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Original Article

Food partitioning of two co-occurring Terapontid fishes, *Terapon jarbua* and *Pelates quadrilineatus*, in coastal areas of Trang Province, Southern Thailand

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Abstract

This study clearly demonstrates that *Terapon jarbua* and *Pelates quadrilineatus* showed obvious food partitioning by their dietary ontogenetic changes. The larvae of both species fed mainly on the calanoid copepods. Juveniles of *T. jarbua* shifted to feed mainly on harpacticoid copepods, crabs and fish scales. Juveniles of *P. quadrilineatus* shifted to fed mainly on harpacticoid copepods and *Lucifer* spp. Adult fish shifted to fed on larger prey size. Adult*T. jarbua* fed mainly on fish and fish scales while adult of *P. quadrilineatus* fed mainly on large benthic animals, amphipods, bivalves, hermit crabs and polychaetes. The study on morphology and feeding structure development indicated that, the development of mouth, jaw, teeth, gill raker and intestinal length were important ontogeneticchange in the diet of fish. The ontogenetic change in the diet was the important strategies to reduce competition between these two coexisting species in coastal area of Trang Province.

Keywords: food partitioning, ontogenetic dietary shift, *Pelates quadrilineatus*, *Terapon jarbua*, Trang Province

1. Introduction

Several studies demonstrated the importance of mangrove and seagrass beds in the tropical coastal ecosystem as feeding grounds for fishes (Hajisamae, Chou, & Ibrahim, 2003; Hajisamae & Ibrahim, 2008; Horinouchi, 2007; Horinouchi *et al.*, 2009, 2012; Ikejima, Thongnunui, Medej, & Taniuchi, 2003; Laegdsgaard & Johnson, 2001;). Habitat type is also one of the important factors influencing the feeding strategy of a species by determining foraging opportunities. A fish 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, but better capture opportunity. A fish may also choose among different habitats that provide different prey diversity and abundance to reduce food competition (Crowder & Cooper, 1982).

Terapontid fishes, *Terapon jarbua* and *Pelates quadrilineatus*, were found to coexist in the coastal area of Trang Province, southern Thailand. They are carnivorous fish feeding on the wide range of food items from both the water column and benthic substrates such as insect larvae, zoo-plankton, fish, zoobenthos and organic matter (Davis *et al.*, 2011; Davis, Pusey, & Pearson, 2012a; Hajisamae *et al.*, 2003; Hajisamae & Ibrahim, 2008; Horinouchi *et al.*, 2012; Kanou, Sano, & Kohno, 2004; Kulbicki*et al.*, 2005; Lugendo, Nagelkerken, Kruitwagen, Velde, & Mgaya, 2007; Nakane, Suda, & Sano, 2011; Rao & Prasad, 2002). Resource partitioning in fish distinguished three resource dimensions; the trophic, spatial and temporal dimension, of which trophic dimension was found to be the most important dimension for

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segregating fish species in community. Thus coexistence of species can be obtained through the differentiation of their ecological niches. Food partitioning is the partitioning of food by two or more species or size classes in a single species, in order to utilize the food supply to its fullest extent (Ross, 1986). Food partitioning may be understood as an efficient way to utilize the total food resource in a habitat. The resource may be split up and used by a different age class in a single species, or the resource may be split up to benefit several species (Gerking, 1994). Food partitioning may be the result of different feeding type or different food source in the same habitat. Ontogenetic dietary shift is one of the important processes in food partitioning with the shift of resources during development. During ontogeny, the growing consumers are expected to change their ecological niche with respect to prey type, prey size and habitat type to meet their increasing basic metabolic demands and optimize their ecological foraging performance (Persson, Leonardsson, & Gyllenberg, 1998; Werner & Gilliam, 1984). The actual timing of the switches in diet usually relates to larvae becoming juvenile or juvenile becoming adult (Blaber, 2000). There is often a correlation between feeding structure and trophic role because morphology determines how fish feed. Size-related of morphological change are important in relation to many aspects of the feeding structures of fishes. These include position of mouth, mouth gape, jaw length, number of gill rakers, and dentition and intestinal length (Davis, Bradley, Pusey, & Pearson, 2012b; Davis, Unmack, Pusey, Pearson, & Morgan, 2013; Eggold & Motta, 1992; Mittelbach & Persson, 1998; Stoner & Livingston, 1984; Wainwright & Richard, 1995). Differences in feeding structure morphology may also be the outcome of food partitioning. The result of food partitioning may be the alternative process in reducing competition for fish sharing the same feeding ground (Blaber, 2000). Should this be true, we would expect clear food partitioning of these two co-occurring terapontid fishes, *T. jarbua* and *P. quadrilineatus*, by examined on diet from stomach content analysis and morphological adaptations in feeding structures.

2. Materials and Methods

2.1 Description of study area and sampling period

The study area is partof Sikao Bay, which located in coastal area of Trang Province on the southwest coast of Thailand. Sikao Bay has relatively a short dry season from January to April and the long wet season from May to December. The study area consists of 8 sampling stations as shown in Figure 1 and Table 1. The two terapontid fishes, *T. jarbua* and *P. quadrilineatus* were found distributed among these sampling stations. The samples were collected monthly from January to December 2013. Food source, mainly zooplankton and macrobenthos, were sampled accordingly in each study site.

2.2 Fish collection

In this study, the developmental pattern of *T. jarbua* and *P. quadrilineatus* were divided into 6 development stages as follows: (1) preflexion larvae (*T. jarbua* standard length (SL)= 1.49-3.39 mm; *P. quadrilineatus* SL=1.64-3.49 mm), (2) flexion larvae (*T. jarbua* SL=3.40-3.99 mm; *P. quadrilineatus* SL=3.50-3.99 mm), (3) postflexion larvae (*T. jarbua* SL=4.00-5.79 mm; *P. quadrilineatus* SL=; 4.00-6.09 mm), (4) transforming larvae (*T. jarbua* SL=5.80-23.15 mm; *P. quadrilineatus* SL=6.10-18.23 mm), (5) juvenile (*T. jarbua* SL=23.16-112.99 mm; *P. quadrilineatus* SL=18.24-98.99 mm), and (6) adult (*T. jarbua* SL= 113.00-231.00 mm; *P. quadrilineatus* SL= 99.00-149.00 mm) (Yoknoi, 2016).

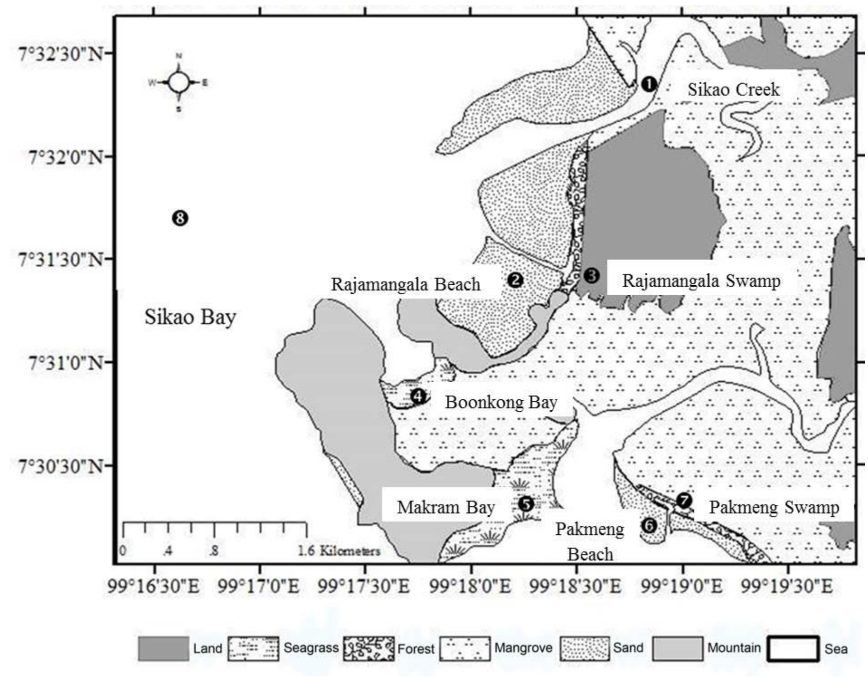

Figure 1. Study area located in Sikao bay of Trang Province on the southwest coast of Thailand.

Table 1. Description of characteristics of each study sites in the coastal area, Trang Province.

	Station	Characteristic		
		Depth (m)	Bottom types	Vegetation
1	Sikao Creek	0.36-1.00	Sand and soft mud	Natural mangrove forest of *Rhizophora apiculata*
2	Rajamangala Beach	0.70-1.15	Sand	Non-vegetated habitat
3	Rajamangala Swamp	0.35-0.75	Sand	Small forest swamp of *Casuarina equisetifalia*, *Rhizophora apiculata* and *Pandanus tectorius*. The swamp dried up during March to April, 2013
4	Boonkong Bay	0.70-1.25	Soft mud	Natural seagrass bed of *Halophila ovalis*, *Cymodocea serrulata*, *Thalassia hemprichii* and *Enhalus acoroides*.
5	Makram Bay	0.43-1.05	Soft mud	Natural seagrass bed of *C. serrulata*, *E. acoroides*, *H.ovalis* and *T.hemprichii*.
6	Pakmeng Beach	0.54-1.20	Sand	Non-vegetated habitat
7	Pakmeng Swamp	0.34-0.80	Sand	Small forest swamp of *Casuarina equisetifalia*, *Rhizophora apiculata* and *Pandanus tectorius*.
8	Offshore area (approximately 2 km from coastline)	10.00-15.00	Sand	Non-vegetated habitat

Preflexion, flexion, and postflexion larvae fish (Planktonic larvae stage) were collected by surface tows using plankton net (0.5 m mouth diameter; 330 µm mesh size) in station 1, 2, 4, 5, 6 and 8. The plankton net was towed by low-speed boat in 3 minutes. Three replicates of planktonic larvae stage samples in station 3 and 5 were filtered using 100 L of seawater with plankton net, due to the shallow depth nature of the habitat. Samples were preserved in 4% neutral formalin. Three replicates of transforming larvae and juvenile fish samples were collected by small seine net with two 5 m long x 0.5 m high wings and 2.5 m long cod end of 2.5 mm stretched mesh. For each tow, the net was initially laid out at the randomly established starting point in order for the net to have the mouth opening at 5 m and pulled by two persons for 20 m. Samples were preserved in 10% neutral formalin. Adult fish were collected from local fisherman using gill net (30 m long, mesh size of 30 mm). Samples were euthanized by rapidly cooling shock and were preserved at 4 ºC.

2.3 Stomach content analysis

Altogether 1,183 specimens of *T. jarbua* and 694 specimens of *P. quadrilineatus* were used for the identification of the major prey item by stomach content analysis. Standard length was measured for each specimen prior to excision of the stomach and viscera from the body cavity. Prey items in the stomach content were identified to the lowest practical taxon. The percentage volume of each small prey item was visually estimated from a 1 mm x 1 mm x 1 mm grid slide under a stereo microscope. The large prey items were estimated from volumetric cylinders. Number, volume and frequency of each prey item in stomach were noted. The main prey item was calculated by Index of relative important (IRI) (Hyslop, 1980).

$$IRI = (\%N + \%V) \times \%F$$

Where IRI represents the index of relative importance of the main prey items, %N represents percentage number abundance as the total number of prey items in all stomach in a sample; %V represents percentage volumetric composition as the total volume of that taxa of prey and %F represents percentage frequency of occurrence based on the number of stomachs in which a prey items was found. A one-way analysis of variance (ANOVA) was used to test for significant difference of the prey item among different stages of terapontids developmental stages.

2.4 Morphological study on feeding structure

Ninety specimens of *T. jarbua* (transforming larvae n=30; juvenile n=30; adult n=30) and 90 specimens of *P. quadrilineatus* (transforming larvae n=30; juvenile n=30; adult n=30) were randomly taken from the catch and used to describe the morphology of feeding structure. Fish measurement such as total length, standard length, body depth, mouth gape, mouth diameter, jaw length, intestinal length were carried out by using a caliper. All measurements were measured down to ±0.001 mm. Morphology of the feeding structure were examined, namely mouth position, teeth, gill raker, shape of stomach, intestine were observed and created illustrations aided by the use of a stereo microscope with camera lucida and optical micrometer attached.

3. Results and Discussion

3.1 Distribution pattern of *Terapon jarbua* and *Pelates quadrilineatus*

Terapon jarbua and *P. quadrilineatus* showed the clear habitat utilization in coastal area of Trang Province among developmental stages. The distribution and abundance of planktonic larvae (preflexion larvae, flexion larvae, and postflexion larvae) and adult, were found only in the offshore area. They utilized this area for feeding and breeding ground. In transforming larvae and juvenile stages, they displayed habitat shift. They showed preferences for different habitat type for feeding and nursery ground. High density of transforming larvae and juveniles of *T. jarbua* were found at mangrove swamp (station 3 and 7) during the wet season. Transforming larvae and juveniles of *P. quadrilineatus* were found in the seagrass beds. Makram bay (station 5) showed the highest density of transforming larvae and juveniles during the dry season.

3.2 Ontogenetic dietary shift and morphological adaptations in feeding structure of *Terapon jarbua*

Ontogenetic dietary shift was evidenced in *T. jarbua*. Main prey items in the stomach of *T. jarbua* in different stages changed as in Figure 2. Minimal seasonal changes in the diet composition of each stage were observed, except in the juveniles that fed more on fish scale in the dry season. Calanoidcopepods was the dominant prey item in the diet of planktonic larval stage. Calanoid copepods was also the major diet component in the transforming larvae with other zooplankton mainly crab zoea and *Lucifer* spp. Harpacticoid copepods played the small part in the diet. The transforming larvae fed mainly in the water column and near bottom. Juveniles of *T. jarbua*fed fed mainly on small benthic organisms on the bottom sediment such as harpacticoid copepods, amphipods and ostracods. Large benthos such as grapsid, hermit crabs, shrimps and isopods were also presented in the diet composition of juveniles. Piscivorous and lepidophagous feeding habits were also evidenced in the juveniles of *T. jarbua.* The feeding habits of piscivores and lepidophagy were more prominent in the adult stage. The prey items were more diversed in the adult *T. jarbua*. Large benthic animals mainly grapsidae crabs, hermit crabs and shrimps also contributed to the diet composition.

The study on morphological adaptations in feeding structure of *T. jarbua* indicated the ontogenetic change in mouth gape and diameter, dentition, gill rakers, stomach and pyloric caeca and intestinal length as in Figure 3. These ontogenetic changes were important in the partition of diet and habitat of this species. The planktonic larvae of *T. jarbua*were found distributed offshore area. Calanoidcopepods was the major prey category offish in this stage. Calanoidcopepods was high density in offshore and made up to 41%of the total zooplankton density. At these stages, the fish larval depend on random feeding because their feeding ability was poor and feeding structure incomplete developed. Size selection is important in larval feeding because the maximum and median lengths of consumed prey were considerably less than fish mouth gape (Gerking, 1994). Therefore, the abundance of calanoid copepods highly affected their feeding ability and survival. In the transforming larvae, a subterminal mouth showing the benthic feeding habitat. Teeth were mainly of villiform type with small teeth forming in bands on the upper and lower jaw. Juveniles and adults of *T. jarbua* had band of villiform teeth with 1 row of conical teeth on the upper and lower law. Adult of *T. jarbua* had sharper and greater numbers of conical teeth than juveniles. Dentition typically provided a reasonable approximation of diet with conical hold teeth corresponding to carnivory (Davis *et al.*, 2012b). The development of teeth on the jaws indicated that the food items must be easily captured. Short gill raker varied from 20-23 slits appeared in the transforming larvae juveniles and adults. As the fish

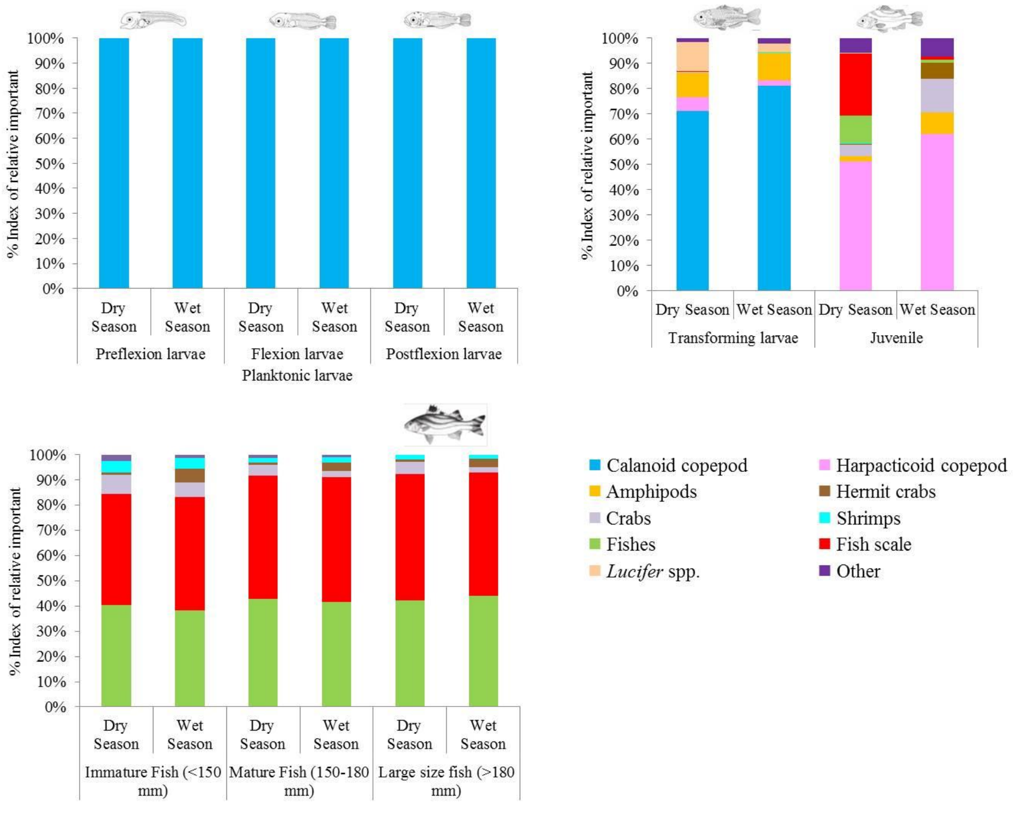

Figure 2. Dietary compositions expressed as percentage of index relative important (%IRI) from stomach content analysis in *Terapon jarbua* (n=1,183) of different developmental stages and seasons from the coastal area of Trang Province.

Figure 3. Comparative studies on feeding structure morphology of *Terapon jarbua* (transforming larvae n=30; juvenile n=30; adult n=30) in coastal area, Trang Province.

consumed zooplankton and small benthos, they seem to pick them up rather than filter them. A reduction number of gill rakers were related to a more benthic feeder. The stomach was V-shape with the pyloric caeca increasing with growth. Number of pyloric caeca ranged from 7 in the transforming larvae to 10 in the juveniles and adults to aid in the digestion of more diverse prey items. The function of pyloric caeca was an adaptation to increase the absorption surface, the nutrient uptake capacity of the gut and allowed to optimize digestion of diverse food items (Rust, 2002). *Terapon jarbua* had the simplest intestinal layout consisted of two-loops (IL/SL < 1.2) throughout the life history. This indicated that this species consume higher proportions of animal prey than plant and/or detrital materials (Davis *et al.*, 2013). The result showed that *T. jarbua* increasingly fed on fish scales from juvenile to adult. Blaber (2000) reported that *T. jarbua* was able to digest the scales, which have a relatively high calorific value. In Figure 2, the large size fish (>180 mm) consumed higher percentage of fish scales in the range of 48.85-50.34 % as compared to the immature fish (<150 mm) of 44.00-45.00 %. The percentage of fish prey also increased with growth. The dietary shift also corresponded to the energy requirement in the mature fish and large size fish. *Terapon jarbua* showed the later shift to piscivory with slow decrease in foraging capacity on non-fish prey with body size. They were more flexible in their resource use (Mittelbach & Perrson, 1998).

3.3 Ontogenetic dietary shift and morphological adaptations in feeding structure of Pelates quadrilineatus

The feeding habit of *P. quadrilineatus* was also carnivores as in *T. jarbua.* Their prey items ranged from zooplankton, small and large benthos and fish scales. Ontogenetic dietary shift was evidenced in *P. quadrilineatus*as in Figure 4. Calanoidcopepods was the dominant prey item in

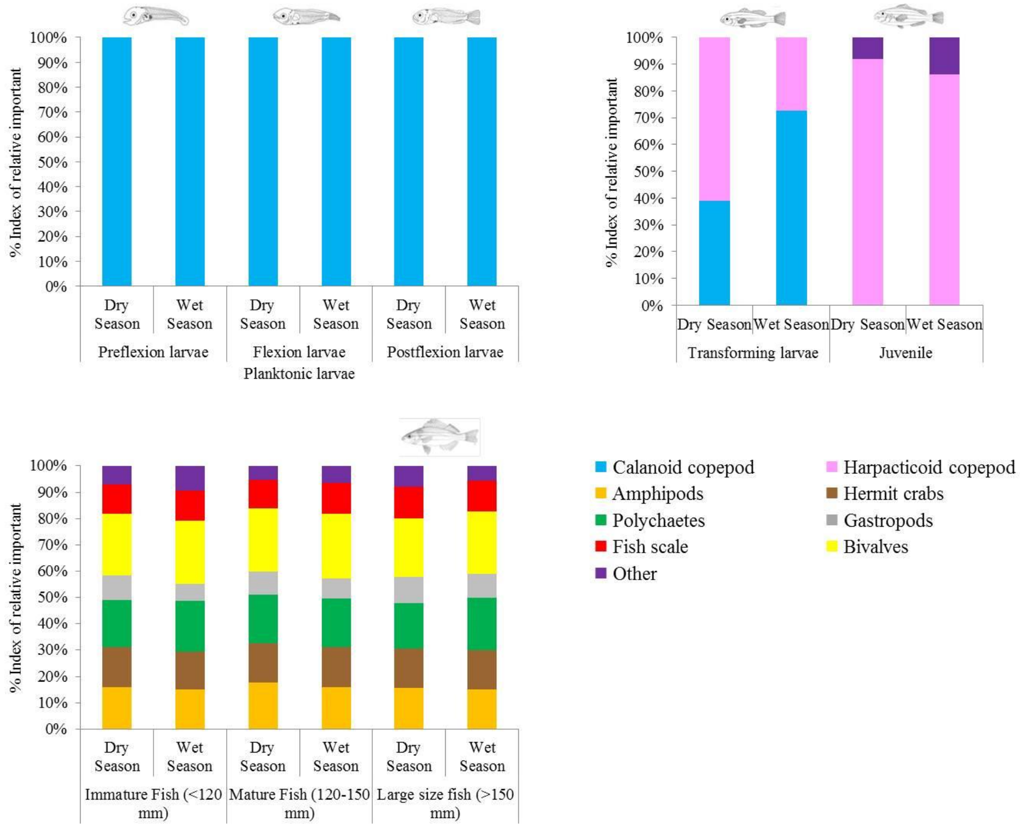

Figure 4. Dietary compositions expressed as percentage of index relative important (%IRI) from stomach content analysis in *Pelates quadrilineatus* (n=694) of different developmental stages and seasons from the coastal area of Trang Province.

the preflexion, flexion and postflexion larvae. Zooplankton, calanoid copepods and small benthos, harpacticoid copepods were the major prey items in the diet of the transforming larvae. Seasonal abundance in the prey items reflected in the importance of the prey items. The transforming larvae of *P. quadrilineatus* fed on both calanoid and harpacticoid copepods in the same proportion during the dry season. Calanoid copepods played the important role in the diet of the transforming larvae of *P. quadrilineatus* during the wet season. As the calanoid copepods were abundant during the wet season, the larvae chose to fed more on the abundant food source. In juvenile *P. quadrilineatus*,the small benthos harpacticoid copepods, was the major prey item. Zooplankton, *Lucifer* spp. and calanoid copepods made up the smaller percentage of diet composition in juvenile. Adult *P. quadrilineatus* fed mainly on large benthic animals and fish scales. Bivalves, amphipods, hermit crabs, polychaetes and gastropods were the major prey items. Lepidophagy in *P. quadrilineatus* were found in adult stage.

The ontogenetic change in the mouth gape and diameter, dentition, gill rakers, stomach and pyloric caeca and intestinal length were observed in Figure 5. Subterminal mouth presented in *P. quadrilineatus.* Calanoidcopepods was the major prey category in planktonic larvae of *P. quadrilineatus*. In these stages, their feeding ability was poor and feeding structure incomplete developed. Therefore, the feeding ability of *P. quadrilineatus* in this stage was affected by abundance of calanoid copepods as in *T. jarbua*. Teeth of *P. quadrilineatus* were mainly of villiform type. Small teeth formed in rows on the upper and lower jaw in all stages. The numbers of row of villiform teeth increased as the fish grow. Amphipods, bivalves, hermit crabs, polychaetes and fish scales were the main prey items in all size of adult of *P. quadrilineatus*. Their villiform teeth were used in crushing the hard shells and exoskeletons of the invertebrate preys. The gill rakers were long with 39-45 slits. The stomach of Y-shape with the number of pyloric caeca varied from 13-15 pieces. The ratio of intestinal length/standard length showed that this species was classified as specialist carnivorous fish corresponded to Davis *et al.* (2013) reported that the ratio of intestine length/standard length of specialist carnivorous fish were 0.9-1.02.

3.4 Food partitioning of *Terapon jarbua* and *Pelates quadrilineatus* in coastal area of Trang Province

The results on the distribution patterns, stomach content analysis, and feeding structure in different stages of *T. jarbua* and *P. quadrilineatus* supported that both species displayed an ontogenetic dietary shift and food partitioning. Planktonic larvae of *T. jarbua* and *P. quadrilineatus* utilized the same area of offshore as the feeding ground. They were competed for the same major food items, calanoid copepods in the water column. However, the feeding ability of fish in this

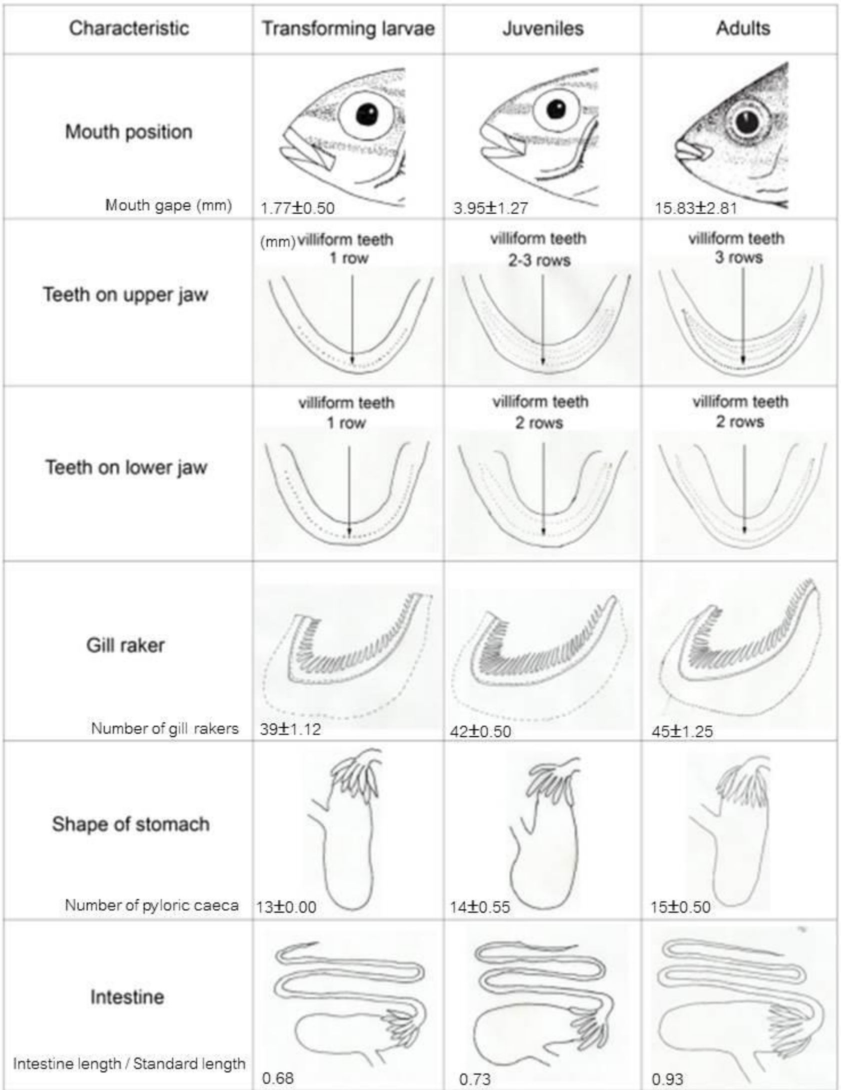

Figure 5. Comparative studies on feeding structure morphology of *Pelates quadrilineatus* (transforming larvae n=30; juvenile n=30; adult n=30) in coastal area, Trang Province.

stage is limited by mouth gape and mouth diameter. They are able to ingest pray of a similar or smaller size to their mouth (Østergaard, Munk, & Janekarn, 2005). The availability of food items has a greater effect on their feeding ability than feeding structure in this growth stage. In addition, the chosen prey were mainly on calanoid copepods which was the dominant zooplankton help to reduce the handling time, searching time and energy spent for capturing their prey.

Both *T. jarbua* and *P. quadrilineatus* displayed habitat shift and food partitioning during transforming larvae and juvenile stages. They showed preferences for different habitat type for feeding ground. High density of transforming larvae and juveniles of *T. jarbua* were found in the natural coastal mangrove swamps. Transforming larvae and juveniles of *P. quadrilineatus* were found in the natural seagrass beds. Living in different habitat types for both species during metamorphosis helped in reducing the interspecific competition between them. The feeding ecology of both species in these stage reveled that transforming larvae of both species still fed mainly on calanoid copepods. However, the importance of calanoid copepods was decreasing. Juveniles of *T. jarbua* shifted to feed mainly on small benthic animals (harpacticoid copepods), large benthic animals (crabs) and fish scales. Juveniles of *P. quadrilineatus* shift to feed mainly on small benthic animals (harpacticoid copepods) and large plankton (*Lucifer* spp.). Juvenile of both species showed a transition feeding from water column to benthic environments (Horinouchi *et al.*, 2012; Kanou *et al.*, 2004). The change in main prey item indicated that *T. jarbua* and *P. quadrilineatus* had food partitioning between transforming larvae and juvenile stage. The increasing of jaw length and mouth size in juveniles helped fish to increase their prey size (Olsen, Evjemo & Olsen, 1999). Juvenile of *T. jarbua* have conical teeth on the upper and lower jaw helped fish to bite their prey.

In the adult stage of both species, they used offshore areas as feeding grounds but they fed on different food source. Adult of *T. jarbua* fed mainly on fish and fish scales while adult stage of *P. quadrilineatus* fed mainly on large benthic organisms such as amphipods, bivalves, hermit crabs and polychaetes. The complete development of feeding structure helps adult fish to easily capture the moving preys such as fish or benthic prey items. Changes in size of feeding structures have been associated with changes in foraging behavior, thus altering the range of exploitable prey items (Brown, 1985). Fish scales were increasing in diet composition with growth in both species. This provided complementing nutrition source. Food partitioning strategy as different feeding habits in the adult of *T. jarbua* and *P. quadrilineatus* helpedto reduce interspecific competition.

Terapon jarbua and *P. quadrilineatus* changed the habitat and diet with growth. Therefore, this study confirms the hypothesis that *T. jarbua* and *P. quadrilineatus* demonstrated the resource partitioning through habitat and dietary shifts in each developmental stages. These strategies helped in reducing the food competition among both species and allow them to coexist in the same area.

4. Conclusions

Coastal areas of Trang Province provided the important of habitat use for feeding ground of fish. *Terapon jarbua* and *P. quadrilineatus* showed the clear habitat utilization between developmental stages. Planktonic larvae and adult of both species lived offshore. The transforming larvae and juveniles moved to shallow near shore habitats. However, they have demonstrated habitat partitioning during metamorphosis. *Terapon jarbua* were found in the natural coastal mangrove swamps while *P. quadrilineatus* were found in natural sea grass beds. In addition, they showed ontogenetic dietary shift. The main prey items of larvae, juvenile and adult in *T. jarbua* changed from small planktonic animal, benthic animal to fish, respectively. The main prey items of larvae, juvenile and adult of *P. quadrilineatus* shifted from small planktonic animal, small benthic animal to large benthic animal, respectively. Prey item changes related to development of feeding structure such as mouth gape, mouth diameter, jaw length, dentition, stomach and intestinal length. This allowed a changed in diet from only small planktonic animal to larger sized prey. This study confirmed that there was food partitioning between the two co-occurring terapontids fish, *T. jarbua* and *P. quadrilineatus* in coastal area of Trang Province. These are the important strategies to reduced competition for fish sharing the same feeding grounds.

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