-	-	-	-	-	-	0.56	3.67	-	-	-	-	-
	algae	-	-	-	-	0.84	4.65	8.35	2.38	-	4.39	2.42	4.23	-	-	-	-	-
	copepod	-	-	-	3.01	15.88	-	8.75	-	-	2.25	2.84	6.06	-	-	0.94	-	-
$B_{2\text{-}1}$	Benthicworms	-	-	-	-	2.04	-	1.29	-	-	2.11	-	-	-	-	-	-	-
	fishscale	-	-	-	3.43	2.43	1.04	-	-	-	10.05	-	-	-	-	-	-	-
	squid	-	-	-	2.36	-	1.35	-	13.57	-	1.53	-	-	-	-	-	-	-
	Larva crustaceans	3.08	1.11	6.35	-.	0.91	-	4.52	-	-	-	-	-	-	-	5.43	0.15	-
$B_{2\text{-}2}$	polychaete	1.19	1.67	3.13	-	-	-	1.29	-	-	-	-	1.17	-	-	0.63	-	-
	bivalve	-	-	-	-	-	-	-	-	-	-	1.83	-	-	-	3.04	0.14	-
	gastropod	-	-	-	-	2.72	-	-	0.48	-	1.19	-	-	3.17	-	13.73	4.47	-
	forams	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.35	2.36	-
$B_{2\text{-}3}$	rubble	-	-	-	-	-	-	-	4.29	-	-	-	-	-	-	0.92	1.04	-
	crab	-	2.50	-	-	-	-	0.38	5.71	8.64	-	0.88	0.55	-	-	-	-	-
	sediment	-	-	-	-	-	-	-	0.71	3.64	-	-	-	-	-	-	4.73	-
	Microcrustaceans	34.00	33.76	33.50	49.70	31.75	56.26	-	-	-	8.94	-	0.16	-	2.08	0.83	0.01	-
	shrimp	22.10	22.49	27.84	20.84	13.80	10.53	22.02	18.57	11.21	16.94	64.62	38.03	-	-	0.00	0.45	-
	Chyme	38.89	31.67	23.33	4.83	7.17	6.25	50.71	52.57	63.00	34.87	25.38	29.70	55.00	43.33	30.00	36.43	16.67
B_1	Calanoid	0.74	2.36	1.67	-	-	-	-	-	-	-	-	1.25	-	-	-	-	-
	FILA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Echinoderm larva	-	-	-	15.82	20.10	19.92	-	-	-	10.19	-	-	4.28	11.00	-	-	20.16
	Fish	-	1.11	-	-	-	-	0.58	-	12.73	0.92	1.48	12.05	9.67	10.50	-	-	43.02
	Nematode	-	2.04	4.18	-	-	-	2.11	1.71	0.79	6.63	-	2.02	27.89	33.08	43.14	50.22	20.16

**depauperate

Table 2 (Continued) Two way coincidence table showing variation in gut contents of the different fish species examined from the Visayan Sea.
***Note:* Table rows are arranged according to prey item assemblages and columns are arranged according to species-size clusters**

chaetognaths were also common in their guts. Sub-groups 1_A and 1_C can be considered as generally planktivorous. Observations on 1_C are consistent with overlapping feeding habits of reef-associated and demersal species in the area, particularly in stations adjacent to shallow coral reefs. For example, the pomacentrid *N. filamentosus* is typically found over soft bottoms of lagoons and inshore reefs around coral outcrops, rocks, and debris (Froese, and Pauly, 2006). Leiognathids in general are bottom living but small individuals feed mostly on copepods and phytoplankton, while large fish feed predominantly on benthic invertebrates. *L. bindus* in particular feeds on calanoid copepods, ostracods, chaetognaths, polychaete larvae, and fishes (FAO, 2001). Similarly, *L. rivulatus* searches for planktonic prey using a protrusible mouth or by sieving potential food through their gill rakers (Froese.and Pauly, 2006).

The high incidence of chyme in subcluster 1_B, however, may not make them typical planktivores, in spite of the occurrence of planktonic prey in their guts as stated above. *P. lineatus* and *A. notatus* for instance are known to be carnivorous, feeding primarily on crustaceans, mollusks, and fishes (FAO, 1999), while *A. notatus* are known to feed on fish and zoobenthos (Froese and Pauly, 2006). Since trawling was done during the daytime, the large amounts of chyme suggest that *P. lineatus* and *A. notatus* fed during the night, making most of the ingested prey partially digested by the time trawling was done.

The second assemblage can also be divided into three sub-groups 2_A, 2_B, and 2_C. These are largely demersal in habit because plankton (e.g., calanoids) are generally absent from their diet and they consume mostly benthic prey. Sub-group 2_A showed a high occurrence of shrimps and microcrustaceans in their guts, while the others showed common occurrences of shrimps, crabs (2_B), and nematodes (2_c) in their diets (Table 2).

Food niche overlap was computed only for 7 demersal species (out of a total of 15) because the objective was to quantify the degree of overlap between size classes of different species. Only species with complete size classes (mostly from assemblage 2) (Fig. 4) were included in this analysis. These include *S. variegatus*, *U. asymmetricus*, *L. bindus*, *S. affinis*, *P. lineatus*, and *A. manillensis.* Generally, the values of niche overlap between size groups of various species were low (Table 3) and inconsistent with the premise that resource overlap decreases with growth. Very few species in this study showed such a trend in resource use. Examples are *L. bindus* and *P. lineatus*, and *U. asymmetricus* and *S. affinis.*

Food niche overlap provides insights on the existence, nature and strength of competitive interactions (del Norte-Campos, 1995). The concept of resource overlap is usually related with the intensity of competition because of the use of common resources. Competing species will necessarily show extensive niche overlap, although high niche overlap does not always mean that there is competition. In the case of *S. variegatus and A. manillensis*, (Table 3), high niche overlap does not necessarily mean there is competition between them, unless food resources are limited. The presence of high prey density may result in high diet overlap between species because there is no need to partition available resources. Although no simultaneous investigation on prey availability was conducted in this study, previous reports on benthic infauna (Mequila et al., 2004) and zooplankton (Campos et al, 2002) surveys in the area show that abundances of prey for demersal and pelagic fishes are relatively high in the area.

Low food niche overlap, on the other hand, may mean that food resources have become well- partitioned as a result of competitive interactions. Divergence over evolutionary time in feeding morphology and behavior of fish for example may result in utilization of different resources, thus lowering the niche overlap among previously competing species (Labropoulou and Markakis, 1998). The feeding behavior of fish examined in this study range from ram feeders (*R. kanagurta* and *S.leptolepis*) and suction feeders (*L. bindus* and *L. rivulatus*), to browsers (*U. asymmetricus*), and crushers (*L. lunaris, A. manillensis* and *P.lineatus*). Whether this is a result of previous competition among these species is uncertain. The high values of food niche width (H') in Table 4, regardless of sizes, indicate that fish consumed a diverse diet, implying that they are generalists in terms of feeding. Although this seems contradictory to the low overlap values, it may mean that fish occupy a wide range of habitats, thus favoring utilization of a large number of resources. According to Amundsen et al. (1996), a population with a broad niche width may be the outcome of either true generalist behavior of each individual of a population (high within-individual variation) or specialization of individuals of the population on different prey (high between-individual variation), as would be the case with ontogenetic changes in diet. The latter, however, was not observed in this study.

	Small	Medium	Large
Sv/Ua	0.17	0.35	0.30
Sv/Lb	0.18	0.32	0.32
Sv/Sa	0.21	0.14	0.19
Sv/Pl	0.18	0.56	0.44
Sv/Am	—	0.61	0.70
Ua/Lb	0.50	0.43	0.41
Ua/Sa	0.60	0.54	0.50
Ua/Pl	0.44	0.43	0.28
Ua/Am	—	0.35	0.28
Lb/Sa	0.16	0.16	0.24
Lb/Pl	0.64	0.34	0.33
Lb/Am	—	0.35	0.30
Sa/Pl	0.08	0.18	0.10
Sa/Am	—	0.13	0.07
Pl/Am	—	0.32	0.37

Table 3. Food niche overlaps between fish species by size class in the Visayan Sea, July 2003
Note: Sv - *Synodus variegatus*; Sa - *Scolopsis affinis*; Pl - *Plotosus lineatus*; Ua - *Upeneus asymmetricus*; Am - *Arothron manillensis*; Lb - *Leiognathus bindus*

High overall productivity in the Visayan Sea is evidenced by consistently high fisheries yield since at least the 1970s (Aprieto and Villoso, 1979), in spite of heavy fishing pressure (Hermes et al., 2004). This is the result of many factors, including its shallow depth and central location, which in turn allows not only water and nutrient exchange with various basins adjacent to it (Campos et al., 2002), but fish movement and recruitment as well. Its being surrounded by deep (>200m) water adds to the many factors that would favor high natural fish abundance in the area and the likelihood of strong competitive interactions. The results of the study, however, are not consistent with strong competition. This is attributed to an overall relative availability of food resulting from a general reduction in the abundance of consumers and a corresponding reduction on predation (consumption) on food resources (Mequila et al., 2004). Constant cropping brought about by heavy fishing, particularly of trawls which have been used in the area since the 1950s (Aprieto and Villoso, 1979) allows this. Thus,

Species	Size range (TL in cm)	L_{max} (cm)	Reference	Niche Width (H') small	medium	large	
Synodus variegatus	12.4 - 24.5	30 SL	Masuda, 1984	0.57	0.50	0.56	
Upeneus asymmetricus	9.5 - 14.2	30	Allen, 1999	0.55	0.67	0.67	
Leiognathus bindus	5.6 - 12.2	12	Allen, 1999	0.78	0.85	0.92	
Scolopsis affinis	12.8 - 21.3	30	Randall et.al., 1996	0.62	0.82	0.57	
Selaroides leptolepis	7.8 - 15.3	17	Masuda, 1984	0.63	0.63	0.62	
Plotosus lineatus	9.9 - 26.4	32	Randall et.al., 1996	0.27	0.31	0.12	
Arothron manillensis	8. - 11.9	45 SL	Masuda, 1984	—	0.64	0.51	
Neopomacentrus filamentosus	6.6 - 13.9	11	Froese.and Pauly, 2006	0.53	0.42	0.70	
Saurida undosquamis	14.4 - 26.8	50 SL	Masuda, 1984	—	0.45	0.73	
Leiognathus rivulatus	7.6 - 13.2	12	Rau and Rau, 1980	—	0.48	0.57	
Lagocephalus lunaris	7.9 - 22.7	45 SL	Masuda, 1984	—	0.51	0.63	
Rastrelliger kanagurta	14.2 - 20.8	35	Randall et.al., 1996	—	—	—	0.68
Apogon notatus	7.1 - 8.5	10	Masuda, 1984	—	—	—	0.32
Pentapodus setosus	11.1 - 16.2	20	Allen, 1999	—	—	—	0.86
Parapercis alboguttata	12.6 - 21.5	22	Allen, 1999	—	—	—	0.64

Table 4. Food niche widths (H') of fish species by size class in the Visayan Sea, July 2003
Note: Maximum total length attained as reported in the literatures are included in the table for comparison with the size observed in this study. Those indicated with SL were species with maximum length reported in standard length.

continuous cropping together with natural high overall productivity promote generalist feeding (high niche widths) in the fish community over a wide range of habitats (low niche overlap).

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