Part 2

Feeding ecology of demersal fish assemblages along coastal area off Pattani and Narathiwas Provinces

Abstract

Food preferences, feeding attributes, trophic guilds, and ontogenetic changes in diet compositions of 45 fish species collected along coastal waters in the southern areas of the South China Sea, Thailand were examined. Most species had high food intake and fed on specific ranges of food types. Shrimp was the most important food (31.7%), followed by calanoid copepod (16.8%), fish (12.7%) and gammarid amphipod (8.3%). These fishes can be categorized into six different trophic guilds and further divided into four categories namely; piscivore, zooplanktivore, zoobenthivore and miscellaneous/opportunist. Numbers of feeding guilds at each depth varies between four and five. Four of these are consistently found throughout the year at all zones; shrimp predator, piscivore, calanoid copepod feeder and a combination of polychaete and other food feeders. Ontogenetic studies indicate that fishes are more likely to group according to species rather than size. This scientific information is important when examining the complex association between fishes and identifying groups of species using similar resources.

Keywords diet composition; feeding habits; functional role; Gulf of Thailand; fish ecology.

Introduction

Knowledge in the trophic ecology of any given system is fundamental in understanding the ecosystem as a whole (Blaber, 1997; Cruz-Escalona et al., 2000). It therefore becomes important to determine not only the feeding mode, but also the extent and nature inter-specific and inter-guild trophic relationships (Elliott et al., 2007). A 'guild' refers to a group of species exploiting the same class of environmental resources in a similar way (Root, 1967). When used in fish community studies, it offers the possibility of dividing a community into functional groups (Schlosser 1982; Ross 1986; Bayley 1988; Gerking1994; Garrison and Linke, 2000). The concept of feeding guild in estuarine fishes was first introduced by de Sylva (1975) who defined groupings of fishes based on their feeding preferences and food web structure. Recently, Elliott et al. (2007) classically identified seven standard categories of the feeding functional groups (FMFG) in estuarine habitat; detritivore, herbivore, omnivore, zooplanktivore, zoobenthivore, piscivore and miscellaneous /opportunist. This FMFG classification is a trophic guild system designed to allow the aggregation of fish species that utilize similar food resources to help understand, explain and use in a management context, the functioning of this habitat.

Spatial and seasonal factors greatly affect the structuring of trophic organizations of fishes in a particular area (Elliott et al., 2002). Seasonal changes of a trophic guild can often be attributed to the changes in life history patterns of food organisms or to the feeding activities of the fishes themselves (Snyder, 1984; Lucena et al., 2000). Foraging success of fish in different habitats is different. Fishes may have to choose between a habitat that provides more abundant and diverse prey, but in which prey is harder to capture, and a habitat which has less prey abundance, but better capture opportunity (Crowder and Cooper, 1982).

Tropical coastal ecosystems in Southeast Asia have been known as important habitats of the world (Blaber, 1997). There are studies investigating on the community assemblages and ecological aspects of fishes in these shallow sheltered estuarine habitats (Pinto, 1988; Chong et al., 1990; Sasekumar et al., 1992; Ikejima, 2003; Hajisamae and Chou, 2003). However, community and feeding ecology studies of fishes are rare, especially for greater depths which sustain the bulk of fishing impacts.

It is hypothesized that diet compositions and trophic attributes differ among fish species and groups of certain fish species form a specific guild in general. Water depths and months play a great role in organizing different guilds. Ontogenetic changes of some selected species occur in this habitat. This study is therefore aimed at investigating diets and feeding attributes of 45 fish species in coastal waters of up to 25m, examining trophic guilds of these fishes in general, at different depths and in different months, and evaluating ontogenetic changes in food compositions of some selected species.

Materials and Methods

Study area

Sampling sites are located along the coasts of Pattani and Narathiwat provinces, southern Thailand. These areas also coincide with the southern areas of the South China Sea, considered to be heavily over-fished (Blaber, 2001). The coastline is characterized by long sandy beaches, semi-diurnal tides with approximately 0.3-0.9m tidal ranges and experiences two different tropical monsoons; the North-East monsoon from November to February and South–West monsoon from May to August. More than 60% of the annual rainfall occurs in November and December. Freshwater inputs from four main rivers including the Takbai, Bangnara, Saiburi and Pattani Rivers drain into this area. Pattani bay, a 74 km^2 semi-enclosed estuarine bay with several ecosystem types, provides shelter for juveniles of many fish species before they migrate to deeper open water areas (Hajisamae et al., 2006).

Four different line transects parallel to the shoreline were selected; sites A, B, C and D. At each site, four different depth contours were selected and marked as zones 1, 2, 3 and 4. The average depths at these zones were 12.3±1.0m, 15.8±1.0m, 19.8±1.0m and 23.3±1.5m, respectively. In general, these areas are characterized by sandy and some muddy bottom, unobstructed by formations except for a small island between stations D3 and D4.

Sample collection and gut analysis

Up to 20 individuals each of 45 species giving a total of 4 603 gut samples were randomly selected from bimonthly catches by a bottom trawl (14m headline, 15m ground rope, and 2.20cm mesh cod-end liner) towing during daylight hours at approximately 2.3 knot for 60 minutes between March 2006 and November 2006. They were immediately preserved in 10% buffered formalin, soaked overnight in freshwater and subsequently stored in 70% ethanol. The gut of individual specimens sorted to known total length intervals were cut open into a Petri dish with the aid of surgical ocular scissors. After the entire gut was removed, its gut fullness, on a scale of 0 (empty) to 6 (fully distended with food), was recorded (Hajisamae and Ibrahim, 2008). Each food was identified to the lowest taxonomic level possible due to lack of suitable expertise. Ten fish species were selected, based on their dominance and/or economic importance, to examine ontogenetic changes in feeding habits.

Data analysis

The raw data were analyzed for:

Volumetric contribution (%V) which is the percentage contribution to the total gut volume present in each of non-empty guts (Platell and Potter, 2001).

Trophic indices have been used to describe the importance of each food type in the diets of different fish species (Hyslop, 1980). *Total number of food* refers to the total number of food types found in all the guts of each species. *Dominant food type* refers to the food type found in the greatest proportion in the guts of each fish species. *Vacuity index (VI)* refers to the number of empty guts as a percentage of the total number of guts examined. *Gut fullness (FL)* refers to an average of the relative gut fullness of all guts examined. *Diet breadth (Bi)* is calculated using Levin's standardized index (Krebs, 1989; Labropoulou and Papadopoulou-Smith, 1999). The formula for diet breadth index is;

$$Bi = \left(\frac{1}{n-1}\right)\left(\left(\frac{1}{\sum_{i,j=1}^{n} P_{ij}^{2}}\right) - 1\right)$$

Where B_i = Levin's standard index for predator "i"; "P_{ij}" = proportion of diet of predator "i" that is made up of food "j"; "n" = number of food categories.

Trophic guild construction:

For a general trophic guild, a Bray-Curtis similarity matrix of the raw data of mean percentage composition of food (%V), no digested items involved, was constructed and a cluster dendogram was developed using the PRIMER statistical package 5.0 (Clarke and Gorley, 2001). A group of species falling in the same cluster was tested for a difference by Analysis of similarity (ANOSIM). Results from ANOSIM, similarity percentage (SIMPER) and together with the raw data of food composition, were used to assess the robustness of the guild. A model of general trophic guild for 45 fish species was then formed. Spatial and monthly trophic guilds were also identified to examine how fishes collected in different months and at different depths formed the guilds applying a similar protocol. Ontogenetic trophic guilds for the ten selected species were constructed.

Results

Dietary attributes

For each of the 45 fish species, between 10 and 507 guts were examined. The vacuity index (VI) of each species ranged from 0 to 56.2, with most of the values falling <10. Nine out of 45 species had a vacuity index of "0", indicating that none of the guts of these fishes was empty. Gut fullness for each species ranged from 1.5 for *Johnius dussumieri* to 4.6 for *Epinephelus sexfasciatus*, with most of them falling between 3 and 4. The total number of food types varied between species, ranging from one for *Trichiurus lepterus* to 18 for *Scolopsis taeniopterus*. The overall diet breadth (*Bi*) ranged between 0.00 and 0.69, with most of the values falling between 0.2–0.5. Fishes demonstrating very low diet breadth included *Caesio cuning*, *Saurida undrosquamis*, *Siganus canaliculatus*, *Trichiurus lepterus*, *Upeneus sulphureus* and *Upeneus tragula*. Details of trophic attributes are illustrated in **Table 1**.

Table 1 Trophic indices and relative composition by volume of food of 45 fish species collected off coastal waters of Pattani and Narathiwas, Thailand between March 2006 and November 2006. VI = vacuity index, FL = mean gut fullness, Bi = diet breadth

Species	No. of sample	Total length (cm)	Trophic attributes				Food types								
			VI	FL	Bi	No. of food type	Shrimp	Calanoid copepod	Polycheate	Gammarid amphipod	Crab	Fish	Crypod	Others	Digested items
Alectis indicus	10	10.1	0	4.4	0.17	3	80	0	0	0	16.5	0	0	3.5	0
Apogon endekataenia	69	6.3	5.8	3.7	0.20	9	54.8	19.0	0.9	3.5	0.3	11.1	2.6	1.5	6.2
Apogon niger	95	7.6	14.7	2.4	0.37	10	34.0	19.1	0.0	7.4	2.2	9.9	0.2	6.2	21.0
Apogon quadrifasciatus	507	7.6	12.6	2.3	0.20	13	44.0	17.3	0.6	4.5	0.9	4.8	0.8	6.6	20.5
Arius maculatus	21	15.8	4.8	3.7	0.22	5	7.5	0.0	6.5	0.0	12.5	0.0	0.0	68.5	5.0
Arius venosus	23	14.3	0	1.9	0.16	9	60.4	0.4	8.3	0.0	1.7	4.3	0.4	7.0	17.4
Caesio cuning	148	8	0	3.2	0.09	8	16.4	75.1	1.1	0.8	0.0	3.2	0.0	1.4	2.0
Callionymus planus	223	9.1	1.3	3	0.27	12	2.6	34.8	12.8	30.4	0.1	0.0	1.5	13.2	4.7
Dactylopus dactylopus	58	9.7	3.4	2.9	0.23	11	7.0	35.6	5.2	37.0	0.0	0.2	4.4	6.1	4.6
Diagramma pictum	31	8.8	3.2	3.2	0.19	8	57.7	21.3	0.0	8.7	0.0	1.3	0.3	4.0	6.7
Epinephelus bleekeri	17	14.4	5.9	2.9	0.64	3	35.0	0.0	0.0	0.0	11.3	28.8	0.0	0.0	25.0
Epinephelus coioides	22	13.6	22.7	2.1	0.58	4	11.8	5.9	0.0	0.0	17.6	23.5	0.0	5.9	35.3
Epinephelus sexfasciatus	14	13.4	56.2	4.6	0.44	2	0.0	0.0	0.0	0.0	0.0	57.1	0.0	14.3	28.6
Gazza minuta	37	12.7	13.5	3.1	0.39	7	8.8	12.5	4.7	0.0	0.0	42.8	22.8	0.6	7.8
Gerres filamentosus	37	15.1	2.7	3.7	0.15	8	7.5	0.8	65.0	11.1	0.0	1.7	0.0	11.1	2.8
Himantura bleekeri	11	16	9.1	3.3	0.24	5	60.0	10.0	18.0	0.0	0.0	4.0	0.0	2.0	6
Inegocia japonica	261	10.9	41.8	3.8	0.15	10	59.1	2.6	2.4	1.6	11.3	6.1	0.2	9.5	7.1
Johnius dussumieri	18	10.3	5.6	1.5	0.38	4	13.5	56.5	0.0	24.1	0.0	0.0	0.0	0.0	5.9
Leiognathus brevirostris	144	7.6	3.5	2.8	0.47	8	18.5	23.2	30.5	14.7	0.0	0.0	2.3	2.8	7.9
Leiognathus equulus	15	13.8	0	3.7	0.13	7	16.3	2.7	70.7	0.0	0.0	0.0	1.3	2.3	6.7
Leiognathus splendens	242	9.2	1.2	3.1	0.12	15	2.5	52.3	24.9	8.0	0.0	0.1	5.4	4.9	1.9
Leiognathus stercorarius	99	7.3	2	2.9	0.18	12	16.5	51.5	14.3	6.3	0.0	0.0	0.8	4.4	6.2
Lieognathus decorus	23	10.5	13	3.0	0.37	8	11.5	42.5	7	5	0	0	21	8.0	5
Lutjanus erythropterus	13	11.4	0	4.7	0.36	4	23.1	0.0	0.0	0.0	17.7	56.9	0.0	2.3	0.0
Lutjanus madras	63	13.3	25.4	2.4	0.18	7	57.7	1.3	2.1	0.4	0.0	16.2	1.9	1.3	19.1
Monacanthus chinensis	29	11.2	3.4	3.1	0.57	9	11.4	22.5	18.9	14.6	7.1	0.0	0.0	7.5	21.4
Paramonacanthus choirocephalus	10	10.4	0	2.3	0.52	7	31.1	17.8	8.9	25.6	0.0	0.0	1.1	15.6	0.0
Nibea soldado	47	9.5	10.6	3.0	0.13	10	56.3	0.3	24.0	0.9	0.9	4.0	0.0	9.9	3.7
Oxyurichthys saru	84	10.7	7.1	3.5	0.16	9	2.8	58.7	4.1	23.5	1.3	0.0	0.0	5.8	3.8

Pentapodus setosus	14	10.8	0	3.9	0.41	8	39.3	11.4	20.4	1.1	3.6	5.0	12.1	7.1	0.0
Plotosus anguillaris	31	8.5	3.2	2.6	0.19	4	72.3	21.0	3.3	0.0	0.0	0.0	0.0	0.0	3.3
Polynemus tetradactylum	10	10.8	0	3.0	0.40	4	25.0	0.0	1.0	54.0	0.0	22.0	0.0	0.0	0.0
Pomadosys maculatus	21	8.4	0	2.2	0.21	5	66.2	0.0	4.8	19.5	0.0	0.0	0.0	9.5	0.0
Priacanthus tayenus	190	10.3	0.5	4.5	0.24	14	36.6	16.0	16.3	18.6	1.9	5.7	2.9	1.5	0.5
Saurida micropectoralis	297	13.8	31	3.4	0.13	10	30.1	0.7	1.9	0.5	1.7	57.5	0.0	3.3	4.4
Saurida undrosquamis	212	9.8	46.7	4.5	0.07	6	7.5	1.8	0.0	0.0	4.0	77.4	0.0	8.4	0.9
Scolopsis taeniopterus	300	13.1	4	3.3	0.16	18	26.9	4.7	40.9	5.5	1.1	0.9	6.2	7.6	6.1
Secutor ruconius	142	7.2	4.9	2.8	0.24	12	17.9	41.7	5.6	0.7	0.0	1.5	14.4	16.9	1.5
Siaganus canaliculatus	139	8.7	3.6	2.8	0.09	13	11.5	3.0	66.8	5.5	0.0	3.4	0.1	8.9	0.7
Sillago sihama	12	13.4	8.3	2.9	0.69	8	18.2	0.0	18.2	22.7	9.1	9.1	0.0	13.6	9.1
Trichiurus lepturus	18	33.2	5.6	3.0	0.00	1	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0
Upeneus sulphureus	382	8.2	1	3.6	0.09	12	62.0	29.8	0.7	2.2	0.9	0.6	1.3	0.8	1.6
Upeneus sundaicus	44	9	2.3	2.8	0.14	8	66.0	11.9	0.0	13.3	1.2	0.0	3.5	1.9	2.3
Upeneus tragula	366	8.8	1.6	3.3	0.06	12	73.3	19.4	0.5	2.6	0.1	0.3	1.2	1.5	1.1
Vincentia chrysura	54	7.1	29.6	2.1	0.18	6	67.1	11.8	0.0	0.0	0.0	10.5	0.0	7.9	2.6
Average	4,603		9.2	3.1	0.30	8.2	31.7	16.8	11.4	8.3	2.8	12.7	2.4	6.9	7.0

Food and dominant food types

Overall relative composition by volume of food found in the guts of all fish samples was examined. Shrimp was the most dominant food type consumed by fishes (31.7%), followed by calanoid copepod (16.8%), fishes (12.7%), polychaete (11.4%), gammarid amphipod (8.3%), crab (2.8%), barnacle cyprid (2.4%), other food types (6.9%) and unidentified digested food (7.0%). Altogether, 20 species fed mainly on shrimp, nine species on calanoid copepod and seven species on fishes (**Table 1**).

General trophic guild

A combination of cluster analysis, ANOSIM and SIMPER significantly characterized 45 dominant and important species according to their trophic organization into six different guilds (**Figure 1**). With the exception of a piscivorous guild, shrimp was considered both major and minor food source types in differing species. The largest guild, in terms of number of species, comprising of seven species such as *Apogon quadrifasciatus*, *Upeneus sulphureus*, *Nibea soldado* and *Alectis indicus* are mainly shrimp predators. The second largest with nine species such as *Oxyurichthys saru*, *Caesio cuning* and *Johnius dussumieri*, featured calanoid copepods as the main food source with some combinations of gammarid amphipod and shrimps. Six species were polychaete predator. *Trichiurus lepturus*, *Saurida undosquamis* and *Epinephelus coioides* were solely piscivorous species. Five species were defined as a combination of fishes and shrimps guild. Six species such as *Polynemus tetradactylum*, *Priacanthus tayenes* and *Sillago sihama* formed a combined-food feeding guild having more than four food types in their diets.

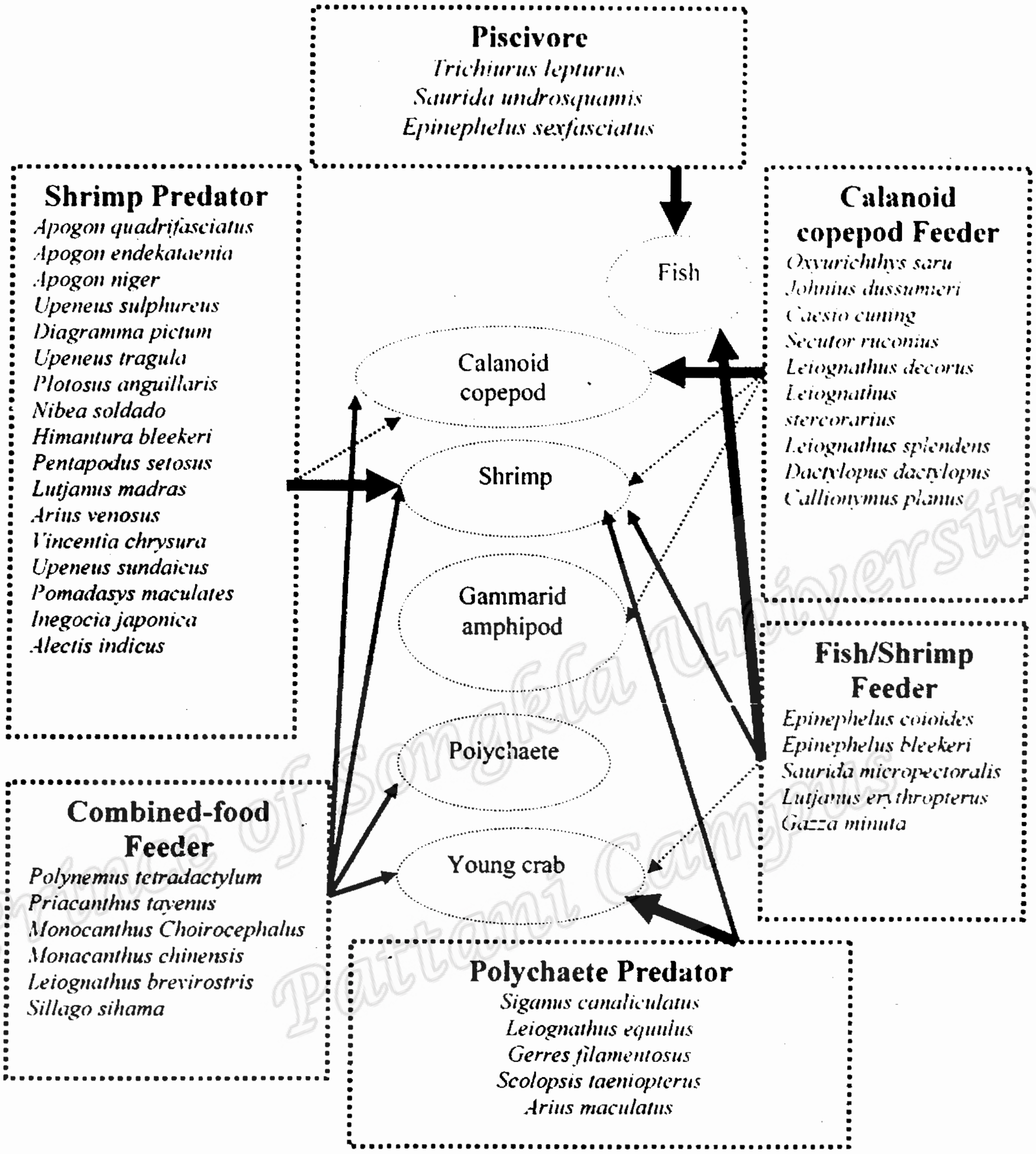


Figure 1 General trophic guilds of fishes collected off coastal waters of Pattani and Narathiwas, Thailand between March and November 2006. thick label = major food type, thin label = minor food type. (ANOSIM Global R = 0.922, *P = 0.001*)

Trophic guilds at different depth

At zone 1, fishes could be divided according to diet composition into four groups (ANOSIM Global R = 0.845, *P = 0.001*) (**Figure 2a**). Results of SIMPER for the percentage contribution of each food type to the formation of guild at different depths are summarized in **Table 2**. The first group was fishes feeding on a combination of polychaete and shrimp. The second group comprised of fishes having calanoid copepod as a major food intake with minor contribution of polychaete. Eleven species formed the third group with shrimp as the great contributing food type. Both *Saurida micropectoralis* and *S. undrosquamis* formed the last group feeding completely on other fishes.

Table 2 Summary results of similarity percentage analysis (SIMPER) on the contribution of food types in the formation of trophic guilds in different months and depth zones. G1-G5 = Trophic guilds 1-6; % = % contribution

Month	Guild	Food types	%
March 06	G1	Calanoid copepod	46.8
		Shrimp	33.2
		Gammarid amphipod	8.5
	G2	Shrimp	91.8
	G3	Polychaete	41.5
		Gammarid amphipod	30.4
		Calanoid copepod	8.1
	G4	Calanoid copepod	55.4
		Fish	36.6
May 06	G1	Shrimp	71.8
		Fish	14.3
	G2	Shrimp	89.2
	G3	Gammarid amphipod	38.8
		Calanoid copepod	28.8
		Shrimp	15.1
		Polychaete	12.5
	G4	Calanoid copepod	86.3
	G5	Polychaete	63.7
		Shrimp	25.1
July 06	G1	Calanoid copepod	63.5
		Gammarid amphipod	22.2
		Polychaete	8.4
	G2	Polychaete	72.1
		Shrimp	19.1
	G3	Shrimp	87.1
		Calanoid copepod	10.0
	G4	Fish	100
Septem 06	G1	Fish	99.3
	G2	Calanoid copepod	97.8
	G3	Polychaete	69.5
		Shrimp	21.3
	G4	Shrimp	72.4
		Calanoid copepod	22.3
Novem 06	G1	Calanoid copepod	92.0
	G2	Shrimp	66.7
		Mantis shrimp	33.3

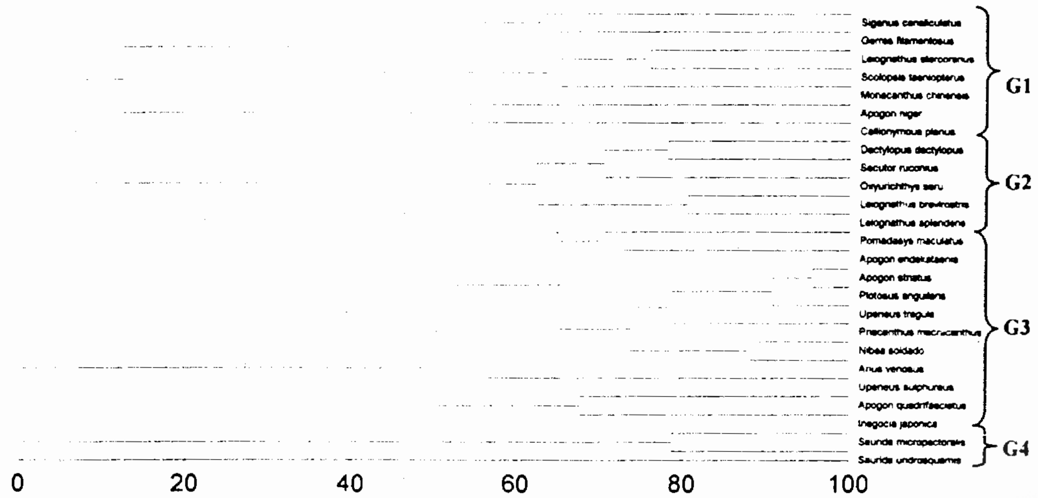
Zone	Guild	Food types	%
1	G1	Polychaete	42.4
		Shrimp	30.8
	G2	Calanoid copepod	80.0
		Polychaete	10.8
	G3	Shrimp	87.7
		Calanoid copepod	8.5
	G4	Fish	100
2	G1	Shrimp	51.9
		Calanoid copepod	39.5
	G2	Fish	95.5
	G3	Polychaete	59.5
		Shrimp	24.7
		Calanoid copepod	7.7
	G4	Calanoid copepod	86.7
		Gammarid amphipod	9.7
3	G1	Calanoid copepod	39.1
		Shrimp	25.5
		Gammarid amphipod	23.1
		Polychaete	5.9
	G2	Shrimp	94.1
	G3	Fish	66.4
		Shrimp	27.5
	G4	Polychaete	85.6
		Shrimp	7.6
	G5	Calanoid copepod	89.6
		Shrimp	6.3
4	G1	Fish	91.1
	G2	Calanoid copepod	96.7
	G3	Shrimp	82.3
		Calanoid copepod	13.0
	G4	Polychaete	58.5
		Shrimp	30.8
		Gammarid amphipod	4.0

Four groups of fishes were separated at the depth zone 2 (ANOSIM Global R = 0.634, $P = 0.001$) **(Figure 2b)**. Fishes formed the first group fed largely on shrimp and calanoid copepod. *Saurida micropectoralis*, *S. undrosquamis* and *Epinephelus coioides* formed the second group that fed almost completely on other fishes. Eight species together formed the third group feeding mainly on polychaetes with high contribution of shrimp and some calanoid copepod. The last group was fishes that had almost entirely of calanoid copepod with some gammarid amphipod.

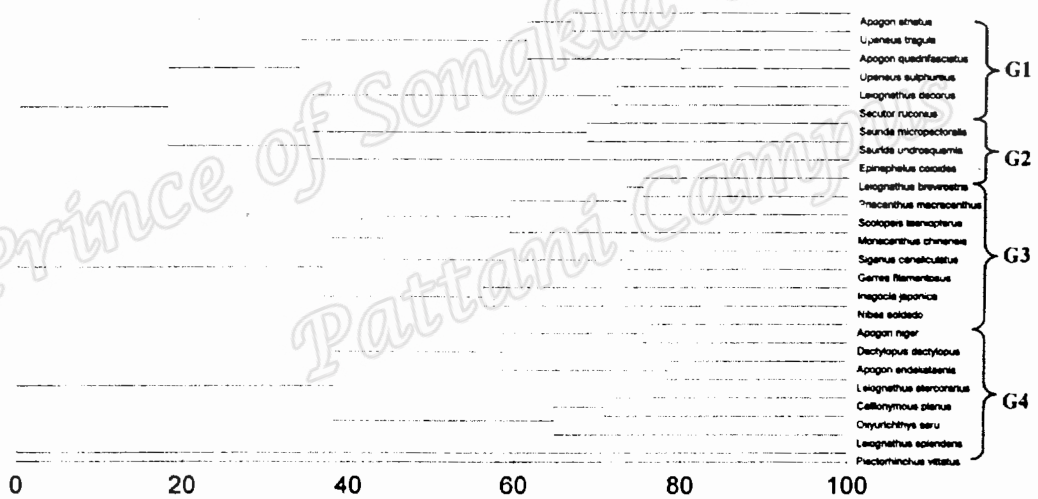
Cluster analysis also demonstrated five trophic groups at the depth zone 3 (ANOSIM Global R = 0.735, $P = 0.001$) **(Figure 2c)**. The first group comprised of species feeding on a contribution of four food types. The second group was almost a complete shrimp predator. The third group was fishes having diets with high contributions of fishes and shrimps. The fourth group was fishes feeding largely on polychaetes with some contribution of shrimps. Diet of the last group, which included six species consisted mostly of calanoid copepod.

At the depth zone 4, fishes could be categorized into four different feeding groups (ANOSIM Global R = 0.849, $P = 0.001$) **(Figure 2d)**. The first group, three species, was piscivorous species feeding almost entirely on other fishes. The second group was calanoid copepod feeders. Ten species formed the third group, feeding largely on shrimp and with some contribution of calanoid copepod. The forth group was fishes feeding on a combination of polychaetes and shrimps.

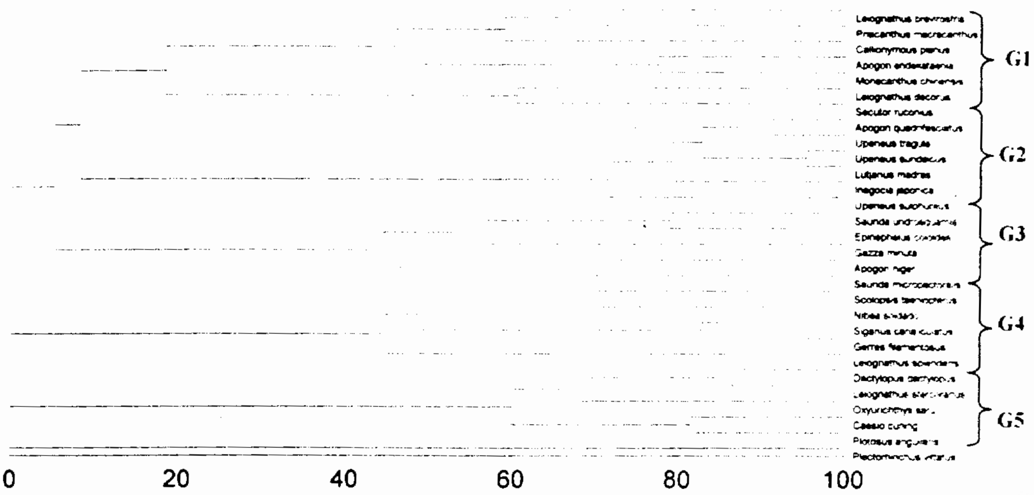
a. Zone 1 (ANOSIM Global R = 0.845, *P = 0.001*)



b. Zone 2 (ANOSIM Global R = 0.634, *P = 0.001*)



c. Zone 3 (ANOSIM Global R = 0.735, *P* = *0.001*)



d. Zone 4 (ANOSIM Global R = 0.849, *P* = *0.001*)

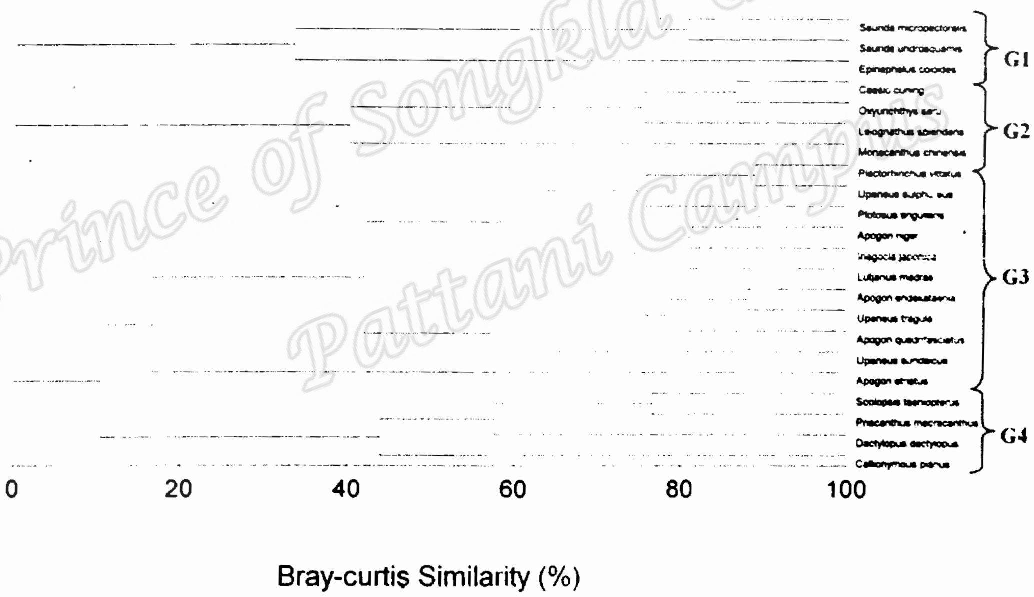


Figure 2 Cluster dendogram demonstrating trophic groups of fishes collected at different depth zones off coastal waters of Pattani and Narathiwas, Thailand between March and November 2006. G1 – G5 = trophic groups.

Trophic guild in different months

Four cluster groups were formed based on dietary contribution in March 2006 (ANOSIM Global R = 0.685, *P* = *0.001*) (Figure 3a). Results of SIMPER for the percentage contribution of each food types to the formation of guild in different months are summarized in **Table 2**. The first group consisted of fishes having a combination of calanoid copepods and shrimps as their main food source. The second group comprised of fishes feeding mainly on shrimps. Six fish species formed the third group, feeding on a combination of polychaetes and gammarid amphipods. The forth group had calanoid copepods and fishes in their diets.

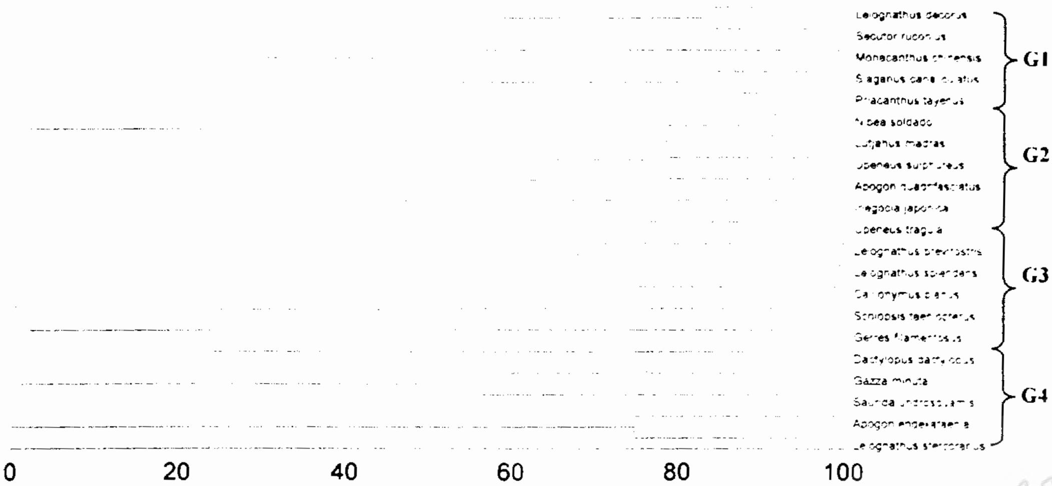
Cluster analysis categorized fishes found in May 2006 into five different groups, the most diverse feeding guild in this study (ANOSIM Global R = 0.792, *P= 0.001*) (**Figure 3b**). Six fish species formed the first group, feeding mainly on shrimps with some contribution of fishes. Six species were categorized in the second group relying heavily on shrimps. Five species formed the third cluster, feeding on a combination of four main food types including gammarid amphipods, calanoid copepods, shrimps and polychaetes. Four species formed the fourth cluster with calanoid copepods as the major food type. Three fish species together formed the fifth group, feeding on a combination of polychaetes and shrimps as the main food types.

In July 2006, four groups of fishes were formed (ANOSIM Global R = 0.941, *P = 0.001*) (**Figure** 3c). The first group was fishes that fed mainly on calanoid copepods and gammarid amphipods. The second group was fishes having polychaetes as the main food source with some contribution of shrimps. Eight species formed the third group, the largest group, comprised of fishes that fed largely on shrimps with a small contribution of calanoid copepods. The last group was fishes feeding completely on fishes.

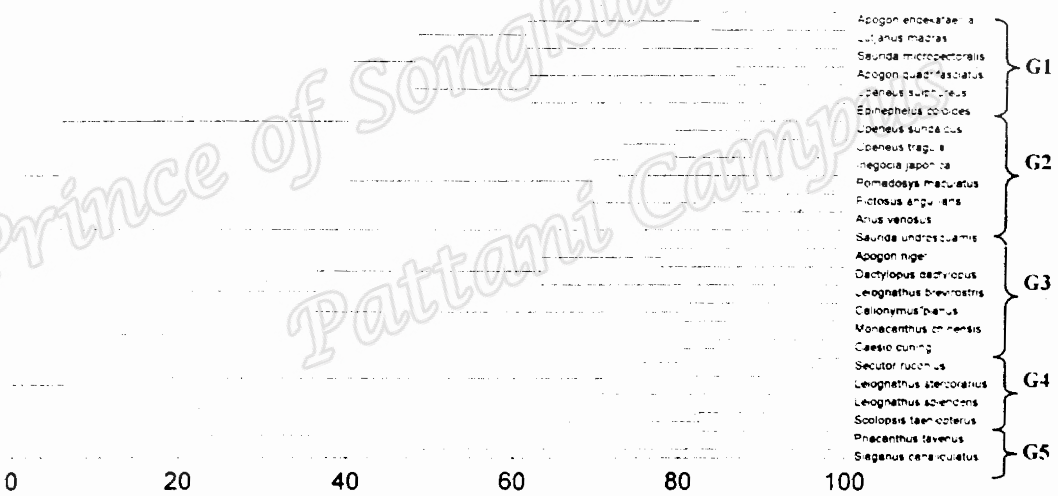
Nineteen species of fishes analyzed in September formed four different guilds and a single species (ANOSIM Global R = 0.886, *P = 0.001*) (**Figure 3d).** Three species formed the first group, feeding completely on other fishes. Three species feeding solely on calanoid copepods formed the second cluster. The third group was fishes that had polychaetes and some contribution of shrimps as their food. Eight species formed the fourth group with a great contribution of shrimps and some calanoid copepods in the diets.

Only seven fish species were analyzed for the month of November 2006 (ANOSIM Global R = 0.98, *P = 0.001*) (**Figure 3e**). Of these, two clusters and a single individual were formed. The first group was fishes feeding mainly on calanoid copepods and the second cluster fed on a combination of shrimps and mantis shrimps.

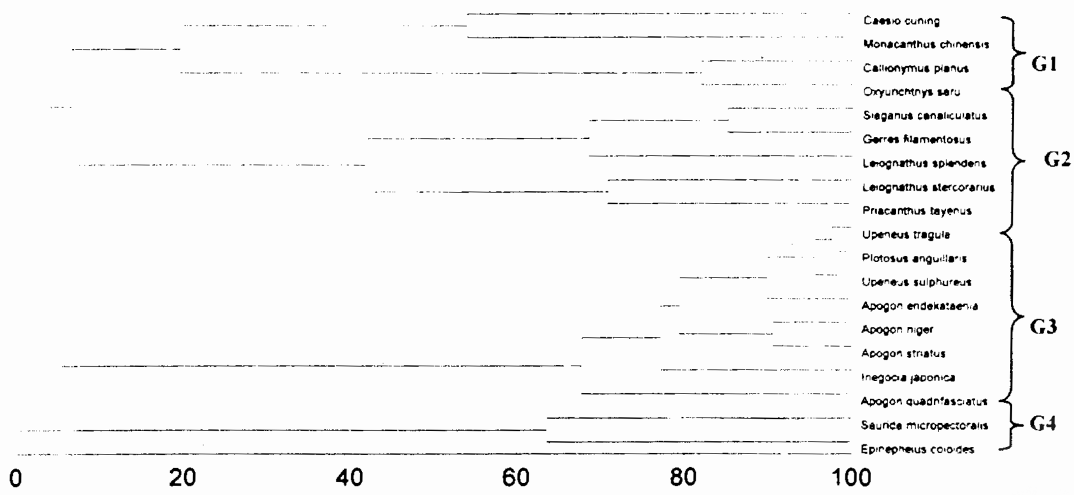
a. March 2006 (ANOSIM Global R = 0.685, *P 0.001*)



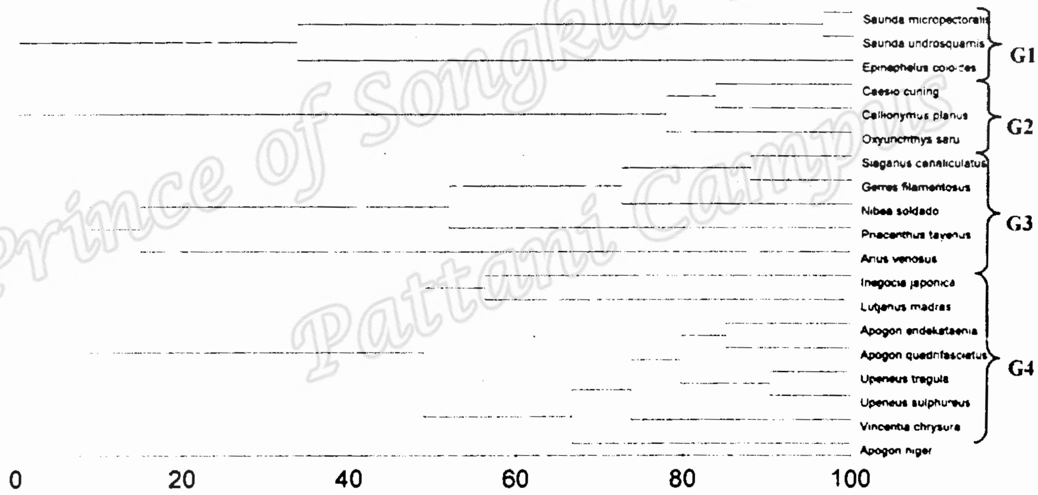
b. May 2006 (ANOSIM Global R = 0.792, *P = 0.001*)



c. July 2006 (ANOSIM Global R = 0.941, *P* = *0.001*)



d. September 2006 (ANOSIM Global R = 0.886, *P* = *0.001*)



e. November 2006 (ANOSIM Global R = 0.98, *P* 0.001)

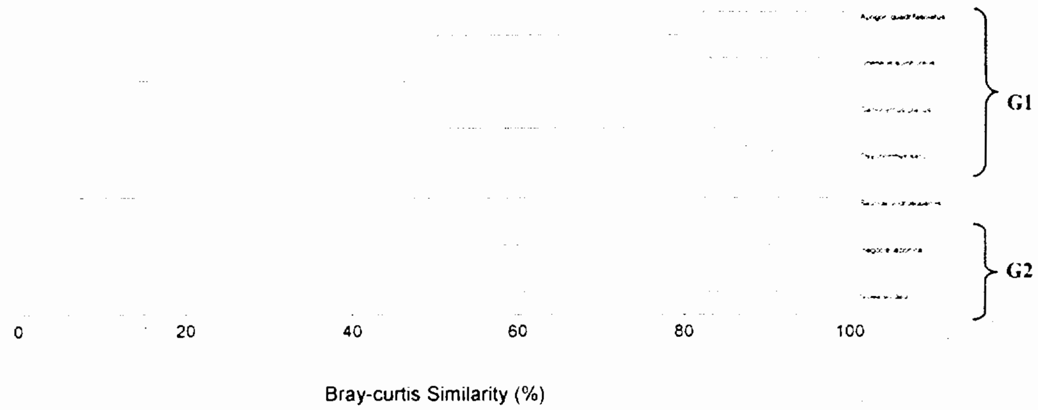


Figure 3 Cluster dendogram demonstrating trophic groupds of fishes collected in different months off coastal waters of Pattani and Narathiwas, Thailand between March and November 2006. G1-G5 = trophic groups

Ontogenetic changes

Trophic attributes for different size intervalss of 10 dominant fish species are shown in **Table 3**. Fullness index, vacuity index and diet breadth for all size intervals of these 10 species ranged from 1.6 to 5.1, 0 to 65.7 and 0.05 to 0.71, respectively. Ontogenetic changes in diet compositions are shown in **Table 3**. Shrimp, fish, calanoid copepod and gammarid amphipod were the most dominant food types for all size classes of the ten species.

Table 3 Trophic indices and and relative composition by volume of food of 10 dominant fishes collected off coastal waters of Pattani and Narathiwas, Thailand March 2006 and November 2006. VI = vacuity index, FL = mean gut fullness, Bi = diet breadth

Species	Length interval (cm)	Trophic indices				Food types										
		VI	FL	Bi	No. of food types	shrimp	calanoid copepod	polycheate	bivalve	gammarid amphipod	crab	fish	cryprid	sand	fish eggs	others
S. taeniopterus	<10.0	0	2.6	0.22	14	38.2	8.8	24.5	2.3	14.4	2.0	1.7	1.3	0.2	0.0	3.0
	10.1-15.0	3.1	3.5	0.14	14	25.4	4.4	49.8	2.6	4.1	0.5	0.4	5.4	0.2	0.0	2.6
	15.1-20.0	6.2	3.1	0.23	13	20.4	3.8	37.9	6.3	2.4	0.2	0.0	7.4	1.4	0.0	5.5
	>20.0	11.1	4.5	0.23	8	7.5	0.0	58.8	0.0	3.8	0.0	0.0	6.3	8.8	0.0	15.0
S. undrosquamis	<6.0	44.4	4.3	0.31	4	19.0	10.0	0.0	0.0	0.0	0.0	63.5	0.0	0.0	0.0	0.0
	6.1-8.0	65.7	4.6	0.06	3	0.0	0.0	0.0	0.0	0.0	4.3	73.9	0.0	0.0	0.0	0.0
	8.1-10.0	50	4.9	0.05	4	1.2	0.0	0.0	0.0	0.0	5.9	81.2	0.0	0.0	0.0	0.0
	10.1-15.0	32	4.2	0.12	4	8.3	0.0	0.0	0.0	0.0	6.9	81.9	0.0	0.0	0.0	0.0
	15.1-20.0	22.2	5.1	0.24	3	20.0	0.0	0.0	0.0	0.0	0.0	80.0	0.0	0.0	0.0	0.0
	>20.0	23.1	5.0	0.08	4	1.0	0.0	0.0	0.0	0.0	0.0	89.0	0.0	0.0	0.0	10.0
S. micropectorails	<10.0	15.3	3.0	0.23	6	34.0	0.0	3.3	0.0	0.0	1.5	51.4	0.1	0.0	0.0	0.0
	10.1-15.0	28	3.3	0.17	9	32.2	2.2	1.5	0.0	1.5	1.6	51.3	0.0	0.0	0.0	2.4
	15.1-20.0	4.8	4.8	0.24	4	28.8	0.0	0.0	0.0	0.0	4.0	83.2	0.0	0.0	0.0	0.0
	>20.0	4.1	4.1	0.17	4	16.0	0.0	0.0	0.0	0.0	0.0	76.0	0.0	0.0	0.0	4.0
L. splendens	<8.0	2	2.7	0.32	10	8.1	34.8	25.3	0.8	15.9	0.0	0.0	5.6	0.0	0.0	2.7
	8.1-10.0	0.8	3.0	0.13	12	0.9	57.2	24.9	0.9	7.8	0.0	0.0	3.0	0.1	0.3	1.8
	>10.0	1	3.4	0.15	12	1.5	55.3	24.3	1.8	3.0	0.0	0.3	8.9	0.0	0.0	3.6
U. sulphureus	<6.0	6.5	3.2	0.10	3	48.8	0.0	0.0	0.0	5.1	0.0	0.0	0.0	0.0	0.0	0.0
	6.1-8.0	0	3.7	0.04	9	57.3	0.0	0.3	0.0	3.2	0.6	1.0	3.5	0.3	0.0	0.1
	8.1-10.0	0.8	3.6	0.02	7	61.6	0.0	0.5	0.3	1.4	0.0	0.0	0.0	0.3	0.0	0.5
	>10.0	0	3.6	0.04	6	83.0	0.0	2.4	0.0	0.0	3.9	1.2	0.0	0.1	0.0	0.0
U. tragula	<6.0	10	3.7	0.50	3	51.1	48.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	6.1-8.0	0	3.4	0.10	9	69.7	26.8	0.0	0.0	1.8	0.2	0.4	0.4	0.0	0.0	0.7
	8.1-10.0	0.7	3.3	0.09	9	70.3	16.9	0.3	0.0	4.7	0.1	0.5	2.4	0.3	0.0	0.0

	>10.0	3.5	3.4	0.05	8	85.7	9.9	1.6	0.4	0.2	0.0	0.0	0.0	1.0	0.0	1.2
C. planus	6.1-8.0	0	3.0	0.28	8	2.3	48.2	12.3	0.9	25.5	0.0	0.0	0.0	5.7	0.0	0.9
	8.1-10.0	2.2	2.8	0.33	10	2.2	33.7	13.2	8.0	29.6	0.1	0.0	1.4	4.6	0.0	2.3
	>10.0	0	3.5	0.30	11	4.3	23.8	11.8	7.1	38.5	0.0	0.0	3.4	5.0	0.0	2.3
S. canaliculatus	<6.0	11.7	1.6	0.71	5	26.7	20.0	20.0	0.0	33.3	0.0	0.0	0.0	0.0	0.0	0.0
	6.1-8.0	6.3	2.7	0.07	6	4.4	0.0	84.9	0.0	0.0	0.0	4.2	0.2	6.2	0.0	0.0
	8.1-10.0	0	2.7	0.13	9	14.7	0.0	67.0	0.0	3.8	0.0	3.6	0.2	7.4	0.0	2.4
	10.1-15.0	0	3.4	0.12	10	7.7	4.5	65.0	3.6	3.2	0.0	4.5	0.0	2.3	0.0	4.1
	>15.0	0	4.1	0.34	6	15.7	0.0	55.7	14.3	0.0	0.0	0.0	0.0	4.3	0.0	8.6
C. cuning	<6.0	0	2.9	0.19	3	15.0	75.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	6.1-8.0	0	3.5	0.09	7	15.5	78.8	1.4	0.0	1.6	0.0	2.3	0.0	0.0	0.0	0.4
	8.1-10.0	0	2.7	0.13	6	22.4	70.0	1.7	0.0	0.0	0.0	0.0	0.0	0.2	0.0	1.0
	>10.0	0	3.4	0.20	5	8.7	72.6	0.0	0.0	0.0	0.0	13.0	0.0	0.0	0.0	5.7
A. quadrifasciatus	<6.0	12.4	2.7	0.17	9	50.0	26.4	1.2	0.0	6.2	1.2	2.4	0.7	0.0	0.0	0.2
	6.1-8.0	16.5	2.3	0.17	9	45.7	12.9	0.2	0.0	0.0	1.9	6.6	0.4	0.0	3.3	2.5
	8.1-10.0	8.9	2.2	0.21	11	42.1	17.4	0.9	0.0	7.2	0.0	5.6	1.2	0.1	7.2	0.9
	>10.0	10.4	2.1	0.45	6	32.6	16.3	0.0	0.0	8.6	0.0	0.0	0.7	0.0	14.0	0.0

Even though a trend of ontogenetic changes in diet of fishes was observed, cluster dendogram demonstrated that fishes were grouped according to species rather than size classes (ANOSIM Global R = 0.859, $P = 0.001$) (**Figure 5**). Five dietary clusters were reconstructed. SIMPER indicated that the first group consisted of fishes feeding mainly on a combination of shrimps (43.6% contribution) and calanoid copepods (42.6%). The second group was fishes that fed mainly on shrimps (78.5%) with some contribution of gammarid amphipods (11.7%). The third group was fishes having an equal combination of polychaetes (25.3%), calanoid copepods (22.9%), gammarid amphipods (18.2%) and shrimps (12.6%). The fourth group comprised of fishes that fed mainly on polychaetes (44.9%) and shrimps (22.0%). The fifth group was species feeding mainly on fishes (68.4%) and shrimps (23.6%).

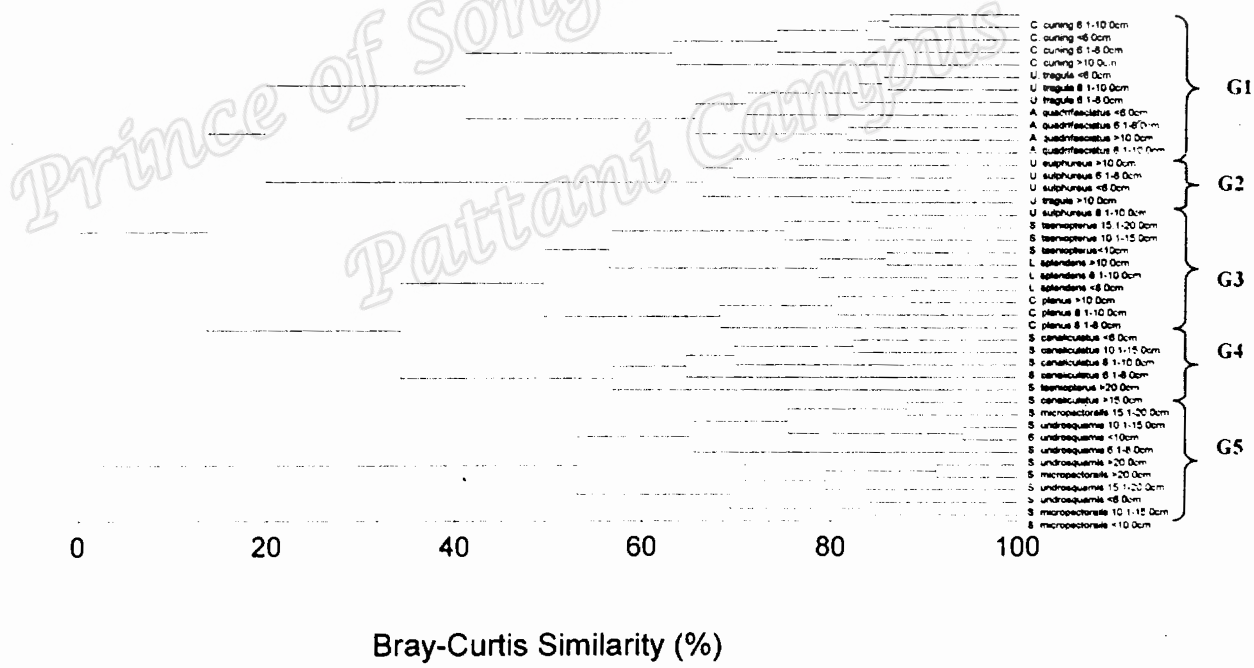


Figure 5 Cluster dendogram demonstrating trophic groups by sizes of 10 dominant fish species collected off coastal waters of Pattani and Narathiwas, Thailand between March and November 2006. G1-G5 = trophic groups

Discussion

The present study includes the largest dataset in the attempt to examine fish trophic guild interactions in the Asian region. Results indicate that fishes have high food intake and feed on a specific range of food types. All taxa, with the exception of *Epinephelus bleekeri* and *Sillago sihama*, are specialist feeders (Bi<0.60), relying on particular food types. Variation of trophic attributes and diet composition of all fishes examined indicate that they all are carnivorous but having different nutritional requirements and adopting different feeding strategies. However, only seven food types were found to be of particular importance, including shrimps, calanoid copepods, fishes, polychaetes, gammarid amphipods, crabs and cyprids of barnacle. Most of these prey-item can be described as real hyperbenthos or as temporary visitors in the hyperbenthic layer (Elliot et al., 2002). Apart from three solely piscivorous species, *Epinephelus sexfasciatus*, *Epinephelus sexfasciatus* and *Trichiurus lepturus*, shrimp, mainly Penaeidae, is considered the most important food source in this habitat as they feature either as the main or supplementary food type. Most fishes fed on more than a single food category. Good vision and prey attacking techniques are two factors considered important when capturing very active swimming organisms such as fishes and shrimps. Recent classification of the feeding functional groups (FMFG) (Elliott et al., 2007) identified seven broad categories. However, only four groups; piscivore, zooplanktivore, zoobenthivore and miscellaneous/opportunist can be categorized in this study. This study differs significantly from a similar nearby habitat, Pattani Bay, (Hajisamae and Ibrahim, 2008) in the absence of copepods nauplii, bivalve larvae, harpacticoid copepods and *Pleurostigma* as main food types. Moreover, herbivorous and omnivorous species are not recorded in this study, which is a different scenario from the majority of tropical estuarine fish species being omnivorous and incorporating plants, algae or macrophytes, in their diets as described by Blaber (2001). It is therefore postulated that the planktivorous guild will be less important in the deeper area of the same locality compared to a near-shore habitat. Moreover, diet of some fish species found in the bay habitat differs from that in this environment. For example, *Leiognathus splendens* and *Epinephelus coioides* in the bay habitat feeds mainly on harpacticoid copepods and shrimp, respectively (Hajisamae and Ibrahim, 2008), and changes to calanoid copepods and fish, respectively in this study.

The occurrence of feeding guilds has been widely discussed as a possible strategy to avoid competition (Pianka, 1980; Angel and Ogeda, 2001) or to optimize available resources (Jacksic, 1981). In general, of the six guilds characterized, four are distinct predators on specific food types. Having compared to trophic guilds in Pattani Bay (Hajisamae and Ibrahim, 2008), most were combined-guilds consisting of at least two food types per guild. A relatively similar trophic guild system is reported from the eastern Johor Strait, Singapore where calanoid copepod feeders, polychaete predators and a shrimp predators are the main guilds characterized (Hajisamae et al., 2003). It is noted that the difference in diet composition of each guild does not imply the dependence on completely different suite of food types.

In general, trophic guild at each depth zone share similar characteristics, where four guilds are consistently formed at all depth zones; shrimp predators, fish predators, calanoid copepod feeders and a combination of polychaete and other food feeders. Shrimp predators form the largest guild with the exception of zone 3. Occurrence of varying combination of food types forming the combined-food guilds may reflect food availability. Monthly guilds vary from two to five. Major food types including shrimps, calanoid copepods, fishes and polychaetes are preyed on by most species throughout the year. The largest trophic group for each month comprised of fishes that fed on a combination of few food types with shrimps as the greatest contributor. Some fishes may differ in the trophic guild they belong to over differing months. For instance, *A. endekataenia* was categorized as a calanoid copepod feeder in March but shifted to being a shrimp feeder in May, July and September. Food availability in the study area and sizes of fishes found in each month are potential factors affecting this circumstance.

Diets of most species change with size (Blaber, 1997) and age (Blaber and Blaber, 1980; Day et al., 1989; Platell et al., 1997). Despite the tendency of most of the fishes in this study to group according to species rather than size classes, ontogenetic changes in feeding habits are still observed. For example, *Scolopsis taeniopterus* fed on shrimps at smaller size classes before shifting to polychaetes when they are larger. Small *Upeneus tragula* preferred calanoid copepods while the larger ones ate shrimps.

Siganus canaliculatus shifted from feeding on calanoid copepods and gammarid amphipods during the younger stages to polychaetes at the larger size classes. There is a general tendency for marine fishes to start as zooplankton feeders, consuming large amounts of calanoid copepods during their young stages, and shifting to other food sources when they grow larger (Elliott et al., 2002). Crustacean zooplankton is a major component in the diets of the young marine fishes throughout the world (e.g. Hales, 1987; Hyndes et al., 1997; Platell et al., 1997; Amara et al., 2001; Hajisamae and Ibrahim, 2008). However, there are some truly zooplanktivorous species that continue feeding on calanoid copepods even when they are larger sizes such as *Leiognathus splendens*, *Callionymus planus*, *Caesio cuning* and *Apogon quadrifasciatus*. Species demonstrating minimal ontogenetic changes in feeding habits include *Saurida undrosquamis*, *Saurida micropectoralis*, *Upeneus sulphureus*, *Leiognathus splendens*, *Upeneus tragula* and *Caesio cuning*.

In conclusion, shrimps were the most important dietary component of fishes in this ecosystem, followed by calanoid copepods, fishes and gammarid amphipods. Fish species concentrated on in this study could be divided into six different trophic guilds, each with a different combination of food. They can be further divided according to feeding functional groups (FMFG) into four categories, namely; piscivores, zooplanktivores, zoobenthivores and miscellaneous/opportunists. Trophic guilds at each depth zones vary between four and six, with four guilds consistently formed at all zones; shrimp predators, piscivores, calanoid copepod feeders and a combination of polychaete and other food feeders. Shrimps, calanoid copepods, fishes, polychaetes and gammarid amphipods were fed on by demersal fishes throughout the year. Ontogenetic studies indicated that fishes were likely to group according to species rather than size classes. Some fishes demonstrated ontogenetic changes in feeding habits. This information is fundamental in understanding complex associations of fishes and fish communities and identifyng groups of species that use similar resources. These information serv as a reference of feeding ecology of fishes found in the lower part of the South China Sea, important in decision making and management of fisheries resources of the region.