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Development patterns and defining length at juvenile of two co-occurring Terapontids, *Terapon jarbua* and *Pelates quadrilineatus*, from Trang province coastal area, Southern Thailand

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Abstract

This study aimed to describe development patterns and define length at juvenile of two co-occurring terapontid fishes. *Terapon jarbua* (n=366, 1.49-48.24 mm) and *Pelates quadrilineatus* (n=314, 1.64-54.13 mm) were collected from coastal area, Trang Province, Thailand. Specimens were divided into five developmental stages: preflexion larvae, flexion larvae, postflexion larvae, transforming larvae, and juvenile by study of morphometric character, meristic character and pigmentation pattern. The length at juvenile was defined by using a multivariate analysis of morphometric characters. The length at juvenile stage of *T. jarbua* and *P. quadrilineatus* began at 23.16 mm and 18.24 mm in standard length, respectively. All morphometric characters were significantly different ($P<0.05$) between transforming larvae and juvenile stage in both species. An understanding in development patterns can aid in the explanation of their ontogenetic niche shifts. Due to the actual timing of switches in diet and habitat, it usually relates to changes in morphology of fish. The increase of mouth and jaw were significant in the ontogenetic dietary shift. The increase of body depth, fin length and eye size were also important to the mobile ability and feeding habitat shift in terapontid fishes.

Keywords: coexist adaptation, larvae, juvenile, morphology, terapontids

1. Introduction

There have long been interests in understanding how similar species or same family coexists despite the pressures of intraspecific competition or interspecific competition. Niche partitioning refers to the process that drives competing species into different patterns of resource use. Ontogenetic niche shifts is one important process in niche partitioning. It helps maximize fitness by reducing competition between coexist species with resource segregation (Werner & Gilliam, 1984). The actual timing of ontogenetic niche shifts usually relates to the time that larvae become juveniles and juveniles become adults. The time reflects changes in morphology of fish (Blaber, 2000). Morphological development in fish is an involving process of growth and adaptation. The changes can also lead to structural defects affecting for developing, feeding and ultimately the survival of the organism (Koumoundouros, Divanach, & Kentouri, 1999). Associating with these changes, there is a sudden shift in diet or habitat for resources segregation (Osenberg, Mittelbach, & Wainwright, 1992).

In Thailand, larvae and juveniles of *Terapon jarbua* (Forsskål, 1775) and *Pelates quadrilineatus* (Bloch, 1790) have been reported coexist in several areas (Chayakul, 2007;

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Duangdee, 1995; Matsuura & Kimura, 2005; Tongnunui, Sailad, & Nopparat, 2010). It is interesting to study how these species, which are in the same family and possessing similar morphology, can coexist in the same area. Urho (2002) reported that the ontogenetic process of fish seemed to be sufficiently flexible to allow larvae to adapt to their environment. The main character of larvae includes the food finding adaptability, predators' avoidance, and gaining enough competitive ability to share resource with juveniles and adults. The understanding in the developmental pattern of both species, can explain their ontogenetic niche shift and their co-occurring in the same area. However, defining the developmental stage in several fishes is not easy, especially the transitional stages between larvae to juvenile. The morphological features of the late larvae stage are very similar to that of the juvenile (Methven & McGowan, 1998). Single morphological character approach has traditionally been used for identifying the transition between larvae and juvenile stages (e.g. until full count of fin ray, beginning of squamation, completed squamation and development of sensory feature or habitat shift). Nevertheless, one-character approach is often inadequate for defying the size at juvenile. This is caused by the fact that individual character has variation and differences in timing and rate of ontogeny (Urho, 2002). For example in *Paralichthys olivaceus*, eye migration completed at 17 mm SL (standard length), squamation began at 14-18 mm SL, and full squamation was not observed until at 39-48 mm SL (Fukuhara, 1986). Therefore, it is difficult to choose only one character for identify the transition between larvae and juvenile stages. In addition, the study only one character often was not enough to explain how fish coexist in the same area. During the development, fish have to develop many characters to utilize resource and survive in their environment. These changes includes increasing mouth gape to accommodate larger food and developing fin rays complement to increase swimming performance to help finding new food source or habitat (Urho, 2002). Nikolioudakis, Koumoundouros, Kiparissis, and Somarakis (2010) used multivariate morphometric analysis to define the mean length at juvenile on newly settled white sea-breams (*Diplodus sargus sargus*). They found almost perfect match was demonstrated between mean length at juvenile and mean size-atmorphological change in white seabream. Then, Nikolioudakis, Koumoundouros, and Somarakis (2014) used this method to find the mean length at juvenile of other fish and found that temperature have effect on morphological change. *Oblada melanura* is a species that recruit during the warmest period of month. They showed close estimation between mean length at juvenile and border between intermediate and juvenile stage. On the other hand, the mean length at juvenile and border between intermediate and juvenile stage in species that recruit the cold period of month were not in close proximity. We adopt to choose their method for estimating the length at juvenile on the basis that *T. jarbua* and *P. quadrilineatus* were tropical species and they should presumably have close estimations between mean length at juvenile and border between intermediate and juvenile stages. Morphometric characters were used in multivariate analysis. When raw measurements were used in principal component analysis (PCA), the PC1 was affected by size variation. PC2 represented shape variation on growth of fish and gave an inflection point where shifts in growth patterns occur between larvae and juvenile stage (Shea, 1985). Therefore, it better reflects the transition point between the larvae and the juvenile (Nikolioudakis, Koumoundouros, Kiparissis, & Somarakis, 2010; Nikolioudakis, Koumoundouros, & Somarakis, 2014). This study, however, focuses on identifying developmental stages of both species by using morphometric character, meristic character and pigmentation. In addition, we adopted a multivariate morphometric analysis to define the transitional point between larvae and juvenile.

The aim of this study is to describe the developmental patterns and defining the length at juvenile of *T. jarbua* and *P. quadrilineatus* with attention to morphometric character, meristic character and pigmentation. The result of this study can be used to explain their ontogenetic niche shift and their adaptation for coexisting in the same area.

2. Materials and Methods

2.1 Fish sample

Specimens of both species were collected from two sources. The first group of specimens (*T. jarbua* n=8 and *P. quadrilineatus* n=6) was captured from offshore area of Rajamangala Beach, Trang Province. The area is 2 km from the shore with depth of 8-10 meters. Samples were collected by using surface tow plankton net (0.5 m mouth diameter; 330 μm mesh size). All samples collected by this method were fixed and preserved in 4% neutral buffer formalin (NBF). Another group of specimens was from Tongnunui, Sailad, and Nopparat (2010) (*T. jarbua* n=358 and *P. quadrilineatus* n=308). These specimens were captured with small beach seine (10 m wide and 1 mm mesh size, with 4.5 m long central purse-beg) from natural coastal swamp at Rajamangala Beach and natural seagrass beach at Libong Island in Trang Province. All specimens were preserved in 10% NBF. Specimens from both collections were sorted and identified on the basis of the identification guide of Okiyama (1986), Leis and Trinski (1989), Jeyaseelan (1998), and Leis and Carson-Ewart (2000).

2.2 Development patterns study

All samples of 366 *T. jarbua* and 314 *P. quadrilineatus* were examined. Terminology and methods for classified stage mainly followed that of Miller and Kendall (2009). Fourteen morphometric characters and 12 meristic characters and pattern of pigmentation were measured and counted. Morphometric characters, (1) standard length (SL), (2) body depth, (3) head length, (4) eye diameter, (5) snout length, (6) jaw length, (7) mouth gape, (8) mouth diameter, (9) predorsal length, (10) length of base of dorsal fin, (11) length of longest dorsal fin spine, (12) length of longest dorsal fin ray, (13) length of longest anal fin spine, and (14) length of longest anal fin ray, were all measured with a micrometer attached to a binocular microscope and a vernier caliper. All measurements were done down to ±0.001 mm. Larvae and juvenile size was reported as SL measurement in millimeter. The meristic characters included (1) dorsal fin spine, (2) dorsal fin ray, (3) anal fin spine, (4) anal fin ray, (5) pectoral fin, (6) pelvics fin spine, (7) pelvics fin ray, (8) postemporal spine, (9) opercular spine, (10) preopercular spine, (11) interopercular spine, and (12) infraorbital spine were counted using a phase contrast microscope. Illustrations were done under stereomicroscope.

2.3 Defining length at juvenile by multivariate morphometric analysis

A total of 666 specimens (*T. jarbua*, n=358, 7.99-48.24 mm and *P. quadrilineatus*, n=308, 9.01-54.13 mm) were used for morphometric analysis. Raw measurements of the 14 morphometric characters (except SL) were subjected to principal components analysis (PCA) (change in oblique orientation: promax, KMO > 0.5 and factor loading >0.3). The variance in principal component 1 (PC1) was mainly explained by size. Therefore, the shape component or principal component 2 (PC2) were plot against SL and fitted with a piecewise regression by Sigma Plot 10.0 in order to identify the transition point from larvae to juvenile. The means of morphometric measurements between transforming and juvenile stage of both species were compared by using Mann-Whitney U test.

3. Results

3.1 Development patterns and defining length at juvenile

The specimens were identified as *T. jarbua* (n=366; 1.49-48.24 mm) and *P. quadrilineatus* (n=314; 1.64-54.13 mm), based on morphometric characters, meristic character and pigment pattern in method, the developmental stages of both species which related to size can be divided into five developmental stages as follows: (1) preflexion larvae, (2) flexion larvae, (3) postflexion larvae, (4) transforming larvae, and (5) juvenile.

3.2 Description of *T. jarbua*

Preflexion larvae (n=2; 1.49 and 3.18 mm): Body was laterally compressed. Mouth opened. Gut compacted with triangular shape. Head size was moderate to large. Snout was short. Dorsal and anal fin formed in finfolds. Pigments were commonly present on head, posterior and ventral side of gut and dot series along base of anal fin (15-16 dots) (Figure 1A).

Flexion larvae (n=3; 3.40, 3.71 and 3.82 mm): This stage began with flexion of notochord. Body was laterally compressed. Gut compacted with triangular shape. Head size was moderate to large. There were two types of spines on head, opercular spine and preopercular spine. The opercular spine was long and strong, extending beyond margin of opercular lobe. Preopercular was strongly serrate and particularly at angle. Pigments were found on head, ventral side of gut and dot series along base of anal fin (3 dots) (Figure 1B).

Postflexion larvae (n=3; 4.00, 4.92 and 5.65 mm): This stage began when dorsal and anal fin formed in ray. Body was laterally compressed. Head size was moderate to large. There were three types of spines on head, opercular spine, preopercular spine, and infraorbital spine. The pigments increased in number on the head, base of pectoral fin, ventral side of the posterior end of the gut to the base of anal fin and upper part of body. Dot series along base of anal fin (3 dots) still remained in this stage (Figure 1C).

Transforming larvae (n=307; 5.80-23.15 mm): This stage began when dorsal and anal fin formed in spine. Body was laterally compressed and moderately deep (24-34% SL). Head size was moderate to large (30-35% SL). Eye was moderate to large (27-44% HL). Predorsal length was long

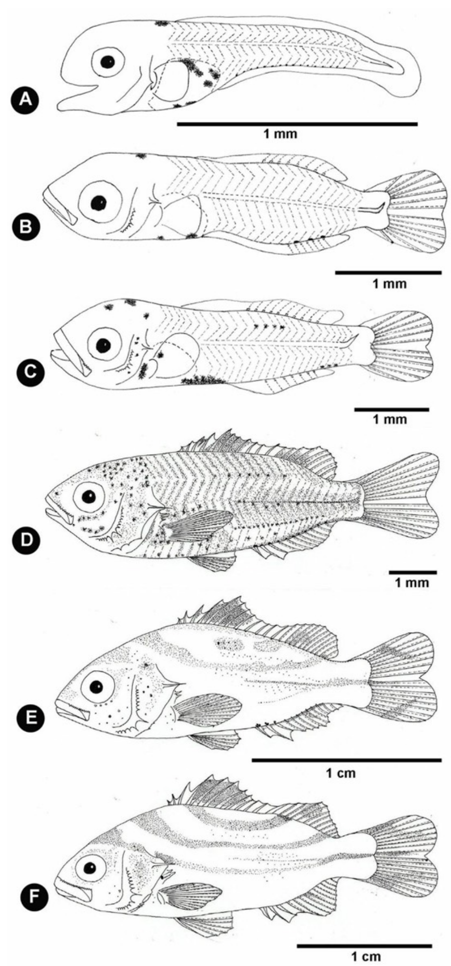

Figure 1. Development series of *Terapon jarbua*. (A) 1.49 mm in SL preflexion larvae; (B) 3.71 mm in SL flexion larvae; (C) 4.92 mm in SL postflexion larvae; (D) 9.02 mm in SL and (E)14.97 mm in SL transforming larvae; F) 24.98 mm in SL juvenile.

(36-45% SL). Mouth was large with mouth gape 29-32% HL, mouth diameter 22-26% HL and jaw length 28-37% HL. Snout length was moderate to large (28-42% HL). There were five types of spines on head, opercular spine, preopercular spine, interopercular spine, infraorbital spine and postemperal spine. Fins had completely developed at 12.00 mm (Dorsal fin: XI-XII, 9-11; Anal fin: III, 7-10; Pectoral fin: 13-15; Pelvic fin: I, 5; Caudal fin: 9+8). Pigmentation changed rapidly with growth by spreading over the head and body. Some pigment appeared on the membranes of dorsal fin and anal fin. Late in this stage, two bands of pigment started to develop discontinuous blackish-brown downwardly curved longitudinal strips on the body. The pigmentation in the dorsal fin membrane was transformed into blackish blotch between the 4th and 8th spine, and smaller one between the 2nd and 6th ray (Figure 1D and 1E).

Juvenile (n=51; 23.16-48.24 mm): Principal components analysis of morphometric measurements using the covariance matrix revealed that there was a prominent change in oblique orientation of PC2 scores when plotted against SL. The fit of the piecewise regression gave an estimate of length at juvenile at 23.16 mm (Figure 4). Predorsal length and eye diameter show high factor loading (>0.3) on the PC2. These characters were important factors that changes between developing stage and influence the identification between the transforming larval and the juvenile of *T. jarbua*. This suggests that juvenile tended to have longer predorsal length and larger eye than transforming larvae (Table 1). Base on morphometric characters, meristic character and pigment pattern, the descriptions of juvenile were as follows: body laterally compressed and moderately deep (34-35% SL); large head (35% SL); large eye (29-32% HL); long predorsal length (35-36% SL); large mouth with mouth gape 31-36% HL, mouth diameter 26-28% HL and jaw length 36-38% HL; long snout length (41-43% HL). There were 5 types of spines on head, opercular spine, preopercular spine, interopercular spine, infraorbital spine, postemperal spine (Figure 3A). Fin rays compliment was completed. Pigment formed in three horizontal downwardly curved bands extending along lateral side of body. The blackish blotch on the dorsal fin membrane was restricted between the 4th and 8th spine. In the dorsal fin ray, the pigmentation was restricted between the 2nd and 6th ray (Figure 1F).

3.3 Description of *P. quadrilineatus*

Preflexion larvae (n=2; 1.64 and 2.98 mm): Body was laterally compressed. Mouth opened. Gut compacted with triangular shape. Head size was moderate to large. Snout was short. Dorsal and anal fin formed in finfolds. Pigments were commonly present on head, ventral midline of the gut and dot series along base of anal fin but number of dot is less than *T. jarbua* (9-10 dots) (Figure 2A).

Flexion larvae (n=2; 3.50 and 3.81 mm): This stage began with flexion of notochord. Body was laterally compressed. Gut compacted with triangular shape. Head size was moderate to large. There were two types of spines on head, opercular spine and preopercular spine. Opercular spine was long and strong but not extending beyond margin of opercular lobe. Preopercular was serrate and larger along vertical

Table 1. Coefficients of the first and second component from the principal component analysis of the morphometric characters for the *Terapon jarbua* (N=358) and *Pelates quadrilineatus* (N=308).

Morphometric character	*Terapon jarbua*		*Pelates quadrilineatus*	
	PC1	PC2	PC1	PC2
Body depth	0.278	-0.160	0.278	0.086
Head length	0.278	-0.102	0.278	-0.156
Mouth gape	0.277	0.056	0.278	0.031
Mouth diameter	0.277	-0.201	0.278	0.092
Predorsal length	0.276	**0.651**	0.277	**0.424**
Base of dorsal fin	0.278	0.034	0.278	-0.083
Snout length	0.277	-0.241	0.277	-0.261
Eye diameter	0.276	**0.593**	0.278	**0.346**
Jaw length	0.277	-0.162	0.278	-0.103
Longest dorsal fin spine	0.278	-0.082	0.276	**0.581**
Longest dorsal fin ray	0.278	-0.130	0.277	**0.387**
Longest anal fin spine	0.278	-0.075	0.278	-0.084
Longest anal fin ray	0.278	-0.177	0.277	0.282
Eigenvalue	12.950	0.027	12.942	0.031
%Variance explained	99.614	0.206	99.556	0.236
Cumulative%	99.614	99.820	99.556	99.792

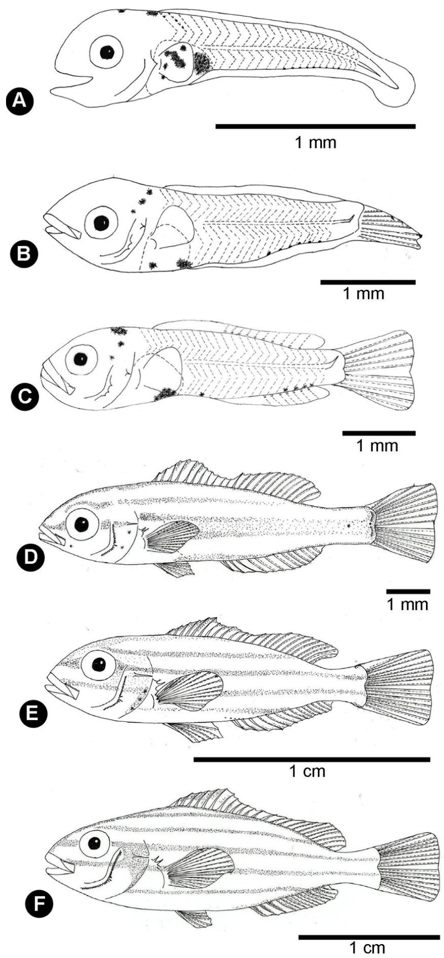

Figure 2. Development series of *Pelates quadrilineatus*. (A) 1.64 mm in SL preflexion larvae; (B) 3.81 mm in SL flexion larvae; (C) 5.12 mm in SL postflexion larvae; (D) 9.01 mm in SL and (E)13.97 mm in SL transforming larvae; F) 24.95 mm in SL juvenile.

edge. Pigments were found on head, ventral side of gut and dot series along base of anal fin (6 dots) (Figure 2B).

Postflexion larvae (n=2; 4.00 and 5.12 mm): This stage began when dorsal and anal fin formed in ray. Body was laterally compressed. There were two types of spines on head, opercular spine and preopercular spine. Pigments were found on head, ventral side of gut and dot series along base of anal fin (4 dots) (Figure 2C).

Transforming larvae (n=140; 6.10-18.23 mm): This stage began when dorsal and anal fin formed in spine. Body was laterally compressed and moderately deep (22-30% SL). Head size was moderate to large (31-34% SL). Eye was moderate to large (29-33% HL). Predorsal length was long (35-38% SL). Mouth was large with mouth gape 26-35% HL, mouth diameter 25-31% HL and jaw length 28-39% HL. Snout length was moderately long (29-33% HL). There were three types of spines on head, opercular spine, preopercular spine and infraorbital spine which found in13.00 mm of SL. Fin rays had completely developed at 13.00 mm (Dorsal fin: XI-XIII, 9-11; Anal fin: III, 9-11; Pectoral fin: 13-16; Pelvic fin: I, 5; Caudal fin: 9+8). Pigmentation changed rapidly with growth. Pigments formed in 1-4 horizontal stripes extending along head and body. In the dorsal fin ray, some pigments appeared on the upper part of dorsal fin membrane (Figure 2D and 2E).

Juvenile (n=168; SL=18.24-54.13 mm): Principal components analysis of morphometric measurements using the covariance matrix revealed that there was a prominent change in oblique orientation of PC2 scores when plotted against SL. The fit of the piecewise regression gave an estimate of length at juvenile at 18.24 mm (Figure 5). Predorsal length, eye diameter, longest dorsal fin spine and longest dorsal fin ray show high factor loading (>0.3) on the PC2. These characters were important factors that changes between developing stage and influence the identification between the transforming larval and the juvenile of *P. quadrilineatus*. This suggests that juvenile tended have to longer predorsal, larger eye, longer longest dorsal fin spine and longer longest dorsal fin ray than transforming larval (Table 1). Base on morphometric characters, meristic character and pigment pattern descriptions of juvenile were as follows: body was moderately deep (30-32% SL); moderate to large head (33-35% SL); moderate to large eye (27-30% HL); long predorsal length (34-35% SL); large mouth with mouth gape 32-38% HL, mouth diameter 32-38% HL and jaw length 36-41% HL; long snout length (31-37% HL). There were three types of spines on head, opercular spine, preopercular spine and infraorbital spine (Figure 3B). Fin rays compliment was completed. Pigment was formed in five horizontal stripes extending along head and body. In the dorsal fin ray, the pigmentation was restricted in the upper portion between the 2nd and 6th spin of dorsal fin in postflexion larvae moved downwards in juvenile (Figure 2F).

All morphometric measurements were significantly different ($P<0.05$) between transforming larvae and juvenile stages in both species. Juvenile have deeper body depth, larger head, larger mouth gape, broader mouth diameter, longer predorsal, longer base of dorsal fin, longer snout, larger eye, larger jaw, longer longest dorsal fin spine, longer longest dorsal fin ray, longer longest anal fin spine, and longer longest anal fin ray than transforming larvae (Table 2).

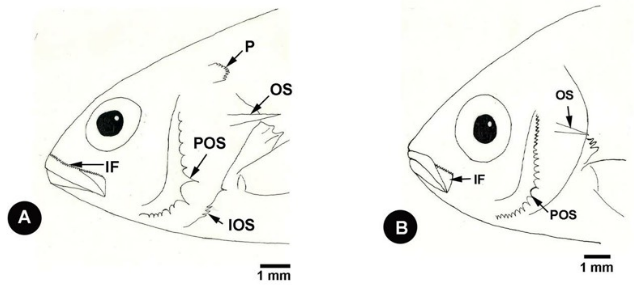

Figure 3. Head spines of *Terapon jarbua* and *Pelates quadrilineatus* in juvenile stage. (A) juvenile of *Terapon jarbua* 24.50 mm in SL and (B) juvenile of *Pelates quadrilineatus* 23.02 mm in SL. PS = Posttemporal spine, OS = Opercular spine, POS = Preopercular spine, IOS = Interopercular spine and IFS = Infraorbital spin

Table 2. Measurement on morphometric character of *Terapon jarbua* (N=358) and *Pelates quadrilineatus* (N=308).

Morphometric character (mm)	*Terapon jarbua*		*Pelates quadrilineatus*	
	Transforming larvae	Juvenile	Transforming larvae	Juvenile
Body depth	5.18±1.53	10.85±2.57	4.06±1.02	7.63±2.20
Head length	5.19±1.51	10.86±2.61	4.81±0.92	8.31±2.31
Mouth gape	1.62±0.52	3.77±0.94	1.57±0.40	2.99±0.89
Mouth diameter	1.36±0.44	2.96±0.73	1.50±0.39	2.98±0.89
Predorsal length	5.82±1.08	10.92±2.70	5.11±0.77	8.38±2.31
Base of dorsal fin	6.79±1.89	14.26±3.46	6.66±0.34	11.68±3.26
Snout length	2.11±0.69	4.61±1.11	1.53±0.31	2.87±0.89
Eye diameter	1.72±0.33	3.12±0.80	1.44±0.24	2.31±0.62
Jaw length	1.90±0.57	4.00±0.97	1.76±0.42	3.24±0.96
Longest dorsal fin spine	2.20±0.67	4.80±1.14	1.74±0.61	3.57±1.01
Longest dorsal fin ray	2.21±0.69	4.41±1.16	1.79±0.55	3.44±0.98
Longest anal fin spine	1.96±0.57	4.17±0.99	1.47±0.32	2.57±0.72
Longest anal fin ray	2.10±0.65	4.54±1.09	1.95±0.53	3.60±0.98

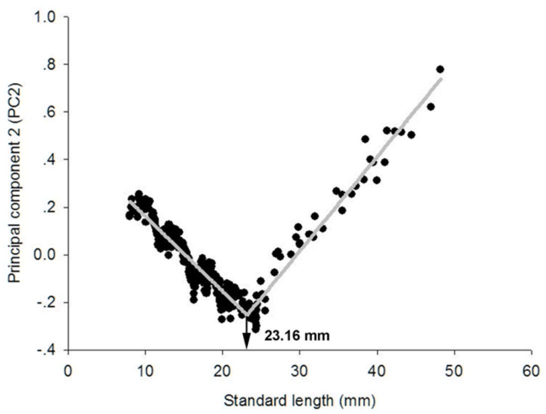

Figure 4. Piecewise regression of principal component 2 (PC2) scores from PCA of 14 morphometric characters on standard length (mm) for estimating length at juvenile in *Terapon jarbua* (n=358). Arrow indicated transition point between larvae and juvenile of *Terapon jarbua*

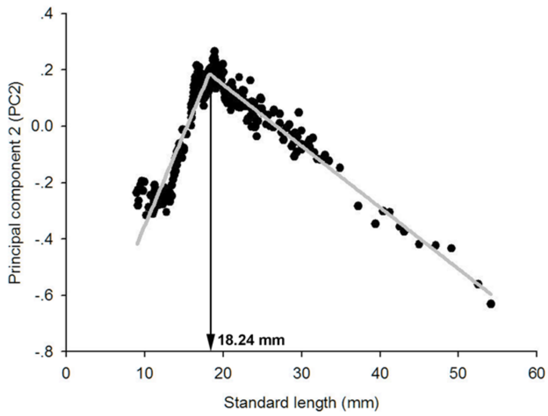

Figure 5. Piecewise regression of principal component 2 (PC2) scores from PCA of 14 morphometric characters on standard length (mm) for estimating length at juvenile in *Pelates quadrilineatus* (n=308). Arrow indicated transition point between larvae and juvenile of *Pelates quadrilineatus*

4. Discussion

There are many criteria for defining the end of the larval period or the beginning of the juvenile period such as, formation of fins, squamation, body pigmentation, development of sensory features, behavioral development and habitat shift (Koumoundouros, Divanach, & Kentouri, 1999; Miller & Kendall, 2009). However, the use of only one character for identifying the length at juvenile of fish is often inadequate (Urho, 2002). The length at juvenile defined by each character can vary. The convert timing to juvenile for individual characters was deference. For example, in the present study, for *T. jarbua*, the formation of scales and fin seemed to complete relatively early at 14.00 and 12.00 mm, respectively while the head spination and pigmentation finished later when the fish was 20.00 and 23.00 mm, respectively. *Pelates quadrilineatus* had the formation of scales, fin and head spination complete relatively early at 14.00, 13.00 and 13.00 mm, respectively while the pigmentation finished later when the fish was 18.00 mm. Differences in rating and timing of the ontogeny for individual characters make recognizing thresholds difficult. Therefore, it is difficult to use only one character for identifying a transitional stage between larvae and juvenile. Multivariate morphometric analysis can largely help in identifying thresholds (Shea, 1985). Therefore, it better reflects the transition point between the larvae and the juvenile (Nikolioudakis, Koumoundouros, Kiparissis, & Somarakis, 2010; Nikolioudakis, Koumoundouros, & Somarakis, 2014). The larger number of characters used to delimit intervals, the better the resolution and the likelihood of delimiting ontogenetic intervals in natural processes (Ditty, Fuiman, & Shaw, 2003). In this study, the length at juvenile of *T. jarbua* and *P. quadrilineatus* from multivariate morphometric analysis was supported by the length which the development of pigmentation completed. The pigmentation was the latest character that developed. The size that show complete pigmentation development of *T. jarbua* and *P. quadrilineatus* was 23.00 mm and 18.00 mm, respectively, while length at juvenile of *T. jarbua* and *P. quadrilineatus* from multivariate morphometric analysis was 23.16 and 18.24 mm, respectively. In addition, the size at juvenile of *T. jarbua* in the present study (23.16 mm) closely matched to the size at juvenile of Jeyaseelan (1998). He studied fish egg and larvae in mangrove forest of Ranong Province, which located at the Andaman Sea, Southern Thailand. He found that early juvenile of *T. jarbua* in this area was 22.50 mm.

The development pattern of *T. jarbua* and *P. quadrilineatus* can be divided into 5 development stages from preflexion larvae, flexion larvae, postflexion larvae, transforming larvae to juvenile. There are changes in morphometric characters, meristic characters and pigmentation pattern during the development. This change of all characters can be used to identify or compare the morphological development of fish (Fuiman, Poling, & Higgs, 1998). In addition, it also identifies ontogenetic niche shifts in resource use of fish (Boglione, Giganti, Selmo, & Cataudella, 2003). The development of mouth gape, mouth diameter, jaw length, body depth, fin length and eye size were important characters to ontogenetic shift and to partition in diet and habitat of fishes. These changes help fish to find food, gain better mobility, avoid predators and find suitable habitat for survival (Urho, 2002).

Preflexion larvae, flexion larvae and postflexion larvae were planktonic stage. In this study, *T. jarbua* and *P. quadrilineatus* in planktonic stage were found coexist in the same period of offshore water of Rajamangala Beach. At these stages, fish depend on random feeding. Their swimming ability was poor. The development of mouth, jaw, body, eye, and fin of them were not completed yet. Prey size selection was considerably less than their mouth gape (Gerking, 1994). Therefore, the abundance of food source, which is the exogenous factor, highly affected their survival. Calanoid copepods, the main food item for the larvae of *T. jarbua* and *P. quadrilineatus* were highly abundant in the study area (Punnarak, 2004). Excessive food items help reducing intraspecific competition and interspecific competition. Therefore, it was not surprising that we found planktonic larvae of both species could coexist in this area. Moreover, at these stages their pigment was not developing. Their body and fin were transparent. This convergence trait helps fish camouflage from predators.

In transforming larvae of both *T. jarbua* and *P. quadrilineatus* moved to shallow near shore habitats. However, they have demonstrated habitat partitioning in this stage. They choose different habitat type for nursery area. Transforming larvae of *T. jarbua* were found in the coastal swamp at Rajamangala Beach while transforming larvae of *P. quadrilineatus* were found in seagrass bed at Libong Island. During the metamorphosis phase, morphological changes and habitat shift occurred. Spawning area do not normally supported the food and habitat requirements of the juvenile. Therefore, distribution and translocation to a nursery area may be vital for survival, especially for fish larvae to avoid the predator and search for food (Urho, 2002). Hence, the morphological changes such as increase of body depth, fin length and eye size during the metamorphosis were important to the mobility, feeding and habitat shift in fishes. Fishes adapted for searching prey in structurally complex habitats tended to have a deep and laterally compressed body (Norton, 1995), extended fins (Webb, 1984), and larger eye (Hobson, 1979). This character permits fish to have well controlled swimming, visual in the turbid habitat, able to catch its prey and avoid their predator.

In juvenile stage, *T. jarbua* still reside in the coastal swamp and *P. quadrilineatus* still reside in the seagrass bed for nursery area and coexisting with their transforming larvae. The morphological changes seem to support and allow the transforming larvae and juvenile stage to coexist in the same area. The mouth gape, mouth diameter and jaw length of both species tended to increase in size when larvae metamorphosis to juvenile. The actual timing of diet shift usually relates to change in developmental stage, with mouth gape and jaw sizes are important determinant for food size (McCormick, 1998). The morphological changes were supported by their diet switching performance from small prey size to larger prey size. It was corresponding to previous studies, which indicated that *T. jarbua* and *P. quadrilineatus* changed prey size with growth. For example, transforming larvae of *T. jarbua* fed mainly on calanoid copepod and then shift to fed mainly on amphipod and polychaetes in juvenile (Kanou, Sano, & Kohno, 2004). The major food item of *P. quadrilineatus* in transforming larvae stage was calanoid copepod larvae and shift to hapacticoid copepod in juvenile stages (Horinouchi *et al.*, 2012). In addition, the subterminal mouth allowed both species change food source from the water column to the benthic environment. The increase of body depth, fin length, and eye size allowed both species to catch prey in structurally complex habitats. This corresponds to downward movement from the water column to the benthic environment when larvae metamorphose to juvenile of both species (Horinouchi *et al.*, 2012; Kanou, Sano, & Kohno, 2004). Moreover, at these stages their pigmentation was completed. The intensive pigment pattern on body of both species help fish can camouflage from predator in the turbidity and structurally complex habitats. The partitioning food source and feeding habitat between transforming larvae and juvenile help decreasing intraspecific competition during their early life stages.

5. Conclusions

Using all morphometric character, meristic character and pigmentation pattern, the developmental pattern of

T. jarbua and *P. quadrilineatus* can be divided into five development stages follows: (1) preflexion larvae, (2) flexion larvae, (3) postflexion larvae, (4) transforming larvae, and (5) juvenile. The length at juvenile stage of *T. jarbua* and *P. quadrilineatus* began at 23.16 mm and 18.24 mm, respectively. Understanding the significance of the similarities and differences in development between fish species within their environment context may provide a more comprehensive view, not only of an appropriate terminology but also of the adaptation for coexistent species. *Terapon jarbua* and *P. quadrilineatus* showed the morphological changes in body depth and fin ray compliment to habitat and feeding shifts. The development of mouth and jaw were important in the ontogenetic shift and partition in diets. The developments of eye and pigment pattern were important to feeding performance and predator avoidance. The changes of these characters allow them to coexist in the same area.

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References

Blaber, S. J. M. (2000). *Tropical estuarine fishes: Ecology, exploitation and conservation*. London, England: Blackwell Science.

Boglione, C., Giganti, M., Selmo, C., & Cataudella, S. (2003). Morphoecology in larval fin-fish: A new candidate species for aquaculture, *Diplodus puntazzo* (Sparidae). *Aquaculture International*, *11*, 17-41. doi:10.1.1.457.4429

Chayakul, R. 2007. *Fish larvae in gulf of Thailand.* Bangkok, Thailand: Department of Fisheries.

Ditty, J. G., Fuiman, L. A., & Shaw, R. F. (2003). Characterizing natural intervals of development in fishes: An example using blennies (Teleostei: Blenniidae). The big fish bang: *Proceedings of the 26th Annual Larval Fish Conference*. Bergen: Norway, July 22-26, 2002, 405-418.

Duangdee, T. (1995). *Identification and distribution of fish larvae in seagrass bed at Had Chao Mai National Park, Changwat Trang* (Master's thesis, Kasetsart University, Bangkok, Thailand).

Fuiman, L. A., Poling, K. R., & Higgs, D. M. (1998). Quantifying developmental progress for comparative studies of larval fishes. *Copeia, 3*, 602-611. Retrieved from http://www.jstor.org/stable/1447790

Fukuhara, O. (1986). Morphological and functional development of Japanese flounder in early life stages. *Bulletin of the Japanese Society for the Science of Fish*, *52*, 81-91. Retrieved from https://www.jstage.jst.go.jp/article/suisan1932/52/1/52_1_81/_article

Gerking, S. D. (2014). *Feeding ecology of fish*. Amsterdam, The Netherlands: Elsevier.

Hobson, E. S. (1979). *Interactions between piscivorous fishes and their prey. In Predator-Prey systems in fisheries management*. Washington, DC: Sport Fishing Institute.

Horinouchi, M., Tongnunui, P., Furumitsu, K., Nakamura, Y., Kanou, K., Yamaguchi, A., Okamoto, K., & Sano, M. (2012). Food habitats of small fishes in seagrass habitats in Trang, southern Thailand. *Fisheries Science, 78*, 577-587. doi:10.1007/s12562-012-0485-5

Jeyaseelan, M. J. P. (1998). *Manual of fish eggs and larvae from Asian mangrove waters.* Paris, France: The United Nations Education, Scientific and Cultural Organization.

Kanou, K., Sano, M., & Kohno, H. (2004). Food habits of fishes on unvegetated tidal mudflats in Tokyo Bay, Central Japan. *Fisheries Science, 70*(6), 978-987. doi: 10.1007/s10152-010-0208-1

Koumoundouros, G., Divanach, P., & Kentouri, M. (1999). Ontogeny and allometric plasticity of *Dentex dentex* (Osteichthyes: Sparidae) in rearing conditions. *Marine Biology*, 135, 561-572. Retrieved from http://link.springer.com/article/10.1007%2Fs002270050657?LI=true

Leis, J. M., & Transki, T. (1989). *The larvae of Indo-Pacific Coal Reef Fishes*. Sydney, Australia: New South Wales University.

Leis, J. M., & Carson-Ewart, B. M. (2000). *The larvae of Indo-Pacific coastal fishes an identification guide to marine fish larvae.* Leiden, The Netherlands: Brill.

Matsuura, K., & Kimura, S. (2005). *Fishes of Libong Island, West Coast of Southern Thailand*. Tokyo, Japan: Oceanic Research Institue, University of Tokyo.

McCormick, M. I. (1998). Ontogeny of diet shifts by a microcarnivorous fish, Cheilodactylus spectabilis: relationship between feeding mechanics, microhabitat selection and growth. *Marine Biology*, *132*, 9-20. doi: 10.1007/s002270050367

Methven, D. A., & McGowan, C. (1998). Distinguishing small juvenile Atlantic cod (*Gadus morhua*) from Greenland cod (*Gadus ogac*) by comparing meristic characters and discriminant function analyses of morphometric data. *Canadian Journal of Zoology, 76*, 1054-1062. Retrieved from http://www.nrcresearchpress.com/doi/abs/10.1139/z98-046#.WRBwEE05Ot8

Miller, B. S., & Kendall, A. W. (2009). *Early life history of marine fishes*. Berkeley, CA: University of California.

Nikolioudakis, N., Koumoundouros, G., Kiparissis, S., & Somarakis, S. (2010). Defining length-at-metamorphosis in fishes: a multi-character approach. *Marine Biology*, *157*, 991-1001. doi: 10.1007/s00227-009-1379-7

Nikolioudakis, N., Koumoundouros, G., & Somarakis, S. (2014). Synchronization in allometric and morphological changes during metamorphosis: Comparison among four sparid species. *Aquatic Biology*, *21*, 155-165. doi: 10.3354/ab00579

Norton, S. F. (1995). A functional approach to ecomorphological patterns of feeding in cottid fishes. *Environmental Biology of Fishes, 44*, 61-78. Retrieved fromhttp://link.springer.com/chapter/10.1007/978-94-017-1356-6_5

Okiyama, M. (1986). *An atlas of the early stage fishes in Japan*. Tokyo, Japan: Tokai University.

Osenberg, C. W., Mittelbach, G. G., & Wainwright, P. C. (1992). Two-stage lift histories in fish: The interaction between juvenile competition and adult performance. *Ecology*, *77*, 255-267. doi: 10.2307/1938737

Punnarak, P. (2004). *Biodiversity of zooplankton in coastal area of klong pak-meng, Trang province* (Master's thesis, Chulalongkorn University, Bangkok, Thailand).

Shea, B. T. (1985). Bivariate and multivariate growth allometry: Statistical and biological considerations. *Journal of Zoology*, *206*, 367-390. doi: 10.1111/j.1469-7998.1985.tb05665.x

Tongnunui. P., Sailad, B., & Nopparat, O. (2010). Fish assemblage in coastal swamps, Sikao District, Trang Province. *RMUTSV Research Journal, 2*(1), 9-16.

Urho, L. (2002). Characters of larvae-what are they? *Folia Zoologica*, 51, 161-186. Retrieved from http://www.mzp.cz/ris/ekodisk-new.nsf/6d13b004071d0140c12569e700154acb/9bab4718c8c79bb6c1257234005bf390/$FILE/Folia%20Zoologia%202002-03.pdf

Webb, P. W. (1984). Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist*, *24*, 107-120. doi: 10.1093/icb/24.1.107

Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics, 15*, 393-425. doi: 10.1146/annurev.es.15.110184.002141