

Ontogenetic Niche Shift in the Spotted Scat, *Scatophagus argus*, in Pak Phanang Estuary, Nakhon Si Thammarat Province, Thailand

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ABSTRACT.— The estuarine fish, *Scatophagus argus*, or spotted cat, utilized the mangrove forests and estuarine waterways in Pak Phanang Estuary, Nakhon Si Thammarat Province, Thailand, as habitat and feeding grounds. At this location, spotted scats revealed flexibility in their feeding ecology being omnivores and opportunistic feeders. Subject to gape-mediated prey size limitations, their diets changed in accordance with the availability or profitability of potential prey items. Morphologically, the subterminal mouth supported that spotted scats were mainly benthic feeders. Optimal food sizes, with respect to the mouth gape, were chosen, so as to maximize food consumed per unit capture. In large fish, smaller and more numerous teeth increasingly appeared on the jaws. Short gill rakers and a U-shaped stomach with pyloric caeca appeared to be the important sites for absorption and increased in number with fish developmental age, as did the ratio of the intestinal to standard fish length, within the range of 0.59 – 4.29. Spotted scats switch from one type of food to another as the relative abundance of the food types changes, whilst the relationship between feeding structure morphology, the diversity of food items and feeding preferences support that spotted scats have an ontogenetic niche shift. Spotted scat larvae predominantly fed on microphytoplankton in the surface water and in the water column. Juvenile fish are a transitional stage feeding both in the water column and the mangrove floor on resuspended benthic diatoms, zooplankton, benthos and detritus. Adults, feed mainly in the midwater level and the mangrove floor, with the most diversified diets ranging from microphytoplankton, protozoan, zooplankton, benthos and detritus. The latter two food items are greatly increased in adult diets.

KEY WORDS: *Scatophagus argus*, ontogenetic niche shift, Pak Phanang Estuary, Nakhon Si Thammarat Province

INTRODUCTION

The spotted scat, *Scatophagus argus* L. 1766 (Perciformes: Scatophagidae), is an euryhaline teleost, which is widely distributed throughout the near shore waters

of the Indo-West Pacific Ocean from southern India and Sri Lanka to southern Japan and Tahiti (Pinto and Punchihewa, 1996; Kottelat, 2001), and including northern to south eastern Australia (Vance et al., 1996), Philippines (Pinto, 1987; Barry and Fast, 1988) and the Southeast Asian coast (Kottelat, 2001; Hajisamae et al., 2006). It has a wide salinity tolerance, although larvae

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tend more towards fresh and brackish and adults towards seawater (Kottelat, 2001; Wongchinawit, 2007). However, as a common species in both natural and replanted mangrove forests and abandoned shrimp farms, they likely have significant ecological roles (Paphavasit et al., 2000; Ikejima et al., 2003; Tongnunui et al., 2007; Wongchinawit et al., 2007).

Because of their attractive pattern, this species is quite common as an ornamental fish (Amarasinghe et al., 2002; Bambaradeniya et al., 2002), and it is also an important food fish in Southeast Asia (Barry and Fast, 1988; Musikasung et al., 2006; Wongchinawit, 2007). However, as a common species in mangrove forest estuaries they not only likely have significant ecological roles, but also become attractive incentives to fishing these delicate and, in some areas, somewhat threatened ecosystems.

Their potential role in mangrove ecosystems, or potential role as bioindicators of mangrove estuary productivity and health (Costello et al., 2002; Wongchinawit, 2007), as well as the ability to economically aquaculture them outside of these ecosystems (Biona et al., 1988A; Biona et al., 1988B) to prevent overfishing mediated damage is, however, unclear since less is known about their dietary requirements during their complete development.

Mangrove estuaries play an important role in sustaining the productivity of inshore and offshore fisheries contributing nutrients to the coastal zone and shelter and nursery grounds for fish and other coastal organisms (Robertson and Blaber, 1992; Chaves and Bouchereau, 2000; Nagelkerken et al., 2000; Sheaves, 2001). The floral benthic detritus in mangrove swamps largely originates from mangrove leaves, but it also contributes to the inner bays and off shore regions for

feeding ground (Vittheesawat, 1999; Somkleeb et al., 2001 and Paphavasit et al., 2004). Combined with the resultant high levels of epibenthic invertebrates, such as shrimps and amphipods, it is not surprising that mangrove estuaries have a relatively high fish species richness and high numbers of individual (Little et al., 1988; Halliday and Young, 1996; Laroche et al., 1997; Lin and Shao, 1999; Tongnunui et al., 2007).

In estuaries, detritivory: herbivory ratios are often high compared to other waters (Lin et al., 2001), with the high efficiency of fish yields leading to the assumption that most estuarine fishes are detritivores, including the spotted scat in Taiwan (Lin et al., 2007). However, spotted scats have been reported to have a much broader diet than detritus including plants and small filamentous algae (Pinto, 1987; Barry and Fast, 1988; Agate et al., 1991; Alcalá et al., 2003), macroinvertebrates and benthic invertebrates (Rainboth, 1996; Miller and Skilleter, 2006). The distribution of such diverse prey items, which would represent a true omnivore, is, however, not congruent between these reports. It is not clear if these discrepancies, with reported specialization in, for example, herbivory or detritivory, represent differences between different populations of spotted scat (Kottelat, 2001), between developmental stages, or simply reflect the differences in available food from the sampling sites. For example, larvae as well as juvenile spotted scats from Thailand have been reported to feed on phytoplankton, zooplankton, benthos and detritus (Boonruang et al., 1994; Vittheesawat, 1999; Musikasung et al., 2006; Wongchinawit, 2007), while adult spotted scats from the Philippines were reported to be primarily herbivorous (Barry and Fast, 1988). Certainly, the development of rows of small rasp-like teeth and elongated intestines

in the adults are well suited for scraping and shredding and digestion of plant materials and, therefore, are consistent with an increasing herbivorous diet in adult scats. In contrast, adult spotted scats from Thailand and Taiwan were reported to be principally detritus feeders (Shinnaka et al., 2007; Lin et al., 2007), although this may well of course be plant-derived material. Elsewhere, within Thailand, spotted scats have been reported to additionally feed on zoobenthos (insects, mollusks, invertebrates, phytoplankton, polychaetes and non-annelid worms), plants (diatoms, benthic algae and weeds) and zooplankton (Monkolprasit, 1994), potentially supporting a more general omnivore classification.

It is therefore clear that further investigations on the life history and habitats of spotted scat in relation to the mangrove forest are needed. However, from these data, subject to the caution of the above caveats of potentially different genetics and bias from temporally and spatially heterogeneous food availability, it is tempting to speculate a pattern of general opportunistic omnivory based upon benthos feeding but with larval stages biased towards phytoplankton, juvenile's biased towards zooplankton and adults biased towards herbivory, including phytoplankton or plant detritus, according to local abundances (Boonruang et al., 1994; Vitheesawat, 1999; Wongchinawit, 2007). Should this be true, we would expect clear developmental changes in the spotted scat digestive system from larval to adult stages as the diet moved from high protein towards a plant or plant-detritus based diet.

To address this question we have chosen Pak Phanang Bay in the southern Thailand, an area with a mature mangrove forest and estuarine waterway as a model system. Ongoing research has established that spotted

scats use the mangrove swamps and coastal regions for feeding and show considerable flexibility in their feeding ecology (Wongchinawit, 2007), and, therefore, it is likely to be a suitable site. As part of this study, in this manuscript we report on the feeding strategies in three different stages of spotted scat development in relation to feeding structure morphology and diverse food sources, leading to ontogenetic niche shift in larval, juvenile and adult spotted scats. All developmental stages of spotted scats were studied in the same area and time so as to allow direct quantitative comparisons between them to elucidate if the diet of spotted scats changes with developmental stages, at least in this population.

MATERIALS AND METHODS

Sample collections

The study site was at Pak Phanang Estuary, a semiclosed muddy bottom estuary fed by several creeks that is situated on the eastern side of Nakhon Si Thammarat Province in the southern part of Thailand (8° 19.9' N; 100° 12' E). Our investigation has focused on the fish communities in the mangrove plantations (PP1 - PP3 in Fig. 1) and the estuarine waterways (PP7 - PP9 in Fig. 1). The mangrove plantations were principally comprised of *Rhizophora mucronata* and *R. apiculata*. Fish larvae were collected by using a plankton net of 103 µm mesh size and a 330 µm mesh size conical net equipped with a flowmeter. The plankton net was towed with a low-speed boat at each station. Two replicates were collected for each sampling station in the mangrove plantations. Samples were then preserved in 4% (w/v) neutralized formalin solution and later sorted for spotted scats. Juvenile fish were collected by using a fry sweeper, a modified push net

of 2 mm mesh size and a 3 mm mesh size trawl net. Towing was conducted at daytime at low tides in the mangrove plantations. Adult fish from study sites were collected by using a 1 cm mesh size local gill net for half an hour, in two replicate samples, during low tide at day time at each station in the mangrove plantations and estuarine

waterways, by moving back and forth along the shoreline in waist-to-chest deep water. Netted fish were preserved in 10% (v/v) neutralized formalin solution and subsequently sorted and the number of individuals recorded. The samples were collected in May and in October in two consecutive years, 2004 and 2005.

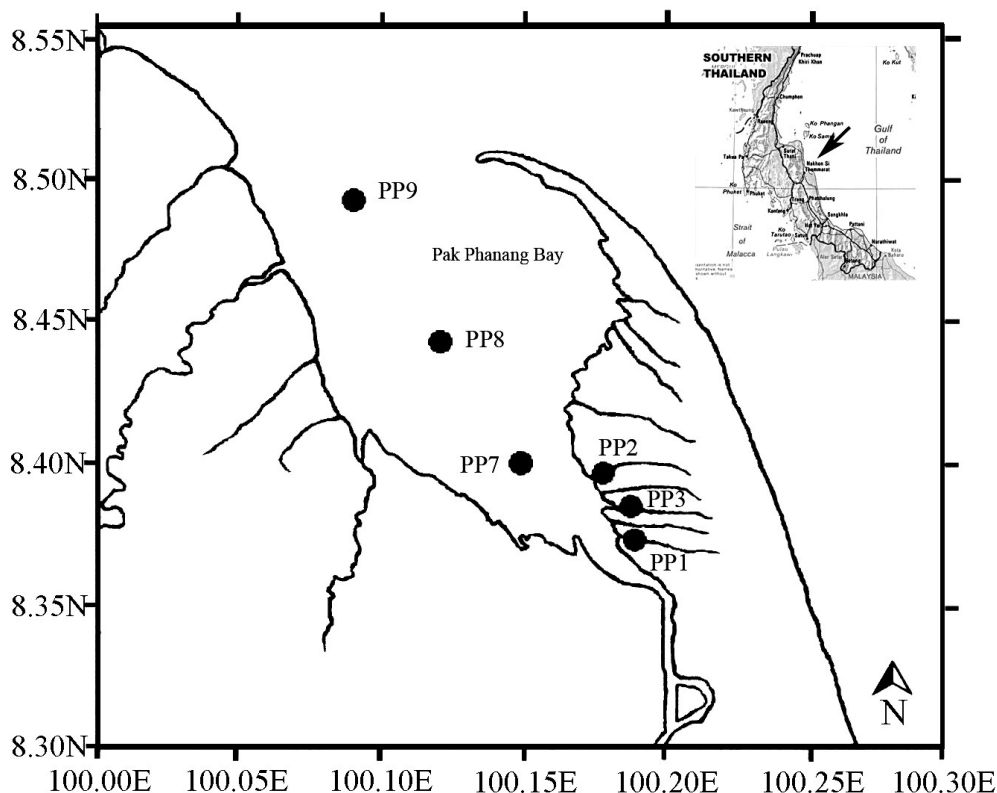


FIGURE 1. Study sites at Pak Phanang Estuary, Nakhon Si Thammarat Province, southern Thailand.

Salinity variations were pronounced in Pak Phanang Estuary, especially between the dry and wet season. Thus the samples were divided to represent the high salinity range of 23.9 - 33.4 psu and a low salinity range of 2.0 - 12.6 psu.

Morphological adaptations for feeding in spotted scats

After identification, captured fish were categorized into three developmental stages based on total body size as larval (1 - 2 cm), juvenile (2.1 - 8 cm) and adult (> 8 cm). A total of 50 individual spotted scat fish in each

of the above three size categories were randomly selected and measured for total length (TL), standard length (SL), width of the mouth gape (WID) and wet weight. The feeding structure morphology in fish, namely the mouth position, teeth, gill rakers, shape of stomach, number of pyloric caeca and intestinal length were examined, the last being to compare the relationship of intestinal: standard body length ratios and the relationship of intestinal: body length ratios. From our preliminary study, sexually mature adult spotted scats were larger than 8 cm. From the total 50 adult individuals examined in this study, with sizes ranging from 8.5 - 20 cm., most were females in the range of 9 - 11 cm. (32 individuals). However, the ovarian stage of these females was not determined. The average width of mouth gape in adults was 0.4 - 0.7 cm. The intestine: body length ratio in adults varied from 1.83 - 3.37 while the same ratio in the females size 9-11 cm, also fell within the same range of 1.83 - 3.30. There were no significant differences in the morphological characters in the adult spotted scats.

Index of relative importance, feeding behavior preference and digestion efficiency

For each of the three size categories, up to 40 spotted scats were randomly taken from the catch collected at each sampling station from the mangrove plantation sites and estuary sites, and the fish were measured in total length (TL) and weight. After dissection, the stomach contents were determined by morphological appearance using a light microscope. For each size category, a total of 10 fish with full or nearly full stomachs of identifiable food items were examined. The main food items were identified using the index of relative importance (IRI) of Pinkas et al. (1971), as

modified by Hyslop (1980). IRI in stomach content of total spotted scats was described for each developmental size category in low and high salinity conditions (see above) using:

$$IRI = (Cn + Cv) \times F$$

where IRI represents index of relative importance of the main food items, taxa or ecological groups; Cn represents percentage numerical abundance as the total number of food items in all stomachs in a sample; Cv represents percentage volumetric composition as the total volume of that taxa of food and F represents percentage frequency of occurrence based on the number of stomachs in which a food items was found.

A feeding behavior preference experiment was conducted by using spotted scats in the three size categories defined above. Two replications of five fish in a 4, 12 or 18 litre pond for larvae, juveniles and adults, respectively, were tested using filtered seawater at a salinity of 20 psu and constant aeration. Fish were starved for one day before initiation of the experiment. Each pond was provided with different food. For fish larvae, different shapes of microphytoplankton, namely *Chaetoceros* sp. and *Skeletonema* sp., were given. For juveniles and adult fish, rotifers and microphytoplankton were provided in the specified quantities. The size range of each prey offered was 6 - 24 μ m in single cell diameter for *Chaetoceros* sp., 2 - 21 μ m cell diameter for *Skeletonema* sp., united in long chains, and finally 80 - 179 μ m wide by 100 - 239 μ m length for rotifers. The prey density of ranged from 1,954 - 3,845, 1,929-6,460 and 4-7 individuals/ml for *Chaetoceros* sp., *Skeletonema* sp. and rotifers, respectively. The microphytoplankton chosen for the feeding

experiment were one of the dominant groups, Bacillariophyceae and Cyanophyceae, in the Pak Phanang Estuary. Food was provided manually from the side of the pond. Feeding preference experiments were calculated from number of food items before feeding (0 hr) and after feeding (24 hr) by Manly's Alpha Preference Index (Krebs, 1989) the formula on estimating alpha is:

$$\alpha_i = \frac{\log P_i}{\sum_{j=1}^m P_j}$$

Where α_i = Manly's alpha (Preference index) for prey type i ; P_i , P_j = Proportion of prey i or j remaining at the end of the experiment ($i = 1, 2, 3, \dots, m$; $j = 1, 2, 3, \dots, m$) = e_i/n_i ; e_i = Number of prey type i remaining uneaten at end of experiment; n_i = Initial number of prey type i in experiment; m = Number of prey types.

The feeding behavior of spotted scats in all developmental stages was also observed during feeding preference experiments. Detailed results of these feeding behavior observations will not be discussed in this paper, but only those relevant observations will be mentioned. A digestion efficiency experiment was also conducted by using spotted scats in the three size categories. Two experimental tanks of 12 litres volume with more than 50 fish larvae each were designated for the rearing of fish larvae. Three tanks of 12 and 24 litres were used for juvenile and adult fish, respectively, in order to allow sufficient space for the fish. Twenty juveniles and five adult fish were used in each rearing tank using filtered seawater at a salinity of 20 psu and an adequate oxygen supply. Water quality was monitored and a daily change of water was provided. Fish were starved for one day before the

experiment. Each rearing tank was provided with different food. Two microphytoplankton, *Chaetoceros* sp. and *Skeletonema* sp., were used in the fish larval experiment. In juvenile and adult experiments, rotifers were used as food in addition to the microphytoplankton. The experiments were carried out over four weeks. Feces were collected daily. Four grams dry weight of the food used for feeding and the fish feces were analyzed by proximate analysis (Association of Official Agricultural Chemists, 1990), the results of which were used to calculate the gross energy (GE), apparently digested energy (DE) and apparent digestibility coefficient of energy (ADC) (National Research Council, 1993).

RESULTS

Distribution of spotted scats

The spotted scat, *Scatophagus argus*, is one of the true resident species in the Pak Phanang Estuary. The total catches of larvae were 229 individuals/100 m³. The highest density of fish larvae was recorded in the 27 year old mangrove plantation (station PP2) during the high salinity period (Fig. 2a). The high abundance of spotted scat larvae in the Pak Phanang mangrove forest demonstrated the importance of the mangrove as a nursery ground. The diversity of microhabitats, formed by the mangrove plant structure, and food sources, including microphytoplankton and zooplankton, in the mangrove forest were used for shelter and food sources of spotted scat larvae, whilst juvenile spotted scats were distributed in the mangrove forest and utilized it as habitat and feeding ground. They seem to often seek a particular microhabitat to reside within (Shinnaka et al., 2007). The total number of juvenile fish recorded was 206 individuals, whilst the

highest density was recorded at the 37 year old mangrove plantation (PP1) during the high salinity period (Fig. 2b). Adult spotted scats were distributed in the estuarine waterway, where the total number of adult fish caught was 224 individuals, but they were mostly distributed in the Pak Phanang

Bay and coastal area (Fig. 2b). However, they often perform feeding-based migration trips into the mangrove habitats where they preferably or exclusively forage. They also migrate into the mangrove areas during the breeding season for spawning.

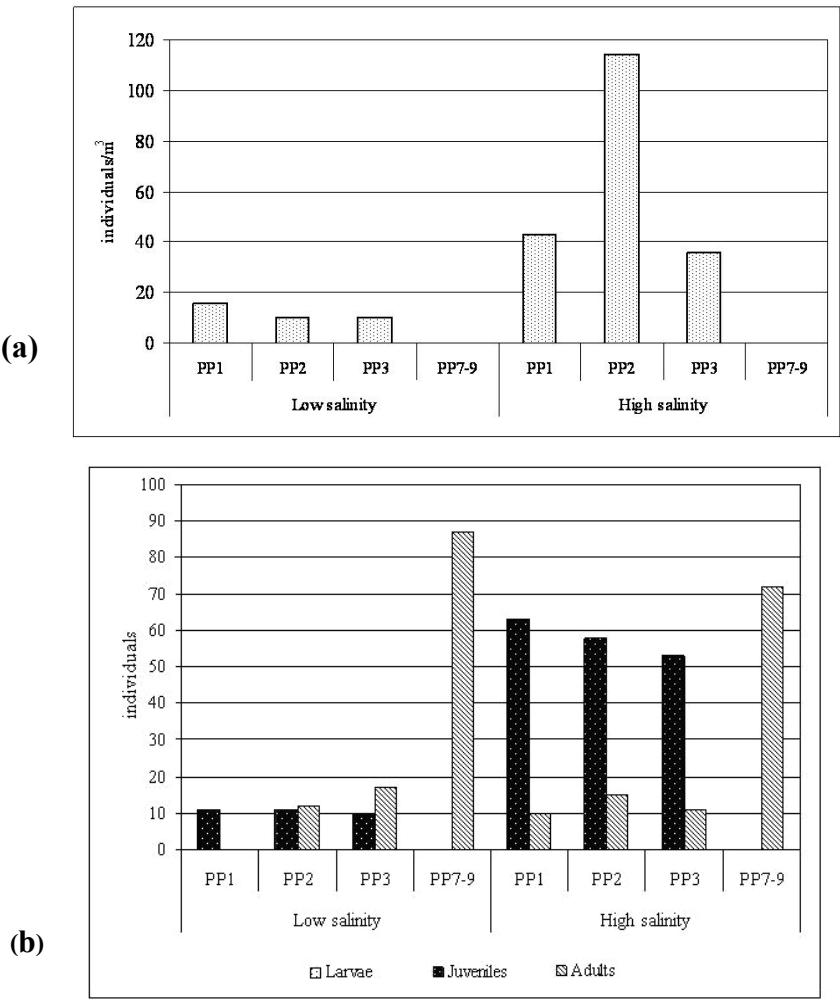


FIGURE 2. Distribution pattern of (a) larval spotted scats and (b) juveniles and adults during low and high salinity in Pak Phanang Estuary, Nakhon Si Thammarat Province, Thailand.

TABLE 1. List of major food items identified in spotted scat stomachs caught at different salinities in mangrove plantations and estuarine waterways, and the index of relative importance (IRI) value of each food category.

Food items	Larvae		Juveniles		Adults			
	Mangrove plantations		Mangrove plantations		Mangrove plantations		Estuarine waterways	
	Low salinity	High salinity	Low salinity	High salinity	Low salinity	High salinity	Low salinity	High salinity
	IRI	IRI	IRI	IRI	IRI	IRI	IRI	IRI
Cyanophyceae	3221	4692	3791	3350	2311	3624	10.8	2674
Chlorophyceae	-	0.38	0.001	3.7	24.4	-	-	-
Eluglenophyceae	0.03	0.013	-	0.000	-	-	-	-
Bacillariophyceae	10265	9243	9622	11272	10610	8240	74.2	8085
Dinophyceae	3.4	6.5	1.4	1.5	-	-	-	-
Dictyochophyceae	-	0.003	-	-	-	-	-	-
Protozoa	1270	1316	874	896	633	659	11701	3694
Zooplankton	819	817	1002	1060	1295	267	5.6	420
Benthos	64.3	71.2	117	86.4	272	514	66.4	2730
Insect	-	-	0.647	0.083	-	0.07	-	-
Detritus	390	801	2403	1346	1024	5354	16.1	2397

Index of relative importance, feeding behavior preference and digestibility

Microphytoplankton were the predominant food items in spotted scat larvae in both low and high salinity periods in mangrove forests. The average density of micro-phytoplankton ranged from 6.51×10^3 to 1.59×10^5 cells/l and 1.28×10^3 to 3.45×10^4 cells/l from in the low and high salinity periods, respectively. The most dominant and most frequent were the Bacillariophyceae and Cyanophyceae, particularly the genera *Nitzschia*, *Gyrosigma/Pleurosigma* and *Oscillatoria*, respectively. Thus, Bacillariophyceae, Pennate diatoms, and Cyanophyceae, *Oscillatoria* spp., were found at 66 and ~55% and at ~21 and 28% of total food items in the low and high salinity periods, respectively (Table 1, Figs. 3 & 4a,b). There was no significant

difference in larval food items between low and high salinity. The results of the food preference experiment for spotted scat larvae showed that the diatom *Chaetoceros* sp., was the preferred food source of optimal prey size and high density (2,435 cells/ml) when compared to *Skeletonema* sp. in a direct competition (choice) assay (α *Chaetoceros* sp. = 0.888, α *Skeletonema* sp. = 0.112). Fish larvae foraged primarily on *Chaetoceros* sp. that fall within the preferred size range (6 - 24 μ m) governed by the mouth size of 1.2 mm for these larvae, in agreement with the observation of food items in the stomach of larvae. First feeding in most marine fish larvae is usually on organisms < 100 μ m in width, which tend to be 1 - 3% of larval length. The prey consumed by fish larvae broaden as larval size increases. The feeding

behavior of spotted scat larvae closely fitted a type 3 Holling's Functional Response, with a sigmoid exploitation feeding curve and an

increase in consumption, over a threshold density for *Chaetoceros* sp. of 1,929 cells/ml. and *Skeletonema* sp. of 2,095 cells/ml.

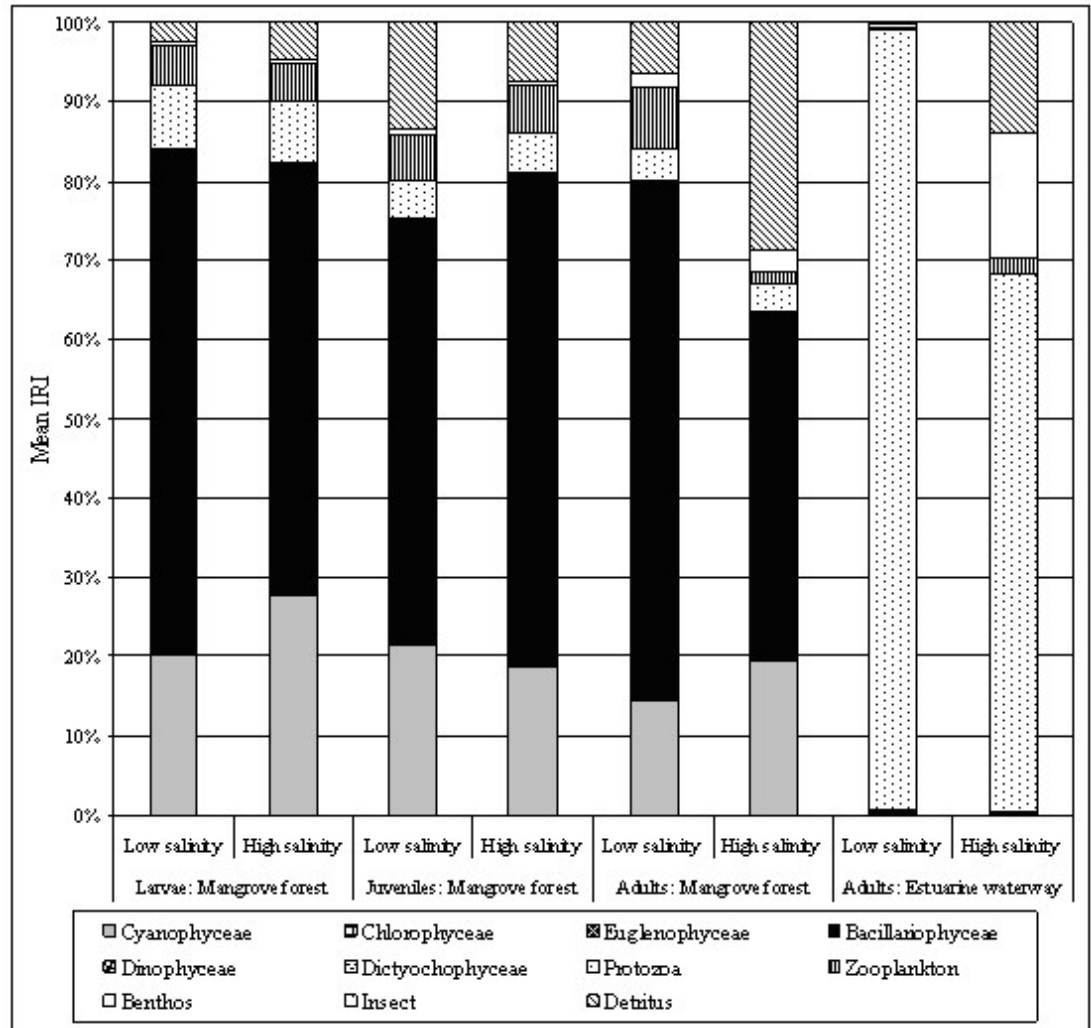


FIGURE 3. Comparative food items in three broad developmental stages of spotted scat in Pak Phanang Estuary, Nakhon Si Thammarat Province

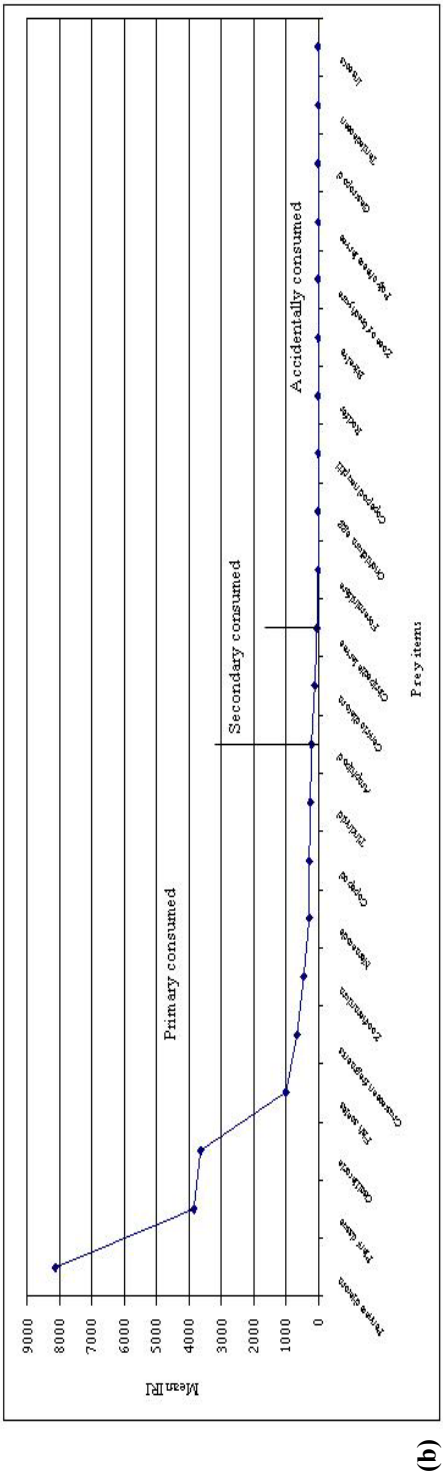
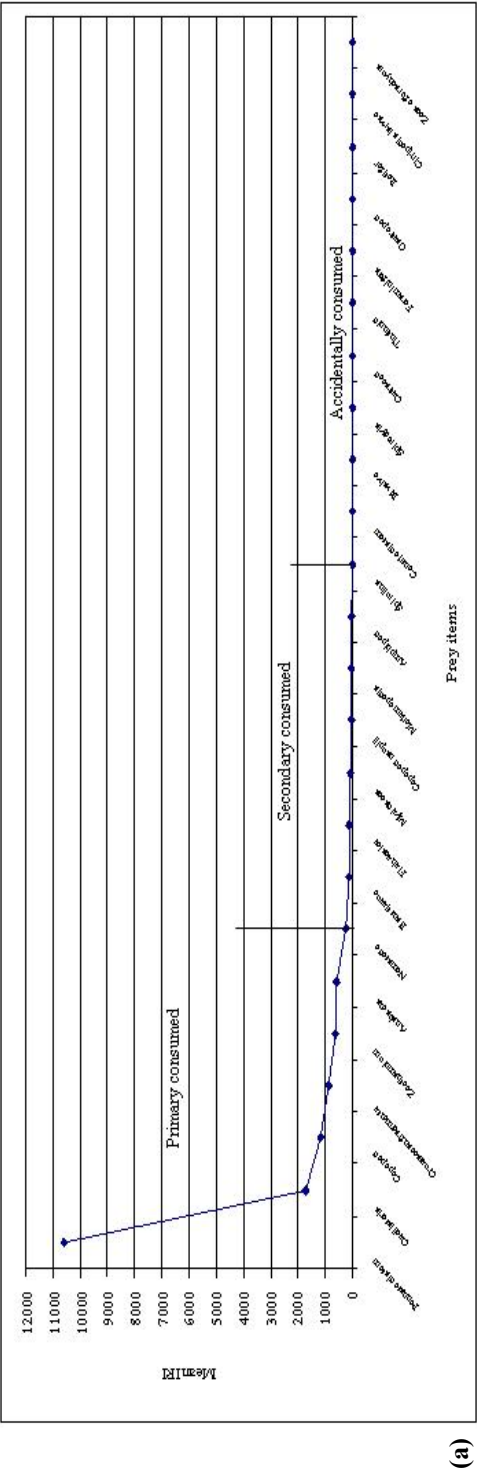


FIGURE 6. Diet preferences of adult spotted seats in mangrove forests during (a) low salinity and (b) high salinity in Pak Phanang Estuary, Nakhon Si Thammarat Province, Thailand.

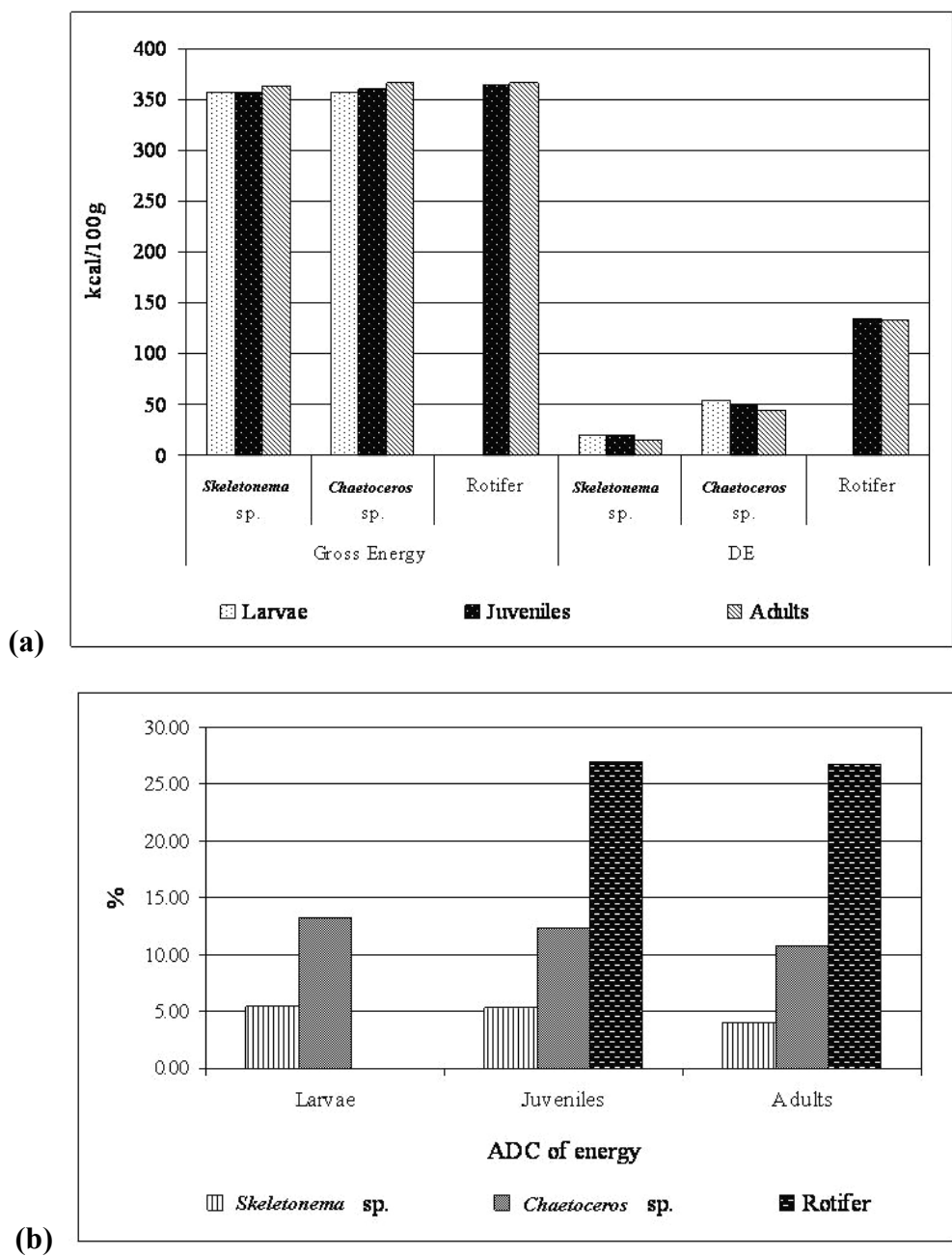


FIGURE 8. (a) Gross energy, apparently digested energy (DE) and (b) apparent digestibility coefficient of energy (ADC of energy) of prey items and feces of spotted scats in three stages.

In juvenile spotted scats, micro-phytoplankton was also the dominant food item in the stomach contents with protozoan, zooplankton, benthos, insect and detritus found in lesser amounts. During both the low and high salinity periods in mangrove forests, the major food item was pennate diatoms at approximately 54 and 63% of the total food items, respectively. *Oscillatoria* spp. was the second most common prey item at 19 - 21% in the low and high salinity periods, whilst the third most important component was detritus at between 13.5 and 7.5% in the low and high salinity periods, respectively. The numerical similarity between prey items in the juvenile fish stomachs between the low and high salinity periods was repeated for all minor prey items (Table 1, Figs. 3 & 5a,b). From the *in vitro* food preference experiment in juvenile spotted scats, the diatom, *Chaetoceros* sp., was the preferred food source of optimal prey size and high density (α *Chaetoceros* sp. = 0.585), compared to *Skeletonema* sp. and rotifers (α *Skeletonema* sp. = 0.266, α rotifer = 0.151). Juveniles selected their food according to the optimal prey size and high density prey similar to spotted scat larvae. Indeed, the feeding behavior of juveniles also conformed to a type 3 Holling's Functional Response with the threshold density for *Chaetoceros* sp. of 3,845 cells/ml. and for *Skeletonema* sp. of 2,916 cells/ml. They focused most of their attention on more abundant foods, switching to less common food only when it exceeded some threshold density. Moreover, they required some learning to exploit food at a maximum rate. At low food densities, as in rotifers at a threshold density of five individuals/ml., they do not have sufficient exposure to a particular food item to fully develop their searching and handling skills.

Within the mangrove forest, Bacillariophyceae, *Nitzschia* spp. and *Pleurosigma*/*Gyrosigma* spp., were the major prey items in adult spotted scats in the low and high salinity periods at 63% and 44% of total food contents, respectively, and were chosen as the first diet preference in both periods. Numerical differences in the relative diet composition of adult scats between the low and high salinity periods were noted in the mangrove forests. Detritus, was the next most common food item during the high salinity period (29%), whilst in the low salinity period Cyanophyceae (14%) was the next most common food. During the high salinity, Cyanophyceae (19%) was the third most abundant component of the spotted scat diet.

In the estuarine waters, in contrast, the diet in adult spotted scats was mainly comprised of protozoa, *Zoothamnium* spp. in the low salinity period, accounting for over 98% of the total food contents. In contrast, during in the high salinity period, the protozoan only accounted for 18% of the much more diverse diet with Bacillario-phyceae being the commonest component (40%) and Cyanophyceae, benthos and detritus all being well represented ranging from 12 - 14% of the total diet each. Adult spotted scats revealed flexibility in their feeding ecology being omnivores and opportunistic feeders. In addition to micro-phytoplankton, zooplankton, benthos and detritus were also chosen by adult spotted scats in both salinity periods in mangrove forests and estuarine waterways (Table 1, Figs. 3, 6a,b & 7a,b). In the *in vitro* selection experiments, diet selection by adult spotted scats depended on the density of the more profitable prey. Adult spotted scats selected *Skeletonema* sp., *Chaetoceros* sp. and rotifer respectively. *Skeletonema* sp. (α *Skeletonema* sp. = 0.613)

was selected due to their chain-like morphology that makes them easily encountered and caught. *Chaetoceros* sp. and rotifers were chosen next (α *Chaetoceros* sp. = 0.273, α rotifer = 0.114). Furthermore, the density of *Skeletonema* sp. was highest as compared to other prey items. Adult spotted scat feeding behavior was consistent with a type 1 Holling's Functional Response where their consumption increased linearly as food density increased up to a maximum feeding rate. Type 1 functional responses are typical for consumers that require little or no time to process their food. The threshold density for *Chaetoceros* sp. was 1,945 cells/ml, for *Skeletonema* sp. was 2,455 cells/ml and for rotifers was four individuals/ml.

The digestibility of any food consumption by fish must be determined by the balance between the energy gain from the food and the energy expending on digestion (Xie, 1999). Generally, digestible energy requirements of fish range from 233 to 410 kcal/100g. diet depending on species and dietary protein levels (National Research Council, 1993). The larvae gained more energy from *Chaetoceros* sp. at 54.25 kcal/100g. (13.17%) compared to *Skeletonema* sp. at 20.34 kcal/100g (5.38%), as revealed from their digestion efficiency (Fig. 8a,b). Apparently digested energy (DE) was the highest in rotifers digested by juveniles and adults. Of the two micro-phytoplankton, *Chaetoceros* sp. had the highest digestion efficiency in all stages of fish.

Spotted scats thus showed a likely niche shift in food items. Although micro-phytoplankton remained the dominant food item in spotted scats of all three developmental stages in the mangrove plantations, they decreased in total proportion of the diet from ~83% in larvae to 78% and 71% in juveniles and adults, respectively. Likewise, protozoa were the highest in larvae

(7.8%), declining in juveniles (4.9%) and adults (3.71%) to become a minor adult diet component. In contrast, benthos and detritus increased in total diet composition from 3.6% in larvae, to 10.5% and 18.3% in juveniles and adults, respectively (Fig. 9).

Morphological adaptations for feeding in spotted scats

The relationship of the feeding structure morphology and diverse food items with feeding preference supported that spotted scats display an ontogenetic niche shift. Larval stages begin feeding on micro-phytoplankton in the water column. They are able to ingest prey of a similar or smaller size to their mouth gape, which varies from 0.11 - 0.13 cm (average $\pm$ 1SD is 0.12 ± 0.001 cm). The ingestion in spotted scat fish larvae is, therefore, limited by the mouth gape size. Teeth were mainly of the villiform type, small and slender forming a band, and appearing in 1 - 2 rows on the upper and lower jaw. Short gill rakers were present and varied from 13 - 16 pieces. Their stomach appeared U-shaped with 7 - 14 pieces of pyloric caeca, and the intestine: standard body length ratio varied from 0.59 - 1.88 (Table 2).

Juvenile fish, showed a transitional stage feeding both in the water column and the mangrove floor, and fed on resuspended benthic diatoms, zooplankton, benthos and detritus. Juveniles have a subterminal mouth with a gape width that varies from 0.17 - 0.28 cm (0.19 ± 0.004 cm). Teeth were mainly villiform type and present in up to 5 - 6 rows, but ciliiform teeth on the tongue for crushing or grinding food are present. Short gill rakers (15 - 20 pieces) are present. The U-shaped stomach of juvenile spotted scats could contain a relatively large volume of food to digest, and the number of pyloric caeca was increased, relative to that in larval fish, to 11

- 22 pieces, which correlated with the increased length of the juvenile fish. The intestine: standard body length ratio was also larger than that of larval fish, varying from 0.63 - 4.29 (Table 2).

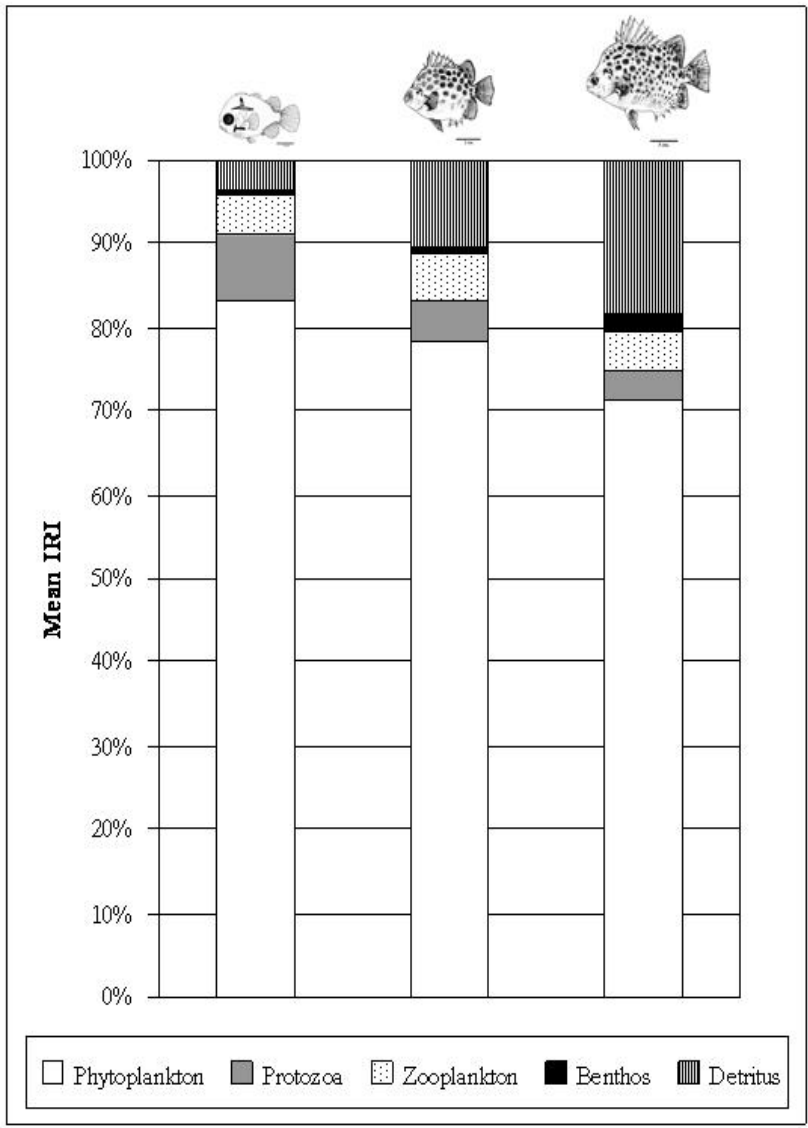
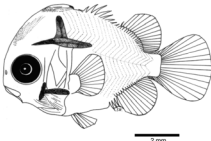
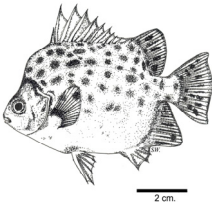
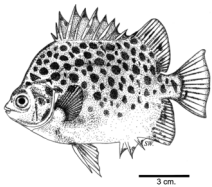
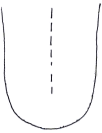
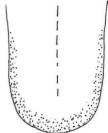
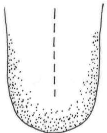
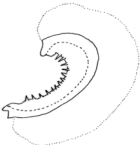
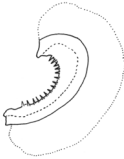


FIGURE 9. Ontogenetic niche shift in spotted scats in mangrove forests at Pak Phanang Estuary, Nakhon Si Thammarat Province, Thailand. Data are based upon 60 samples per category.

TABLE 2. Comparative measurement of feeding structure morphology of spotted scats. Data are shown as either the mean (± 1 SEM) or the range (lower – upper limits) and are derived from 50 individuals each.

Structure morphology	Larvae	Juveniles	Adults
	(Mean $\pm$ SE)	(Mean $\pm$ SE)	(Mean $\pm$ SE)
Total length (TL) (cm.)	1.17 - 1.84	2.05 - 7.44	8.50 - 20.00
Average total length (cm.)	1.49 $\pm$ 0.02	4.41 $\pm$ 0.23	11.18 $\pm$ 0.35
Standard length (SL) (cm.)	1.11 $\pm$ 0.01	3.41 $\pm$ 0.18	8.89 $\pm$ 0.28
Body depth (BD) (cm.)	0.72 $\pm$ 0.01	2.24 $\pm$ 0.12	5.37 $\pm$ 0.14
Head length (HL) (cm.)	0.55 $\pm$ 0.01	1.41 $\pm$ 0.07	3.08 $\pm$ 0.07
Width of the mouth gape (WID) (cm.)	0.12 $\pm$ 0.001	0.19 $\pm$ 0.004	0.61 $\pm$ 0.01
Intestine length (cm.)	1.51 $\pm$ 0.06	9.35 $\pm$ 0.70	28.31 $\pm$ 0.78
Wet weight (g.)	0.10 $\pm$ 0.003	3.49 $\pm$ 0.43	44.54 $\pm$ 4.06
Head length/body depth	0.65 - 0.86	0.57 - 0.75	0.50 - 1.19
Head length/total length	0.34 - 0.42	0.29 - 0.37	0.20 - 0.31
Body depth/total length	0.44 - 0.52	0.47 - 0.55	0.17 - 0.54
Total length/body depth	1.92 - 2.25	1.82 - 2.13	1.85 - 5.95
Intestine length/total length	0.44 - 1.42	0.49 - 3.37	1.83 - 3.37
Intestine length/standard length	0.59 - 1.88	0.63 - 4.29	2.31 - 4.17
Number of gill rakers	15.00 $\pm$ 0.13	16.98 $\pm$ 0.15	17.00 $\pm$ 0.21
Number of pyloric caeca	10.52 $\pm$ 0.26	15.74 $\pm$ 0.29	16.10 $\pm$ 0.28

TABLE 3. Comparative study on the feeding structure morphology of spotted scats

Characteristic	Larvae	Juveniles	Adults
Body form			
Mouth position (subterminal mouth)			
Teeth on upper jaw	 Villiform teeth 1-2 rows	 Villiform teeth 4-5 rows	 Villiform teeth 5-6 rows
Teeth on lower jaw	 Villiform teeth 1-2 rows	 Villiform teeth 4-5 rows	 Villiform teeth 6-7 rows
Teeth on tongue	 Not found	 Ciliiform teeth	 Ciliiform teeth
Gill rakers			
Shape of stomach	 U-shape	 U-shape	 U-shape

Adult spotted scats have a subterminal mouth that supports a benthic feeding habit. The width of mouth gape varied from 0.40 - 0.80 cm with an average mouth gape of 0.61 ± 0.01 cm. Teeth were mainly of the villiform type but increased to 6 - 7 rows present in adult spotted scats whilst the number of ciliiform teeth present on the tongue also increased. Short gill rakers were present (13 - 20 pieces). The stomach appeared U-shaped with 10 - 20 pieces of pyloric caeca. The intestine: standard body length ratio varied from 2.31 - 4.17 (Table 2). Thus, their morphology showed a good relationship with the food being utilized for all developmental stages. Adults being omnivores and opportunistic feeders mainly fed in the midwater level and mangrove floor, and have the most diversified food items in their diet, which ranges from microphytoplankton, protozoan, zooplankton, benthos and detritus. The latter two food items greatly increased in adult diets. In addition, organic detritus was found in the stomach contents indicating that spotted scats feed on microphytoplankton and plant organic detritus. The results relate to the high organic detritus in the form of forest biomass in the mangrove plantations of Pak Phanang Estuary.

Spotted scats showed a niche shift in relation to the change in food selection. Ontogenetic differences in feeding habits of spotted scats have resulted from increases in the mouth gape size, changing numbers of gill rakers, jaw teeth and development of the digestive system (Tables 2 and 3). The mouth gape increases in size from 0.12 cm in larvae to 0.61 cm in adults allowing a diet change from exclusively on microphytoplankton in larvae to inclusively with larger prey items in the benthos, such as polychaetes and tanaidacean.

Accordingly, the rows of teeth increased from 1 - 2 rows of the upper and lower jaw in larvae to 6 - 7 rows in adults, and ciliiform teeth are found from juvenile stages onwards increasing in numbers to adults. Therefore, they have an increased ability to catch and chew prey. Gill rakers varied in number from 13 - 20 increasing the ability to filter and collect food items. The enlarged stomach in large (adult) fish show the large consumption volume of food to digest. In addition, the intestine: standard body length ratio increased from 0.6 - 1.9 in larvae to 2.3 - 4.2 in adults, showing an increasing ability for high digestion and assimilation. Therefore, the variations in the component of food items were related to the feeding morphology structure in each stage.

DISCUSSION AND CONCLUSIONS

The distribution pattern of the spotted scat community clearly showed the high abundance of larvae in Pak Phanang mangrove forest, demonstrating the important of mangroves for nursery grounds and food sources for this species. This finding agrees with those from other tropical mangrove forests and estuaries, such as the mangrove estuary of the Tanshui River Estuary, Taiwan (Tzeng and Wang, 1992), a mangrove forest in northern Australia (Vance et al., 1996) and Negombo Estuary, Sri Lanka (Pinto and Punchihewa, 1996). As fish grow a shift in habitat from mangroves to adjacent mudflats is a response to changes in diet, foraging efficiency and vulnerability to predators (Wootton, 1992; Whitfield, 1998; Blaber, 2000). *S. argus* of a total length of 12 - 85 mm was the most common size collected in mangrove forests at this study site and

were often associated with prop roots and pneumatophores which offer shelter from predation (Shinnaka et al., 2007). This is in agreement with other findings at Trang Province (Tongnunui et al., 2002; Ikejima et al., 2003), Klong Ngao, Ranong Biosphere Reserve (Macintosh et al., 2002), a shallow semi-enclosed estuarine Pattani Bay, Pattani Province (Hajisamae et al., 2006) and a mangrove plantation and mudflat at Pak Phanang Bay, Nakhon Si Thammarat Province (Paphavasit et al., 2004), Pagbilao mangrove forest, Philippines (Pinto, 1987), Australian mangrove areas (Morton, 1990) and in Fisherman Island mangrove forest (Laegdsgaard and Johnson, 1995). Adult spotted scats at this study site were mostly distributed in the Bay (Pak Phanang) and coastal area rather than the mangrove forest itself, which is again consistent with reports for other estuaries, such as Tsengwen Estuary (Kuo and Shao, 1999), Fitzroy River (Morgan et al., 2002) and the Kakadu region, northern Australia (Allen et al., 2002). Few adults were distributed in the mangrove forests due to the shallow and turbid water. Turbidity limits fish vision, which can interfere with social behavior, foraging (Gregory and Northcote, 1993; Vogel and Beauchamp, 1999) and predator avoidance (Meager et al., 2006).

Spotted scats demonstrated clear ontogenetic changes that reflect their morphological changes. Ontogenetic differences in the feeding habits of spotted scats have resulted from changes, including the increasing mouth gape size, changing numbers of gill rakers, number and type of jaw and tongue teeth and development of the digestive system, allowing a change in diet from only microphytoplankton to additionally include increasing levels of larger sized prey in the benthos such as polychaetes and tanaidacean. However,

spotted scats selected optimal prey size with respect to their mouth gape. The main prey items found in larvae were microphytoplankton, protozoan and zooplankton, which have an average size less than the width of the mouth gape of the larvae (0.11 - 0.14 mm), juveniles (0.15 - 0.32 mm) and adults (0.4 - 0.8 mm). The most common prey items were *Pleurosigma* spp., average size 117.71 μ m in length and 20.68 μ m in width, and *Nitzschia* spp., 67.56 μ m and 10.63 μ m in length and width, respectively. The size measurement of these microphytoplankton were enumerated from 30 cells each. Zooplankton such as rotifers had an average size of 100 μ m width, whilst cirripedia larvae had a maximum size of 0.9 mm. Benthos, such as foraminifera, had an average size of 150 μ m - 1 mm in width and nematodes averages 200 μ m. A rapid increase in the jaw and gape size during the first few days helps the larvae to increase the size of food and ingestion (Olsen et al., 2000), and, thus, the proportion of total food types available. consequentially, the actual timing of diet switches usually relates to juveniles becoming adults, where mouth gape size is an important determinant of food size (Peterson and McIntyre, 1998). The optimal food particle size is expected to change during ontogenetic development. Prey sizes are often found to be selected to be close to the optimum in size.

At this stage the rows of teeth increased from 1 - 2 on the upper and lower jaw in larvae to 6 - 7 in adults, which, along with ciliiform teeth being found from juvenile stages onwards, implies that the food items could increasingly be those that have to be captured. That the teeth of spotted scats are villiform for crushing or grinding seems to correlate with their stomach contents being mainly microphytoplankton, a trend which has also been seen in other omnivorous and

herbivorous fish, i.e. juvenile *Lates calcarifer* (Food and Agriculture Organization of the United Nations, 1988). However, this would not adequately explain the increase in the number of villiform teeth observed in adults, which instead may also support the herbivorous grazing nature of adult scats (Barry and Fast, 1988). Whilst the gill rakers varied in number from 13 - 20, and thus the ability to filter and collect food items, the reduction in the number of gill rakers was related to food items. For example, members of the Syngnathidae and Fistulariidae have totally degenerate gill rakers, yet their chief food components are plankton and benthic diatoms (Kramer and Bryant, 1995A). Such a reduction is a potential advantage for species that live close to the substrate and stir up mud. If the gill raker slits closed tightly, the suspended particles would be swallowed, whereas instead, they were eliminated more easily.

Spotted scats have a U-shaped stomach which again is related to the bulk of food items that are consumed per unit time, being largest in species that consume large, single food items or sporadically eat high volumes of food, whereas the stomach is smaller in continually feeding planktivores (Kramer and Bryant, 1995B). The pyloric caeca are an important site for lipid digestion and are an adaptation to increase the absorption surface area (Sire et al., 1981, Kramer and Bryant, 1995B), the nutrient uptake capacity of the gut and allow optimal digestion of diversified food items. As spotted scat fish develop, the number of pyloric caeca also increase and, with the inner wall of the pyloric caeca extensively folded with the presence of large numbers of villi of mucosa (Rust, 2002), will result in an increased absorption rate. In addition, the ratio of intestine: standard length increased in larvae to adults from 0.59 - 4.29, which is within the observed average

of 2.88 (range 2.59 - 2.93) in detritus feeding scats found in mangrove swamps in Vietnam (Phuang et al., 2004) and 3.0 for herbivorous adult scats in the Philippines (Barry and Fast, 1988). Based upon the relative intestine lengths of 0.5 - 2.4 for carnivores, 0.8 - 5 for omnivores, and 2 - 21 for herbivores (Rust, 2002), this ratio for spotted scats is not inconsistent with the suggestion from their stomach contents that although omnivorous, they are increasingly herbivorous with age. In the case here they feed principally on phytoplankton but with larger fish consuming proportionally less phytoplankton and protozoa and more benthos and detritus, whilst elsewhere this maybe algae (Barry and Fast, 1988) or seagrasses. Therefore, the variations in the components of food, including microphytoplankton, protozoan, zooplankton, benthos and detritus, were not only related to the diet availability, but also to the feeding morphology structure in each of the three broad developmental stages examined here. Certainly this trend, including the significant increase in benthos and detritus in the adult diets, would benefit from further analysis of both narrower developmental stages and from different habitats, and thus available prey species and relative abundances.

Pak Phanang mangrove plantations also supported coastal fertility in terms of food sources. Microphytoplankton, diatoms and cyanobacteria were most dominant groups (Piumsomboon et al., 2004, Wongchinawit et al., 2007). Zooplankton diversity was dominated by arthropod crustaceans in both the holoplankton and meroplankton. The high organic content in the sediment corresponded to the high organic detritus in terms of underground, pneumatophore and seedling biomass in the mangrove plantations as compared to the natural mangrove forests. Dense tree canopy in the mangrove

plantations contributed to the high organic detritus in terms of forest biomass as the mangrove plantation aged. These organic detritus in turn will become important food sources for aquatic species. However, although a low diversity of benthos has been recorded in the mangrove plantations of Pak Phanang Estuary (Paphavasit et al., 2004), this was due to the hypoxia condition in the Pak Phanang Bay and in the mangrove forests. The fish avoided this unsuitable condition by feeding mainly in the water column. They have the ability to take advantage of the most profitable food source at a particular time.

Spotted scats from this area showed reasonable flexibility in their feeding ecology. They switch from one type of food to another as the relative abundance of the prey types changes and selected food items that maximize fitness and energy gain. The ontogenetic changes related with optimal foraging theory on the presence of food items in diet. Prey density is the major factor for the selection of food in all stages. As the density of prey increases, the number attacked increases. Spotted scats also spent some of the available time in capture and handling prey. Density of prey items and prey capture in spotted scats follow a type 3 Holling's Functional Response in larvae and juveniles which focus most of their attention on more abundant foods, switching to less common food only when it exceeds some threshold density.

In the larval stage, they predominantly feed on microphytoplankton in the water column. The prey diversity consumed by fish larvae broadens as the larval size increases. Juveniles are transition stages from feeding in the water column to the substrata taking resuspended benthic diatoms, zooplankton and especially meroplankton rather than holoplankton, benthos and detritus. Adults

feed on substrata taking the whole prey items, including the benthic diatoms, benthos and detritus. The latter two food items are greatly increased in adult diets. Adult spotted scats show a Type 1 feeding response where their feeding rate increases linearly as the food density increases and then levels off abruptly at some maximum feeding rate. Thus spotted scats, at least from this area, showed flexibility in their feeding ecology. Being omnivores and opportunistic feeders, their diets range from microphytoplankton, protozoans, zooplankton, benthos and detritus. Spotted scats have feeding adaptation and flexibility in food item responding to changes in the availability, relative abundance or profitability of potential prey. Prey items were more diversified during high salinity periods. During the low salinity period, adult spotted scats in estuarine waterways feed predominantly on *Zoothamnium* spp. The presence of a food item in a diet depends on its availability, its detection by the fish and its selection as food. Selection may depend on the mechanical ability of the fish and profitability of the prey (Wootton, 1999). Spotted scats can select diets on the basis of a high nutritional and energy value to obtain prey profitability. The diatom, *Chaetoceros* sp., is the reliable food source of optimal prey size and high density for larvae and juveniles, but diet selection in adult spotted scat depends on the density of the more profitable prey. *Skeletonema* sp. was the first choice, *Chaetoceros* sp. and rotifers were chosen next. Thus, our study supports that the ontogenetic differences in feeding habits have resulted from acquiring high energy diets to accompany growth and changes in the morphology of feeding structure and digestive system.

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