การใช้ทรัพยากรของปลาข้างตะเภา *Terapon jarbua* และ *Pelates quadrilineatus* ในบริเวณชายฝั่งทะเล จังหวัดตรัง

นางสาวหนึ่งฤทัย ยกน้อย

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรดุษฎีบัณฑิต
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RESOURCE UTILIZATION OF TERAPONTID FISHES *Terapon jarbua* AND *Pelates quadrilineatus* IN COASTAL AREA, TRANG PROVINCE

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A Dissertation Submitted in Partial Fulfillment of the Requirements
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หนึ่งฤทัย ยกน้อย : การใช้ทรัพยากรของปลาข้างตะเภา *Terapon jarbua* และ *Pelates quadrilineatus* ในบริเวณชายฝั่งทะเล จังหวัดตรัง (RESOURCE UTILIZATION OF TERAPONTID FISHES *Terapon jarbua* AND *Pelates quadrilineatus* IN COASTAL AREA, TRANG PROVINCE) อ.ที่ปรึกษาวิทยานิพนธ์หลัก: รศ. ณิฏฐารัตน์ ปภาวสิทธิ์, อ.ที่ปรึกษาวิทยานิพนธ์ร่วม: อ ดร. เจษฏ์ เกษตระทัต, 226 หน้า.

ปลาข้างตะเภา *Terapon jarbua* และ *Pelates quadrilineatus* พบการกระจายตัวอยู่ร่วมกันบริเวณชายฝั่งทะเลจังหวัดตรัง โดยอาศัยบริเวณชายฝั่งทะเลจังหวัดตรังเป็นแหล่งผสมพันธุ์และวางไข่ แหล่งอนุบาลปลาวัยอ่อน และแหล่งอาหาร ซึ่งเป็นที่น่าสนใจว่าปลาที่มีลักษณะสัณฐานที่ใกล้เคียงกันสามารถปรับตัวและอาศัยอยู่ร่วมกันได้อย่างไร โดยทั่วไปการอาศัยอยู่ร่วมกันของปลาชนิดต่างๆ ในระบบนิเวศจะมีการแบ่งสรรทรัพยากรอาหารและที่อยู่อาศัยระหว่างปลาแต่ละชนิดและระหว่างแต่ละขนาดเพื่อลดการแก่งแย่งทรัพยากร ในปลาส่วนใหญ่จะพบการเปลี่ยนแปลงอาหารและที่อยู่อาศัยระหว่างการเติบโตของร่างกาย ซึ่งเป็นกลไกการแบ่งสรรการใช้ทรัพยากรที่เกิดจากความแตกต่างทางด้านโครงสร้างของร่างกาย พฤติกรรมการกินอาหาร ระยะที่เติบโต และการใช้พื้นที่ เพื่อลดการแข่งขันระหว่างปลาชนิดเดียวกัน การศึกษาครั้งนี้มีวัตถุประสงค์เพื่อที่จะศึกษา (1) ระยะพัฒนาการและหาขนาดเมื่อเข้าสู่ระยะวัยรุ่นของปลาข้างตะเภาทั้งสองชนิด (2) การกระจายในแหล่งที่อยู่อาศัยต่างๆ ของปลาข้างตะเภาทั้งสองชนิดในระยะวัยอ่อน วัยรุ่น และโตเต็มวัย และนิเวศวิทยาการสืบพันธุ์ของปลาข้างตะเภาทั้งสองชนิดในระยะโตเต็มวัย (3) องค์ประกอบในกระเพาะอาหารและพัฒนาการของโครงสร้างที่ใช้ในการกินอาหารของปลาข้างตะเภาทั้งสองชนิดในระยะวัยอ่อน วัยรุ่น และโตเต็มวัย เพื่อนำผลการศึกษาที่ได้มาอธิบายการใช้ทรัพยากรร่วมกันของปลาข้างตะเภา *Terapon jarbua* และ *Pelates quadrilineatus* ในบริเวณชายฝั่งทะเล จังหวัดตรัง

ผลการศึกษาพบว่าสามารถแบ่งระยะพัฒนาการของปลาข้างตะเภาทั้งสองชนิดออกเป็น 6 ระยะ คือ ลูกปลาวัยอ่อนระยะแรก ลูกปลาวัยอ่อนระยะที่กระดูกหางท่อนสุดท้ายได้โค้งงอขึ้น ลูกปลาวัยอ่อนระยะหลัง ลูกปลาวัยอ่อนระยะที่มีการเปลี่ยนแปลงรูปร่าง ระยะวัยรุ่น และระยะโตเต็มวัย โดย *T. jarbua* จะเข้าสู่ระยะวัยรุ่นเมื่อมีขนาด 23.16 มิลลิเมตร และมีขนาดแรกสืบพันธุ์ 156.92 มิลลิเมตร และ 153.77 มิลลิเมตร ในเพศเมียและเพศผู้ตามลำดับ ส่วน *P. quadrilineatus* จะเข้าสู่ระยะวัยรุ่นเมื่อมีขนาด 18.24 มิลลิเมตร และมีขนาดแรกสืบพันธุ์ 120.31 มิลลิเมตร และ 124.02 มิลลิเมตร ในเพศเมียและเพศผู้ตามลำดับ เมื่อศึกษาการกระจายในแหล่งที่อยู่อาศัยต่างๆ ปลาข้างตะเภาทั้งสองชนิดพบว่ามีการกระจายในพื้นที่ที่แตกต่างกัน โดยพบการกระจายของลูกปลาระยะวัยอ่อนที่ดำรงชีวิตเป็นแพลงก์ตอนและปลาในระยะโตเต็มวัยอาศัยอยู่บริเวณนอกชายฝั่ง ซึ่งแสดงให้เห็นว่าปลาทั้งสองชนิดใช้บริเวณนี้เป็นแหล่งผสมพันธุ์และวางไข่ อย่างไรก็ตาม *T. jarbua* และ *P. quadrilineatus* มีการแบ่งการใช้พื้นที่เพื่อผสมพันธุ์ในฤดูกาลที่แตกต่างกัน โดย *T. jarbua* มีฤดูกาลสืบพันธุ์แบ่งออกเป็น 2 ช่วง คือ เดือนเมษายนถึงเดือนมิถุนายน และ เดือนกันยายนถึงเดือนตุลาคม ส่วน *P. quadrilineatus* มีฤดูกาลสืบพันธุ์ที่สั้นเพียงช่วงเดียว คือ เดือนพฤศจิกายนถึงเดือนธันวาคม การที่มีฤดูกาลสืบพันธุ์ที่ไม่ตรงกันเป็นกลยุทธ์หนึ่งในการแบ่งสรรทรัพยากรที่อยู่อาศัยโดยการเข้ามาใช้ในช่วงเวลาที่แตกต่างกันส่งผลให้ลดการแข่งขันและเพิ่มโอกาสรอดให้กับลูกปลา ส่วนลูกปลาวัยอ่อนระยะที่มีการเปลี่ยนแปลงรูปร่างและลูกปลาระยะวัยรุ่นพบการกระจายเข้ามาในบริเวณแหล่งน้ำตื้นใกล้ชายฝั่ง ในระยะนี้ปลาทั้งสองชนิดจะแยกแหล่งที่อยู่อาศัยกันอย่างชัดเจนเพื่อลดการแก่งแย่งทรัพยากรที่อยู่อาศัยและอาหาร โดย *T. jarbua* เข้ามาอาศัยอยู่บริเวณบึงน้ำชายฝั่งที่เชื่อมต่อกับทะเล ส่วน *P. quadrilineatus* เข้ามาอาศัยอยู่บริเวณแหล่งหญ้าทะเล ทั้งสองบริเวณมีความเหมาะสมที่จะเป็นแหล่งอนุบาลปลาวัยอ่อนเนื่องจากโครงสร้างของระบบนิเวศมีความซับซ้อนสามารถป้องกันตัวจากผู้ล่าและมีความอุดมสมบูรณ์ของแหล่งอาหาร ในส่วนของการใช้ทรัพยากรอาหารพบว่าปลาทั้งสองชนิดมีการกินอาหารที่เหมือนกันในลูกปลาระยะวัยอ่อนที่ดำรงชีวิตเป็นแพลงก์ตอนและลูกปลาวัยอ่อนระยะที่มีการเปลี่ยนแปลงรูปร่างคือกิน คาลานอยด์โคพีพอด เป็นอาหารหลัก ในระยะวัยรุ่นและระยะโตเต็มวัยมีการใช้ทรัพยากรอาหารที่แตกต่างกัน สัตว์หน้าดินขนาดเล็ก ฮาแพคติคอยด์โคพีพอด เป็นอาหารหลัก สำหรับ *T. jarbua* ในระยะวัยรุ่น นอกจากนี้ยังกินสัตว์หน้าดินขนาดใหญ่ ปลา และเกล็ดปลาเป็นอาหาร ส่วน *T. jarbua* ระยะโตเต็มวัยกินอาหารที่อยู่ในมวลน้ำเป็นหลัก เช่น ปลา และเกล็ดปลา ส่วน *P. quadrilineatus* กินอาหารที่อยู่บริเวณหน้าดินเป็นหลัก โดยในระยะวัยรุ่นกินสัตว์หน้าดินขนาดเล็ก ฮาแพคติคอยด์โคพีพอด และระยะโตเต็มวัยกินสัตว์ทะเลหน้าดินขนาดใหญ่ เช่น หอยสองฝา และไส้เดือนทะเล รวมทั้งเกล็ดปลา ซึ่งการเปลี่ยนแปลงชนิดของอาหารในปลาแต่ละระยะเป็นผลมาจากความต้องการพลังงานที่มากขึ้นเมื่อปลามีขนาดที่โตขึ้น จากการศึกษาพัฒนาการของลักษณะสัณฐานวิทยาภายนอกและโครงสร้างที่ใช้ในการกินอาหารพบว่ามีความสำคัญต่อการเปลี่ยนแปลงแหล่งที่อยู่อาศัยและชนิดของอาหารของปลา โดยการเปลี่ยนแปลงความกว้างของลำตัวและความยาวของก้านครีบมีผลต่อการเคลื่อนที่ซึ่งนำไปสู่การเปลี่ยนแปลงแหล่งที่อยู่อาศัยและแหล่งอาหาร พัฒนาการของปาก ขากรรไกร ฟัน ซี่เหงือก และความยาวลำไส้ มีผลต่อการเปลี่ยนแปลงชนิดของอาหารเมื่อร่างกายมีขนาดที่โตขึ้น การพัฒนาของตาและจุดสีส่งผลต่อประสิทธิภาพในการหลบหลีกจากผู้ล่า ผลการศึกษาครั้งนี้สรุปว่าปลาทั้งสองชนิดมีการเลือกใช้ทรัพยากรที่อยู่อาศัยและอาหารที่ต่างกันในแต่ละช่วงของชีวิตตลอดจนมีรูปแบบและช่วงเวลาการสืบพันธ์ที่ต่างกัน ซึ่งเป็นกลยุทธ์ที่สำคัญในการอยู่ร่วมกันในบริเวณชายฝั่งจังหวัดตรัง

ภาควิชา	วิทยาศาสตร์ทางทะเล	ลายมือชื่อนิสิต ....
สาขาวิชา	วิทยาศาสตร์ทางทะเล	ลายมือชื่อ อ.ที่ปรึกษาหลัก ....
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NUENGRUETAI YOKNOI: RESOURCE UTILIZATION OF TERAPONTID FISHES *Terapon jarbua* AND *Pelates quadrilineatus* IN COASTAL AREA, TRANG PROVINCE. ADVISOR: ASSOC. PROF. NITTHARATANA PAPHAVASIT, CO-ADVISOR: JES KETTRATAD, Ph.D., 226 pp.

Terapon jarbua and *Pelates quadrilineatus* are found coexisted in the coastal area of Trang Province for spawning ground, nursing ground and feeding ground. It is interesting to understand how similar species coexisted despite the pressure of competition. Resource partitioning between species or between size classes is an adaptation to reduce the competition in shared resources. The ontogenetic niche shift in term of diet and habitat is one important process in resource partitioning. Ecomorphology in fishes oftens described the patterns of association between morphology and resource use. Therefore this study had focus on (1) the development pattern and definding length at juvenile of two terapontid fishes (2) the distribution patterns of fishes in different stages and reproductive ecology of adult fish of two terapontid fishes (3) the feeding structure development and stomach content analysis in these two terapontid fishes. The understanding on morphological development and distribution as well as reproductive biology and feeding ecology of both species can help to explain the resource utilization and partitioning between the coexisting species in the coastal area of Trang Province.

Terapon jarbua and *Pelates quadrilineatus* can be divided into 6 development stages: (1) preflexion larvae, (2) flexion larvae, (3) postflexion larvae, (4) transforming larvae, (5) juvenile (6) adult. The length-at-juvenile of *T. jarbua* and *P. quadrilineatus* were 23.16 and 18.24 mm, respectively. The size at first maturity of female and male of *T. jarbua* are 156.92 mm and 153.77 mm, respectively while the size at first maturity of female and male of *P. quadrilineatus* are 120.31 mm and 124.02 mm, respectively. *Terapon jarbua* and *Pelates quadrilineatus* showed the clear habitat utilization between developmental stages which planktonic larvae stage (preflexion, flexion and postflexion) and adult mostly inhabit in offshore. This indicated that the offshore area is the spawning ground of adult fish. However, they showed the clear differences in spawning period. *Terapon jarbua* had two peak of spawning periods during April to June and September to October. *Pelates quadrilineatus* had only a short discrete period for spawning from November to December. The differences in spawning period lead to temporal resource partitioning in planktonic larvae stage of both species. This also help to reduce food competition between their offspring. Transforming larvae and juveniles moved inshore and distributed in the coastal habitats. Transforming larvae and juveniles of *T. jarbua* distributed in the coastal swamps while transformation larvae and juveniles of *P. quadrilineatus* distributed in the seagrass beds. The complexity of microhabitat structure in the coastal swamps and seagrass beds are suitable for nursery area and refuge from predators. *Terapon jarbua* and *Pelates quadrilineatus* demonstrated the ontogenetic dietary shift. Larval stage of *T. jarbua* consumed predominantly on calanoid copepods and shifted to feed on small benthos harpacticoid copepods, large benthos, fishes and fish scales in juvenile stage. Adult stage feed mainly on fish and fish scales. The major food items of larval stage of *P. quadrilineatus* was also calanoid copepod and shifted to feed on small benthos harpacticoid copepods in juvenile stage. Adult stage feed mainly on large benthic animal such as, bivalves, polychaetes and fish scales. The ontogenetic differences in feeding habits have resulted from acquiring high energy diets for growth and development of fish. The study on morphology and feeding structure development indicated that body shape, eye, mouth, jaw, teeth, gill raker, intestinal length and fins were important characters which showed relationship between the morphological development and ontogenetic niche shifts. The morphological change in body depth and fin ray support mobility in the habitat shifts. The development of mouth, jaw, teeth, gill raker and intestinal length were important in the ontogenetic dietary shifts. The developments of eye and pigment pattern enhanced the feeding performance and predator avoidance. The differences in habitat and food utilization in the two terapontid species in each stage as well as the reproductive patterns and spawning periods are the important strategies to reduce competition between the two coexisting species in coastal area of Trang Province.

Department:	Marine Science	Student's Signature	
Field of Study:	Marine Science	Advisor's Signature	
Academic Year:	2016	Co-Advisor's Signature	

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INTRODUCTION

A. General Background and Hypothesis

Coastal area is one of the ecologically dynamic and productive areas for resource utilization in fishes. These areas provided abundance of food and various habitat types for fishes to reside in, such as sandy beaches, mangrove forests and seagrass beds. This allowed fishes to utilize coastal resources in term of food and habitats for foraging, reproduction and shelters (Paterson & Whitfield, 2000). Numerous studies of fish communities have elucidated differences in resource utilization among similar species inhabiting the same habitat, which leads to coexistence of species (Davis *et al.*, 2011; Davis *et al.*, 2012a; Hajisamae *et al.*, 2003; Horinouchi *et al.*, 2012; Kulbicki *et al.*, 2005; Lucena *et al.*, 2000; Nakane *et al.*, 2011; Norton, 1995; Piet, 1998; Sala & Ballesteros, 1997; Wainwright, 1988). The definition of coexisting species as defined by Holt (2001) is the state of two or more species being found in the same place at the same time. Amarasekare (2003) further extended the definition that coexistence resulted when populations of several species that utilize the same limiting resource manage to persist within the same locality. When resource are limited, resource partitioning and/or resource competition are evidenced in the coexistence of species (Osenberg *et al.*, 1992; Piet, 1998; Ross, 1986; Wainwright, 1988; Young *et al.*, 2010). Piet (1998) concluded that the positions of coexisting species in a community were usually described along differences resource dimension of an ecological space. These position depended on the availability of resources and on ecological processes such as interspecific competition or predation. Whenever interspecific competition predominated, the interacting species would evolved to specialized on exploitation of specific resources according to their morphological, behaviourial and physiological characters. Resource partitioning was an important mechanism for competing species to coexist. Over evolutionary time, resource partitioning of competing species could be facilitated by divergent changes of morphological characters. Habitats and food types are the two major resource partitioning usually observed. The clarification of resource utilization patterns has been a topic of considerable interest in the coexisting species. Resource partitioning is the process that drives competing species into different patterns of resource use or occupied different niches. Resource partitioning in fish communities distinguished three resource dimensions: the trophic, spatial and temporal dimension, of which trophic dimension was found to be the most important dimension for segregating fish species in a community. Thus, coexistence of species can be obtained through the differentiation of their ecological niches (Ross, 1986). Species living in the same habitat may partitioned their food by feeding on different food types. On the other hand, species that feed on the same diet may seek to live in different habitats in order to reduce competition when resources are restricted (Chakrabarty & Homechaudhuri, 2015). Ontogenetic niche shifts is one of the important process in niche partitioning with the shift of resources during development. Size imposes important constraints on the animal’s energetic requirement, its potential for resource exploitation, its susceptibility to natural enemies and the competitive ability. During ontogeny, the growing consumers are expected to change their ecological niche with respect to prey type, prey size or habitat type to meet their increasing basic metabolic demands and optimise their ecological foraging performance. The diets of most fish species change with growth (Werner & Gilliam, 1984). Ontogenetic niche shifts help maximize fitness by reducing competition between coexisting species with resource segregation by reducing predation risk through habitat shifts (Werner *et al.*, 1983), and by increasing growth through dietary shifts (Olson, 1996).

Terapon jarbua and *Pelates quadrilineatus* (Perciformes: Teraponidae) are widely distributed in the coastal areas of the tropical, especially in the Indo-West Pacific region (Blaber, 2000; Leis & Rennis, 1983). Both species are partial resident fish in the estuary, which larvae tend to reside towards brackish water and adults tend to reside towards seawater (Vidthayanon & Premcharoen, 2002). They are carnivores in the estuarine ecosystem (Hajisamae & Ibrahim, 2008; Whitfield, 1985). These two fish species were also found to coexist in the coastal area of Trang Province on the southwest coast of Thailand. Many previous studies reported that planktonic larvae and adults of both species were found offshore (Horinouchi *et al.*, 2012; Horinouchi *et al.*, 2009; Ikejima *et al.*, 2003; Matsuura *et al.*, 2005). Transforming larvae and juveniles of *T. jarbua* were found distributed in the coastal swamps and mangrove forests while the transforming larvae and juveniles of *P. quadrilineatus* were found distributed in the seagrass beds (Duangdee, 1995; Horinouchi *et al.*, 2012; Horinouchi *et al.*, 2009; Ikejima *et al.*, 2003; Tongnunui *et al.*, 2002; Tongnunui *et al.*, 2001; Tongnunui *et al.*, 2010). The distribution patterns of larvae, juveniles and adults of *T. jarbua* and *P. quadrilineatus* reflecting the habitat utilization model in the coastal area of Trang Province can be hypothesized in Figure 1.1 as summarized from various studies. The resource utilization of the two terapontid fishes can be hypothesized that *T. jarbua* use the coastal swamps as nursery ground and feeding ground during the larval and juvenile stages. On the other hand, *Pelates quadrilineatus* use the seagrass beds as nursery ground and feeding ground during larval and juvenile stages.

However, adults of both species utilized offshore area as spawning ground and feeding ground.

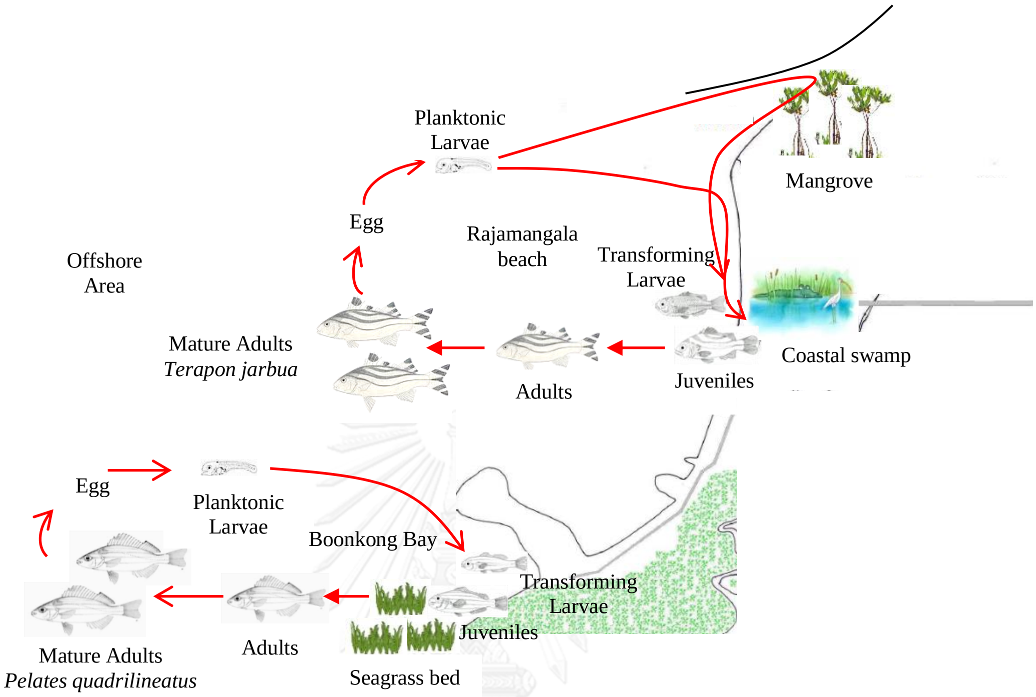


Figure 1.1 Habitat utilization of *Terapon jarbua* and *Pelates quadrilineatus* from the coastal area of Trang Province as hypothesized from Duangdee (1995); Tongnunui (1997); Tongnunui *et al*., (2002); Ikejima *et al*. (2003); Matsuura and Kimura (2005); Horinouchi *et al*. (2009); Tongnunui *et al*. (2010) and Horinouchi *et al*. (2012).

As outline above, *T. jarbua* and *P. quadrilineatus* are found coexisted in the coastal area of Trang Province for spawning ground, nursing ground and feeding ground. There have long been interested in understanding how similar species coexisted despite the pressure of competition. Resource partitioning refers to the process that drives competing species into different patterns of resource use or occupied different niches. Many studies suggest that, resource partitioning in sharing resources in fishes may be an adaptation to reduce the competition between species or size class (Ross, 1986). Ontogenetic niche shifts is one of the important processes in resource partitioning. The shift of resources during development corresponed to changes in morphology (Hjelm *et al.*, 2003; Persson *et al.*, 1998). The ontogenetic niche shifts were often detected as clear shifts in diet or habitat use with increasing body size (Wainwright, 1988). Ontogenetic niche shift in fishes was dued to the functional morphological limitation on prey choice and habitat use (Osenberg *et al.*, 1992; Wainwright, 1988). Mouth, jaw, body shape, eyes, and fins are important characters that demonstrated the relationship between the morphological development and ontogenetic niche shifts (Hjelm *et al.*, 2003; Hobson, 1979; McCormick, 1998; Norton, 1995; Webb, 1984). The study on the development pattern and defínding length at juvenile of terapontid fishes is essential in understanding their ontogenetic niche shift. The distribution patterns of fishes in different stages as well as the gonadal maturation can be used for identifying the habitat utilization for spawning ground and nursing area of these two coexisting species. The spawning area is defined by the area with high abundant of mature adults and fish larvae while the nursery area is where high abundance of juvenile fish is found (Ellis *et al.*, 2012). Food partitioning is the alternative process in reducing competition for fish sharing the same feeding ground (Blaber, 1997). Feeding structure development and stomach content analysis in these two terapontid fishes can be used to identify the main diets and feeding area in each stage. Therefore, the understanding on morphological development and distribution as well as reproductive biology and feeding ecology of both species can help to explain the resource utilization and partitioning between the coexisting species in the coastal area of Trang Province. The result of this study will provide in depth knowledge of resource utilization in coexisting fishes. Moreover, the results can be used as the guidelines in the management of fishery resources. It can also be used to promote these two terapontid fishes as one of the important aquaculture species.

B. Conceptual Framework of Research

Partitioning of resources, in particular food and habitat is thought to be a mechanism facilitating the coexistence of competing fish species when resources are limited (Ross, 1986; Young *et al.*, 2010). Partitioning of available resources may be determined by differences in morphology, physiology or behavior, which allow a species to exploit a portion of the available niche more efficiently than competing species (Tilman, 1987). In the coastal area of Trang province, *T. jarbua* and *P. quadrilineatus,* two terapontid fishes, were found to coexist. In this study, the attempt to investigate how these terapontid species with similar morphology can coexist in the same habitat. Morphological development in fish involves the process of growth and adaptation. The changes of morphology can also lead to structural defects affecting the development and feeding in fishes (Koumoundouros *et al.*, 1999). Associating with these changes, there is a sudden shift in diet or habitat

(Osenberg *et al.*, 1992). This enhance the resources segregation (Werner & Gilliam, 1984). Therefore, the **first topic** of this study is to investigate the developmental patterns in *T. jarbua* and *P. quadrilineatus* with respect to the change of morphometric characters, meristic characters and pigmentation. To ascertain the morphological changes (i.e. mouth gape, mouth diameter, jaw length, body depth, fin length and eye size) in fishes during growth in each stage can be used to explain how these fishes feed and move to the new habitat in order to partition resource. Size specific shifts in food types have been documented in ontogenetic niche shifts in a great variety of fish species. These shifts are often associated with or caused by shifts in habitat (Werner & Gilliam, 1984). The abilities to detect, pursue, capture and successfully handle prey in fishes may have an underlying functional basis related to morphology (Wainwright, 1988). The development of mouth gape, mouth diameter and jaw length determined the fish feeding ability. Mouth gape and jaw size are the important determinant for food prey size (Hjelm *et al.*, 2003; Hyndes *et al.*, 1997; McCormick, 1998; Olsen *et al.*, 1999). Larger fish eat larger prey and hence there will be gradual changes in size of prey with growth. The increase of body depth, fin length and eye size with fish growth enhance the fish mobility to facilitate shift to new habitat for feeding and to reside in. The development of these characters allow fish to have strong controlled swimming ability and better visual in the turbid habitat and able to catch its prey (Hobson, 1979; Norton, 1995; Webb, 1984). The coastal area is ecologically dynamic and productive areas used by many fishes for reproduction and nursery areas (Paterson & Whitfield, 2000). Fish have to choose habitat that provide high survival rate of their offspring. Therefore, the **second topic** of this study is to investigate the habitat utilization as the spawning and nursing area in *T. jarbua* and *P. quadrilineatus*. This is carried out by the study on distribution and abundance of both species in each stage. The gonadal maturation in each species and spawning period were also determined in relation to distribution. The spawning area can be determined by an area of high abundance of mature adult and fish larvae. High abundance of juvenile fish in the nursery area (Ellis *et al.*, 2012). Movement pattern in adult fish is also carried out. In addition, these results can explain the spatial and temporal resource partitioning by the two coexisting species.

Food is the one important factor for the survival of fish. Fish use food resource in their environment for growth. Fish must have the main prey items in each stage and diet shift to gain suitable energy for growth and reduce food competition. Many fishes show distinct ontogenetic changes in feeding habits and prey selection (Davis *et al.*, 2011; Davis *et al.*, 2012a; Horinouchi *et al.*, 2012; Jobling, 1995; Kanou *et al.*, 2004; McCormick, 1998; Wainwright, 1988). The actual timing of switches in diet usually relates to larvae becoming juveniles or juveniles becoming adult which related to changes in feeding structure (Blaber, 2000; Persson *et al.*, 1998; Wainwright, 1988). Difference 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, 1997). For example, Hjelm *et al.* (2003) reported that diet of *Rutilus rutilus*, smaller than 150 mm in total length was mainly consisted of zooplankton in water column, whereas *R. rutilus*, larger than 150 mm mainly fed on benthic macroinvertebrates. This change of diet and feeding habitat corresponded to body shape and the morphology of the feeding apparatus. *Rutilus rutilus* body shape gradually changed from fusiform into deeper body, larger mouth and longer gill rakers as well as narrower inter-raker distances during the development. These changes helped them in utilizing different food sources and coexist in the same area. Therefore, the **third topic** of this study is to investigate the diets of *T. jarbua* and *P. quadrilineatus* in each stage by studying the morphology of feeding structure and identifying the stomach contents. In addition, the availabled food sources in the coastal habitats were determind. This result can revealed the ontogenetic niche shift and food partitioning in the two coexisting species.

The conceptual framework of the research "Resource Utilization of Terapontid Fishes *T. jarbua* and *P. quadrilineatus* in Coastal Area, Trang Province" is outlined in Figure 1.2. The results of this study can be used as the guidelines in the management of fisheries resources and promoting *T. jarbua* and *P. quadrilineatus* as one of the important aquaculture species.

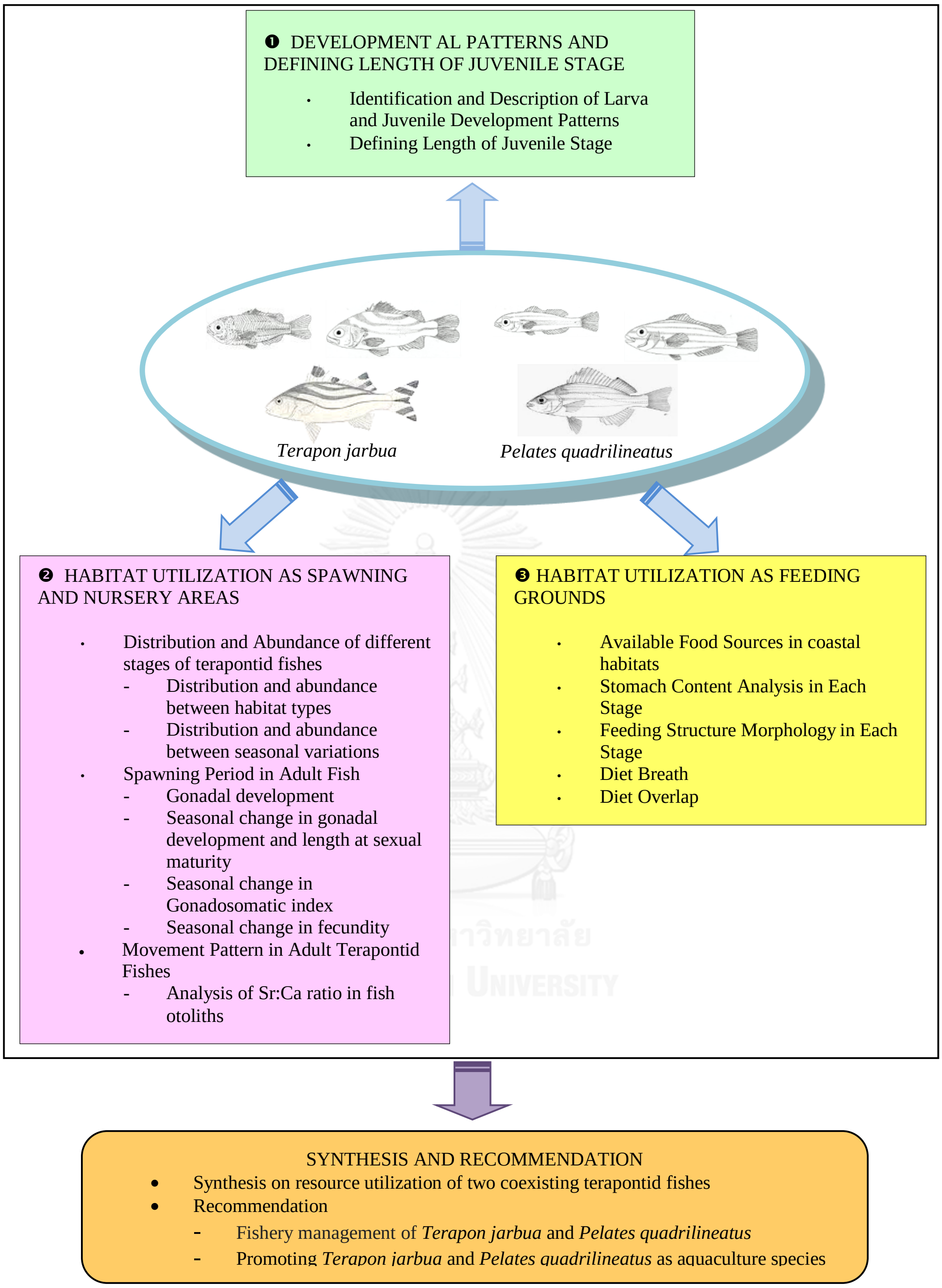


Figure 1.2 Conceptual framework of research on Resource Utilization of Terapontid Fishes, *Terapon jarbua* and *Pelates quadrilineatus* from the Coastal Area of Trang Province.

C. Description of Study Area and Sampling Period

The study area is a part of Sikao Bay, which located in coastal area of Trang Province on the southwest coast of Thailand. The bay is approximately 40 km long with the opening width of 30 km into the Andaman Sea**.** The coastal area is covered by various habitats such as mangrove forest, sandy beach, coastal swamp and seagrass bed which subjected to tidal influence. Sikao Bay has relatively a short dry season from January to April and the long wet season from May to December. The dry season is usually accompanied by light winds from the Northeast monsoon while strong winds associated with the Southwest monsoon occurred during the wet season. The study area consists of 8 sampling stations as shown in Figure 1.3. The two terapontid fishes, *T. jarbua* and *P. quadrilineatus* are distributed among these sampling stations. The samples were collected monthly during January to December 2013.

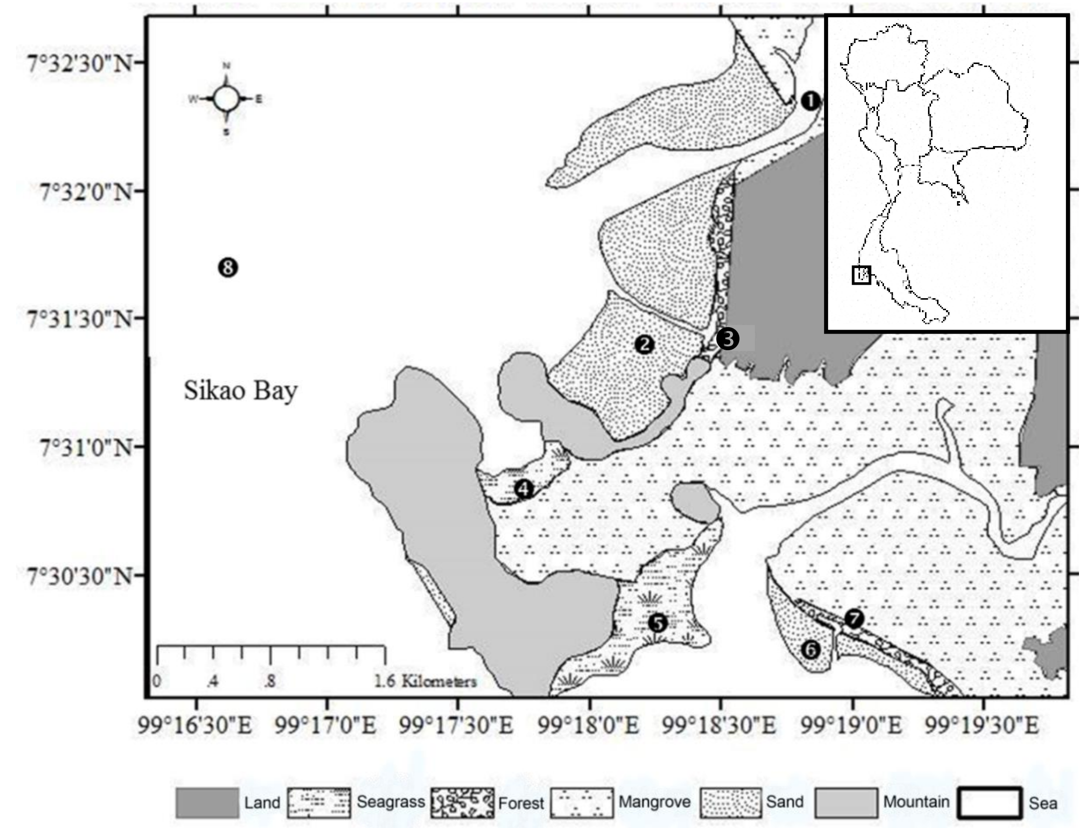


Figure 1.3 Study area located in the coastal area of Trang Province on the southwest coast of Thailand (❶ : Sikao Creek, ❷ : Rajamangala Beach, ❸ : Rajamangala Coastal Swamp, ❹: Boonkong Bay, ❺: Makham Bay, ❻: Pakmeng Beach, ❼: Pakmeng Coastal Swamp and ❽: Offshore area).

Station 1: Sikao Creek (N 7^{o}32’49.1”, E 99^{o}18’02.6”)

This area was the part of Sikao creek opening into Sikao bay. The width of the creek was approximately 25 meters. The bottom consisted of sand and soft mud sediment. Sikao creek was lined by the natural *Rhizophora apiculata* mangrove forest (Tongnunui *et al.*, 2002) (Figure 1.4). This area was always under tidal influence. Ikejima *et al.* (2003) had reported the temperature range at this station of 26.0-34.5 ^{o}C and the salinity range of 22.0-33.0 psu. During this sampling period from January to December 2013, the average water depth was in the range of 0.69±0.11 m in the dry season and 0.72±0.19 m in the wet season. The average water temperature was 28.88±0.63 ^{o}C in the dry season and 27.61±0.36 ^{o}C in the wet season. The average salinity were 27.20±0.24 psu recorded in the dry season and 27.43±0.90 psu in the wet season.

Figure 1.4 Sikao Creek (Station 1) located in the coastal area of Trang Province.

Station 2: Rajamangala Beach (N 7^{o}31’94.1”, E 99^{o}18’82.3”)

This area located in the intertidal zone of Rajamangala beach. The coastline was 2.2 kilometers in the length. The bottom sediment was mainly sand (Figure 1.5). Ikejima *et al.* (2003) reported the temperature range at this station was 28.0-34.0 ^{o}C and the salinity range of 27.0-32.5 psu. The environmental monitoring during this sampling period from January to December 2013 revealed the average water depth recorded 1.00±0.13 m in the dry season and 0.92±0.19 m in the wet season. The average water temperature was 29.38±0.48 ^{o}C in the dry season and 27.94±0.50 ^{o}C in the wet season. The average salinity was 29.88±0.63 psu in the dry season and 28.88±0.79 psu in the wet season.

Figure 1.5 Rajamangala Beach (Station 2) located in the coastal area of Trang Province.

Station 3: Rajamangala Coastal Swamp (N 7°31’98.5”, E 99°18’82.4”)

Natural coastal swamp, Rajamangala coastal swamp, was connecting to the Rajamangala Beach. The area of this natural coastal swamp was 18 meters in length and 3.5 meters in width. The catchment area of this coastal swamp was about 30 m^3. The bottom sediment was mainly sand. Small forest lined the coastal swamp with dominant trees of *Casuarina equisetifalia*, *Rhizophora apiculata* and *Pandanus tectorius*. Tongnunui *et al.* (2010) recorded the temperature and salinity range at the Rajamangala coastal swamp were 27.0-30.0 °C and 15.0-28.0 psu, respectively. During this sampling period from January to December 2013, this coastal swamp dried up during March to April (Figure 1.6). The average water depth was 0.51±0.08 m in the dry season and 0.55±0.15 m in the wet season. The average water temperature was 28.25±0.35 °C in the dry season and 27.64±0.56 °C in the wet season. The average salinity recorded 29.65±0.21 psu in the dry season and 28.38±0.88 psu in the wet season.

Figure 1.6 Rajamangala Coastal Swamp (Station 3) located in the coastal area of Trang Province.

Station 4: Boonkong Bay (N 7^{o}31’58.1”, E 99^{o}17’59.5”)

This station located in the natural seagrass bed of Boonkong Bay. This seagrass bed consisted of *Halophila ovalis* (71.47%), *Cymodocea serrulata* (23.23%), *Thalassia hemprichii* (5.04%) and *Enhalus acoroides* (0.26%). The bay was 750 meters in length and 525 meters in width. The bottom sediment was soft mud (Kongwatmai, 2015) (Figure 1.7). Horinouchi *et al.* (2016) reported the temperature range at this seagrass bed was in the range of 31.0-35.0 ^{o}C and the salinity range of 27.0-30.0 psu. During this sampling period from January to December 2013, the average water depth was 0.98±0.25 m in the dry season and 0.90±0.14 m in the wet season. The average water temperature was 29.25±0.65 ^{o}C in the dry season and 28.06±0.34 ^{o}C in the wet season. The average salinity was 30.35±0.72 psu in the dry season and 29.25±0.65 psu in the wet season. The average immersion period was 4 hours/day at lowest low tides.

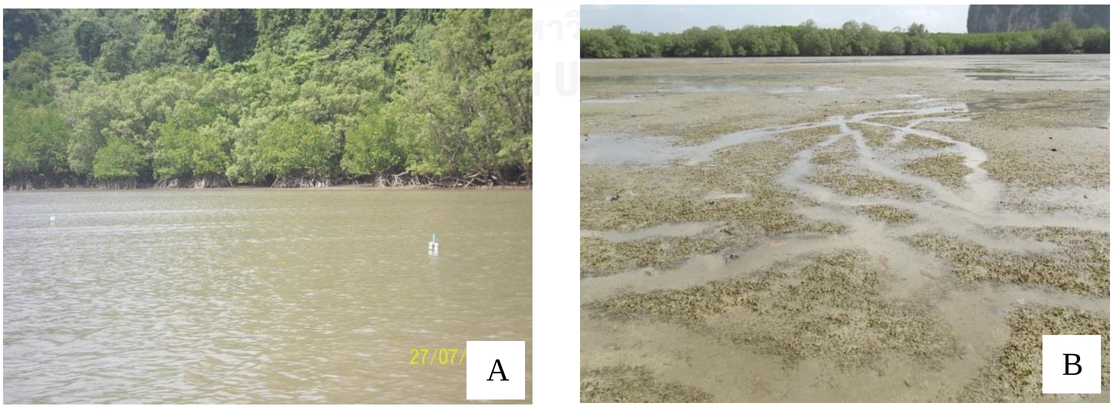


Figure 1.7 Boonkong Bay (Station 4) located in the coastal area of Trang Province. A: Boonkong Bay during high tide, B: Boonkong Bay during low tide.

Station 5: Makham Bay (N 7°30’075.6” E 99°18’86.1”)

This station was located in the natural seagrass bed of Makham Bay. Makham Bay seagrass bed was dominented by *Cymodocea serrulata* (87.0%), *Enhalus acoroides* (9.0%), *Halophila ovalis* (1.0%) and *Thalassia hemprichii* (1.0%). The bay was 720 meters in length and 550 meters in width (Kongwatmai, 2015). The bottom sediment was soft mud (Figure 1.8). During this sampling period from January to December 2013, the average water depth was recorded at 0.77±0.26 m in the dry season and 0.80±0.17 m in the wet season. The average water temperature was 29.00±0.41 °C in the dry season and 28.08±0.33 °C in the wet season. Similar to previously recorded by Phinrub *et al.* (2015) of the average temperature of 27.61 °C. The average salinity was 29.88±0.63 psu in the dry season and 29.25±0.80 psu in the wet season which corresponded to the average salinity of 31.17 psu previously reported by Phinrub *et al.* (2015). This seagrass bed also had the imersion period 4 hours/day at lowest low tides.

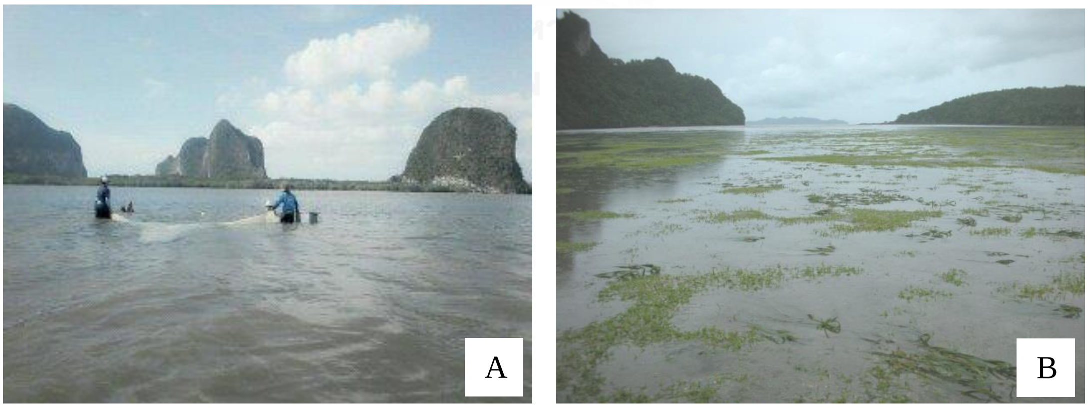


Figure 1.8 Makham Bay (Station 5) located in the coastal area of Trang Province. A: Makham Bay during high tide, B: Makham Bay during low tide.

Station 6: Pakmeng Beach (N 7°30’08.0”, E99°18’42.2”)

This sampling station was located in the sandy intertidal zone of Pakmeng beach (Figure 1.9). The total coastline was 4.7 kilometers in length. The water depth at this station was previously recorded by Punnarak (2004) in the range of 6.0-7.3 m in the nearshore water. Punnarak (2004) also reported the temperature range of 28.4-32.4 °C and the salinity range of 31.7-34.4 psu. During this sampling period from January to December 2013, the average water depth was 0.85±0.25 m in the dry season and 0.88±0.20 m in the wet season. The average water temperature was 28.75±0.65 °C in the dry season and 28.03±0.56 °C in the wet season. The average salinity was 30.25±0.65 psu in the dry season and 29.66±0.71 psu in the wet season.

Figure 1.9 Pakmeng Beach (Station 6) located in the coastal area of Trang Province.

Station 7: Pakmeng Coastal Swamp (N 7°30’07.3”, E 99°19’45.5”)

Natural coastal swamp, Pakmeng Coastal Swamp, was connected to Pakmeng Beach. The coastal swamp was 15 meters in length and 2 meters in width. The catchment area of this coastal swamp was approximately 15 m^3. The bottom sediment was mainly sand. The coastal swamp was dominanted by various plants such as, *Casuarina equisetifalia*, *Rhizophora apiculata* and *Pandanus tectorius* (Figure 1.10). During this sampling period from January to December 2013, the average water depth was 0.48±0.12 m in the dry season and 0.95±0.15 m in the wet season. The average water temperature was 28.13±0.25 °C in the dry season and 27.90±0.46 °C in the wet season. The average salinity was 30.20±0.40 psu in the dry season and 28.43±0.35 psu in the wet season.

Figure 1.10 Pakmeng Coastal Swamp (Station 7) located in the coastal area of Trang Province.

Station 8: Offshore Area (N 7°31'01.3", E 99°17'83.9")

The sampling station representing the offshore area was in front of Rajamangala Beach being 2 km from the coastline (Figure 1.11). The water depth at this station was previously recorded by Punnarak (2004) in the range of 14.1-14.2 m. During this sampling period from January to December 2013, the average water depth was 12.25±2.06 m in the dry season and 11.75±2.19 m in the wet season. The average water temperature was 28.63±0.75 °C in the dry season and 28.04±0.29 °C in the wet season. The average salinity was 30.38±0.48 psu in the dry season and 30.21±0.51 psu in the wet season.

Figure 1.11 Offshore area (Station 8) approximately 2 km from coastline of Trang Province.

D. Research Methodology

The study on resource utilization of terapontid fishes *T. jarbua* and *P. quadrilineatus* in coastal area, Trang Province were divided in 4 parts, consisted of (1) developmental pattern and defining length of juvenile stage in terapontid fish, *Terapon jarbua* and *Pelates quadrilineatus*, (2) habitat utilization as spawning and nursery areas in terapontid fish, *Terapon jarbua* and *Pelates quadrilineatus*, (3) habitat utilization as feeding ground in terapontid fish, *Terapon jarbua* and *Pelates quadrilineatus*, and (4) synthesis and recommendation. The research methodology in each part were as followed in Table 1.1.

Table 1.1 Research methodology on "Resource Utilization of *Terapon jarbua* and *Pelates quadrilineatus* from the Coastal Area of Trang Province".

Research Attributes	**Research Methodology**
Developmental pattern and defining length of juvenile stage in terapontid fish, *Terapon jarbua* and *Pelates quadrilineatus* 1. Fish Sample	• Planktonic fish larvae were sampled from offshore area of Rajamangala Beach, Sikao Bay, by surface tows using a plankton net and preserved in 4% neutral formalin. • Transforming larvae and juvenile fish were sorted trom the collections of Tongnunui (2010) in Rajamangala University of Technology Srivijaya Fish Collection.
2. Identification of Larval and Juvenile Development	• All samples of *T. jarbua* and *P. quadrilineatus* were identified following, Okiyama (1986) Leis and Trinski (1989) Jeyaseelan (1998) and Leis and Carson-Ewart (2000). • Fifteen morphometric characters, 14 meristic characters and pattern of pigmentation were measured and counted for the identification of larval stage and juvenile stage.
3. Defining Length of Juvenile Stage	• Defining length at juvenile by multivariate morphometric analysis followed Nikolioudakis *et al.* (2014). Raw measurements of the 13 morphometric characters were subjected to Principal Components Analysis (PCA) (change in oblique orientation: promax, KMO > 0.5 and factor loading > 0.3). The shape component or principal component 2 (PC2) were plot against standard length (SL) and fitted with a piecewise regression by Sigma Plot 10.0 in order to identify the transition point from larvae to juvenile.

Table 1.1 Continued.

Research Attributes	**Research Methodology**
Habitat utilization as spawning and nursery areas in terapontid fish, *Terapon jarbua* and *Pelates quadrilineatus*	
1. Fish Collection	• Preflexion larvae, flexion larvae and postflextion larvae were sampled by plankton net and preserved in 4% neutral formalin. • Transforming larvae and juvenile were collected by small seine net and preserved in 10% neutral formalin. • Adult fish were collected from gill net (30m long, mesh size of 30 mm) fishery landings. All samples were kept on ice and preserved in the refrigerator at 4^{o}C in the laboratory.
2. Environmental Parameter	• Salinity, temperature and water depth were recorded insitu monthly in each station. Salinity and temperature were measured by salinity and temperature meter AZ8371. Depth of water was measured by depth measuring rope.
3. Distribution and Abundant	• Number and abundance of fish in each stage were compared in each station and season variations.
4. Histological Examination	• All gonad specimens were processed using standard histological techniques (Humason, 1979). The middle part of gonad was cut about 5 mm. The gonad tissues were dehydrated in a series of ethanol. Tissues were then cleared in xylene and embedded in paraffin. The paraffin blocks of gonadal tissue were serially sectioned at 6 µm thickness and stained with Mayer hematoxylin and 1% Eosin G Aqueous solution. • Developmental stages of gonad were categorized according to Brown-Peterson *et al*. (2011). Sex was determined by examination of the gonads.
5. Gonadosomatic Index (GSI)	• The gonadosomatic index (GSI) of females and males were calculated as the proportion of the weight of the gonad to the weight of eviscerated body in percent.
6. Fecundity	• The fecundity of gravid females was estimated individually using the gravimetric method.
7. Movement Pattern in Adult Terapontid Fish	• Analysis Sr:Ca ratio in fish otoliths was analyzed by an electron probe microanalyzer (EPMA).

Table 1.1 Continued.

Research Attributes	Research Methodology
Habitat utilization as feeding ground in terapontid fish, *Terapon jarbua* and *Pelates quadrilineatus* 1. Available Food Sources in the Coastal Habitat	• Zooplankton samples were collected by using plankton net and preserved in 4% neutral formalin for further sorting and identifications. • Macrobenthic fauna were collected by core sample and fixed in 10% neutral formalin for further sorting and identifications.
2. Stomach Content Analysis	• Food items in stomach contents of three stages of terapontid fishes were identified to taxon and the main food items were identified using the index of relative important (IRI) of Pinkas *et al*., (1971), as modified by Hyslop (1980).
3. Feeding Structure Morphology Study	• The development of feeding structure morphology namely mouth position, teeth, gill rackers, shape of stomach and intestinal length in fish of four stages were determined.
4. Diet Breath	• Diet breadth is calculated using Levin’s standardized index.
5. Diet Overlap	• Diet overlap is calculated using Bray-Curtis similarity index.
Synthesis and recommendation 1. Synthesis	• The resource utilization of *Terapon jarbua* and *Pelates quadrilineatus* in coastal area of Trang Province.
2. Recommendation	• Fishery management of *Terapon jarbua* and *Pelates quadrilineatus*. • Promoting *Terapon jarbua* and *Pelates quadrilineatus* as potential aquaculture species.

E. Objectives

1. To study developmental pattern and defining length of juvenile stage of *Terapon jarbua* and *Pelates quadrilineatus* in coastal area, Trang Province.
2. To identify habitat utilization as spawning and nursery areas of *Terapon jarbua* and *Pelates quadrilineatus* in coastal area, Trang Province.
3. To identify habitat utilization as feeding grounds of *Terapon jarbua* and *Pelates quadrilineatus* in coastal area, Trang Province.

F. Expected Results

1. The results provide in depth knowledge in morphology, distribution, reproductive biology and feeding ecology of *Terapon jarbua* and *Pelates quadrilineatus*.
2. The results can be used as the guidelines of the *Terapon jarbua* and *Pelates quadrilineatus* fishery resources management.
3. The results can be used as the basic information in promoting *Terapon jarbua* and *Pelates quadrilineatus* as one of the important aquaculture species for commercial fish and ornamental fish.

CHAPTER 2

DEVELOPMENTAL PATTERNS AND DEFINING LENGTH OF JUVENILE STAGE IN TERAPONTID FISHES, *Terapon jarbua* AND *Pelates quadrilineatus*

A. Introduction

There have long been interests in understanding how similar species or species with in the 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 (Blaber, 1997; Gerking, 1994). Ontogenetic niche shifts is one of the important process in niche partitioning with the shift of resources during development. Size imposes important constraints on the animal’s energetic requirement, its potential for resource exploitation, its susceptibility to natural enemies and the competitive ability. During ontogeny, fishes 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 optimise their ecological foraging performance. It helps maximize fitness by reducing competition between coexist species with resource segregation (Werner & Gilliam, 1984). Morphological development in fish is an involving process of growth and adaptation. During the development, larvae undergo extreme changes in morphology, metabolism and behavior in order to transform to juveniles. The changes can also lead to structural defects affecting for developing, feeding and ultimately the survival of the organism (Koumoundouros *et al.*, 1999). 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). The demersal fish complex life cycles involve the ontogenetic changes in morphology, physiology and behaviour as their pelagic larval stages colonize benthic habitats. The term “metamorphosis” is used to encompass the changes in structure and function that occur as a fish takes on its juvenile form, which often coincides with settlement. Metamorphosis is thought to occur because individuals must possess characteristics that maximize survival in each environment. The loss of larval characters and the development of the juvenile form can be gradual, but often it occurs abruptly, especially in fish that are demersal as adults (Leis & Carson-Ewart, 2000; McCormick *et al.*, 2002). Associating with these changes, there is a sudden shift in diet or habitat for resources segregation (Osenberg *et al.*, 1992; Werner & Gilliam, 1984).

Ecomorphology in fishes oftens described the patterns of association between morphology and resource use. Several studies have identified a strong association between fish morphology and diet such as intestinal length commonly correlated to the degree of herbivory and mouth gape strongly correlated to prey size and the degree of piscivory (Davis *et al.*, 2011; Davis *et al.*, 2012a; Davis *et al.*, 2010; Davis *et al.*, 2013; Elliott & Bellwood, 2003; McCormick, 1998; Mittelbach & Persson, 1998; Norton, 1995; Piet, 1998; Wainwright & Richard, 1995). Dentition also shows correlations to feeding types in fishes with conical holding teeth corresponding to carnivory and flattened cutting teeth to herbivory (Stoner & Livingston, 1984). Most ecomorphological studies of fish have placed emphasis on the comparisons of the adult morphologies of different species in the terminal morphologies. Ontogenetic differences in resource use, particularly diet, within fish species can not be ignored (Davis *et al.*, 2012a; Hjelm *et al.*, 2003; Mittelbach & Persson, 1998; Piet, 1998; Stoner & Livingston, 1984; Wainwright & Richard, 1995; Werner & Gilliam, 1984).

Stoner and Livingston (1984) concluded from their work on sympatric sparid fishes from seagrass meadows that ontogenetic and interspecific variations in the diets of the fishes was correlated with differences in external morphology related to locomotion, mouth dimensions and ontogeny of dentition. The ontogenetic process of fish seemed to be sufficiently flexible to allow larvae to adapt to their environment. The important characteristics of fish larvae includes the ability of finding food, predators avoidance and gaining competitive ability to be able to share resources with juveniles and adults (Urho, 2002). Boglione *et al.* (2003) clearly described the four ontogenetical stages of sharpsnout seabream, *Diplodus puntazzo* (Spiridae): larval, post-larval, transitional and juvenile stages based on the ontogenetic sensory development, except vision in relation to diet change. McCormick *et al.* (2002) also concluded the importance of ontogenetic shift in demersal fish life cycles in particular the metamorphosis occurred during the juvenile stages which often coincides with settlement. Demersal life stages have markedly different energy requirement, with an energy regime devoted to growth and reproduction, and are exposed to differing sensory stimuli and mortality agents. Thus, the understanding in the developmental patterns in fishes can help to explain their relationships between functional morphology and difference in resource utilization of fishes.

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, squamation began 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 of only one character was often 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 prey items and developing fin rays complement to increase swimming performance to help finding new food source or habitat (Urho, 2002). Nikolioudakis *et al.* (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-at-morphological change in white seabream. Then, Nikolioudakis *et al.* (2014) used this method to find the mean length at juvenile of other fishes and found that temperature have effect on morphological change. *Oblada melanura* is a species that was recruited during the warmest period of the 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 was recruited during the cold period of month were not in close proximity. *Terapon jarbua* and *P. quadrilineatus* were tropical species and presumably should have close estimations between mean length at juvenile and border between intermediate and juvenile stages. The method to calculate length-at-metamorphosis based on the multi-character approaches as introduced by Nikolioudakis *et al.* (2010) and Nikolioudakis *et al.* (2014)can be used for the two coexisting terapontid fishes. Morphometric characters were used in multivariate analysis. When raw measurements were used in principal component analysis (PCA), the PC1 was represented by size variation. PC2 was represented shape variation on growth of fish and gave an inflection point where shifts in growth patterns occurs between larvae and juvenile stage (Shea, 1985). Therefore, it better reflects the transition point between the larvae and the juvenile (Nikolioudakis *et al.*, 2010; Nikolioudakis *et al.*, 2014).

In Thailand, larvae and juveniles of *Terapon jarbua* (Forsskål, 1775) and *Pelates quadrilineatus* (Bloch, 1790) have been reported to coexist in several areas (Chayakul, 2007; Duangdee, 1995; Matsuura *et al.*, 2005; Tongnunui *et al.*, 2010). It is interesting to understand how these species, which are in the same family and possessing similar morphology, can coexist in the same area. The aims of this study are to address 1) development patterns of both species, *T. jarbua* and *P. quadrilineatus*, by using morphometric character, meristic character and pigmentation; 2) defining the length at juvenile of both species by adopting a multivariate morphometric analysis to define the transitional point between larvae and juvenile; 3) the allometric relationships of morphological variables and size in order to understand the ontogenetic differences in resource utilization. The result of this study can be used to explain the morphological changes during ontogeny in relation to resource utilization in the coexisting species.

B. Literature Review

1. Terminology and Development of Larvae and Juvenile Fish

Terminology of the developmental stages of fishes has been the subject of much debate and many attempts have been made to define a universal system. Mostly this has resulted in confusion. Because there is so much diversity in the way in which fishes develop. Various terminologies have been proposed to define the stages of development in fishes (Balon, 1975; Hubbs, 1943; Kendall, 1984). The terminology used here is based on the widely used and complete development of fish (Kendall, 1984). The end of larval period was defined with the attainment of full external meristic characters and the squamation. Kendall (1984) divided the development pattern of fish into 3 primary developmental stages as follows:

1.1 Egg: This phase covers the period from fertilization to hatching of the egg. During incubation, the embryo is nourished by the egg yolk and other storage food sources.

1.2 Larva: This phase is the development phase from hatching until the number of fin rays reach completion as in adult. Fish goes through extreme morphological changes during the larval stage. The larval stage can be divided into 5 subdivision; yolk-sac larva, preflexion larva, flexion larva, postflexion larva and transformation larva.

1.2.1 Yolk-sac larvae stage, most fish have yolk sac for nourishment unit hatching. When hatching, the yolk is absorbed.

1.2.2 Preflexion larvae stage begins at the end of yolk-sac larval stage and lasts until the notochord starts to flex. The notochord is straight and the larva is just starting to feed. Sensory and locomotors power are developing rapidly. The preflexion larvae have functional eyes, movable jaws and complete gut in order to capture pray. The fin is usually continuous finfold, not divided into separate fins. Pectoral fins are well developed and used for positioning. The appearance of pigmentation is observed.

1.2.3 Flexion larva stage is the stage when the tip of notochord bends dorsally and caudal fin develops. This stage ends when notochord flexion is completed. During this stage in several fishes, there are the rapid development of fin rays, changes in body shape, changes in locomotors ability accompanied with the changes in feeding behavior.

1.2.4 Postflexion larva stage begins when notochord flexion is complete and ends when all of fin rays have been formed. Larval specializations are more developed and larva grows in size.

1.2.5 Transformation larva stage is the transitional stage, between larva and juvenile stages. This is considered in several fishes as the change from planktonic to demersal habitats. Two ontogenetic processes occur during this stage of transition between larva to juvenile are loss of specialized larva characters and attainment of juvenile characters. These changes include pigmentation pattern, body shape, fin migration, photophore formation, loss of elongate fin rays and head spines, and eye migration as well as scale formation.

1.3 Juvenile: This stage begins when fin ray compliment are fully developed and scale formation begun. The juvenile stage ends when the fish enters the adult population or attains sexual maturity.

The study on the developmental pattern in fishes is not only important for taxonomy and fish identification but also for the understanding of ontogenetic shifts in resource uses in fishes (Boglione *et al.*, 2003). Dietary shifts in fish often correlated to morphological development. Piet (1998) demonstrated that the morphological variations in some fish assemblages contributed to the observed ontogenetic changes in diet directly to changes in the body size.Feeding not only correlated to morphological features but also to ontogeny and to the availability of suitable food types which may be influenced by environmental factors (Eggold & Motta, 1992). Morphological characters that determine feeding performance as fish increase in size is also the key factor where correlated with ontogenetic diet shifts (Cassemiro *et al.*, 2008; Kramer & Bryant, 1995; Piet, 1998; Wainwright & Richard, 1995). As many studies failed to identify the transition from the larval to juvenile periods. This has caused many larvae to be regarded as juveniles. Urho (2002) suggested the important of identifying the transition from larva to juvenile based on the dominant morphological changes in body proportion and coloration, combined with behavioral aspects and habitat changes.

2. Defining Length at Juvenile of fish

Most marine fishes have indirect development and complex life cycles with distinct intervals: embryo, larva, juvenile, adult and senescent (Balon, 1975; L. A. Fuiman *et al.*, 1998). The clear definition of the development stages in fish is essential when one begins to apply ontogenetic scales for interspecific comparisons of morphological and behavioral development of fish (L. A. Fuiman *et al.*, 1998), or to identify ontogenetic shifts in resource use of fish (Boglione *et al.*, 2003). However, the study of the development pattern and defining stage of fish are not easy, especially the transition stage between larva to juvenile. The later stages of the larval stage share several characteristics as in the juvenile but with less developed features (Methven & McGowan, 1998; Renaud *et al.*, 1986). Defining the onset of juvenile period (end of larval period) is rather arbitrary in most species with indirect development due to the lack of detailed information on larval and juvenile development (Copp & Kovác, 1996; Ditty *et al.*, 2003; Urho, 2002). Single morphological character approach (univariate morphometric analysis) has been traditionally used for identifying the transition between larvae and juvenile stages, include the full count of fin ray, completed squamation and development of sensory feature as well as habitat shift. The transition from larval to juvenile development is associated with a shift in allometric growth or shape coupled with abrupt or gradual changes in morphological characters such as disappearance of finfold, acquisition of the adult complement of fin spines and rays, adult pigmentation and squamation (Ditty *et al.*, 2003; McCormick *et al.*, 2002; Urho, 2002). One character approach is further complicated by the individual fish variation and differences in the timing and rate of ontogeny for individual characters. Therefore, one character approach is largely inadequate for a unified, unambiguous definition of size/age at metamorphosis (Ditty *et al.*, 2003; Urho, 2002).

Nikolioudakis *et al.* (2010) developed the techniques to define the transition from larval to juvenile development as mean length-at-metamorphosis in white sea-breams, *Diplodus sargus sargus*, using morphometric as well as morphological characters as the multi-character approaches. The morphometric analysis was based on principles of multivariate allometry whereas the analysis of morphological on assigning a suite of selected characters into larval, transforming and juvenile stages. When raw measurements were used in principal component analysis (PCA), the PC1 was affected by size variations while the PC2 represented shape variations on growth of fish (Shea, 1985). When PC2 were plotted against SL, an inflection point appeared where a shift in growth patterns occurred between larvae and juvenile stage. Therefore, it reflects the transition point between the larvae and the juvenile (Nikolioudakis *et al.*, 2010). Nikolioudakis *et al.* (2014) used this method to find the mean length at juvenile of other fishes and found that temperature was the important factor in determining the size at metamorphosis and degree of synchronization of changes in morphological character. *Oblada melanura* is a species that was recruited during the warmest period of the 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 was recruited during the cold period of month were not in close proximity. *Terapon jarbua* and *P. quadrilineatus* were tropical species and presumably should have close estimations between mean length at metamorphosis and border between intermediate and juvenile stages. Therefore, the multivariate morphometric analysis as introduced by Nikolioudakis *et al.* (2010) and Nikolioudakis *et al.* (2014) can be used for defining length at juvenile of two terapontid fishes, *T. jarbua* and *P. quadrilineatus*.

3. Developmental Patterns in Terapon jarbua and Pelates quadrilineatus

Data on developmental patterns in the two terapontid fishes, *T. jarbua* and *P. quadrilineatus* is largely incomplete. In addition, the details on morphological characters as related to dietary habits are limited.

3.1 *Terapon jarbua*

Terapon jarbua has moderate body depth and laterally compressed. There is 25 myomeres on the body (6-11+14-19) (Leis & Carson-Ewart, 2000). The developmental pattern in *T. jarbua* in each stage are as follows:

3.1.1 Preflexion larvae were oval in shape, sturdy and light-greenish pigments throughout the body excluding the larval finfolds as in Figure 2.1. Along the base of finfold there were series of black pigments (Jeyaseelan & Vannucci, 1998; Okiyama, 1988).

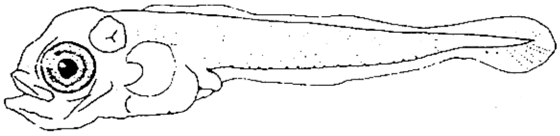


Figure 2.1 *Terapon jarbua* in preflexion larvae stage (2.3 mm). Figure was after Okiyama (1988).

3.1.2 Postflexion larvae as in Figure 2.2 were more advanced at a given size with more developed head spination, deeper bodies, larger head and smaller gap between anus and anal fin as compared to *P. quadrilineatus* (Leis & Carson-Ewart, 2000). There were 6 kinds of spine in the operculum namely; opercular spine (located the top of the opercular margin is long, strong and extending beyond margin of opercular lobe), preopercular spine (serrations spine located on preoperculam), posttemporal spine, cleitral spine and interopercular spine. No variations in number of spines and rays in fins among postflexion larvae, juveniles and adults. Pigmentation with black stellate pigments spreaded throughout the body and head (Jeyaseelan & Vannucci, 1998).

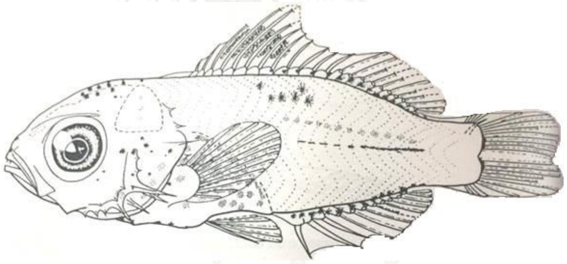


Figure 2.2 *Terapon jarbua* in postflexion larvae stage (5.3 mm). Figure was after Leis and Carson-Ewart (2000).

3.1.3 Juvenile had moderate body depth and laterally compressed as in Figure 2.3. Mouth gape usually obliqued with equal jaws. Upper jaw located in anterior margin of eye in the juvenile and center of orbit in adult. Opercular spine was very long and strong, extending beyond margin of opercular lobe. Preopercular spine strongly serrated. Posttemporal bone expanded, exposed and serrate posteriorly. The body color was silvery greyish dorsally and silvery white ventrally, 3 or 4 dark brown or back downwardly curved longitudinal stripes on body, spinouts portion of dorsal fin with a blackish blotch dorsally on membranes between 3rd and 6th spines and 5th and 7th rays, both caudal fin lobe with dark tips and transverse band (Jeyaseelan & Vannucci, 1998).

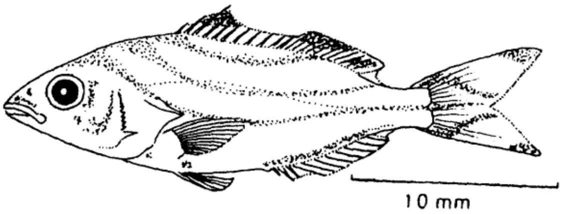


Figure 2.3 *Terapon jarbua* in juvenile stage (22.5 mm). Figure was after Jeyaseelan and Vannucci (1998).

3.2 *Pelates quadrilineatus*

Pelates quadrilineatus has moderate body depth and laterally compressed. There is 25 myomere on the body (6-11+14-19) (Leis & Carson-Ewart, 2000). The descriptive morphology of *P. quadrilineatus* in each stage are as follows:

3.2.1 Preflexion larvae were oval in shape, sturdy and light-greenish pigments throughout the body excluding the larval finfolds as in Figure 2.4. Along the base of finfold, series of black pigment were presented but the number of the pigment were less than *T. jarbua* (Leis & Carson-Ewart, 2000).

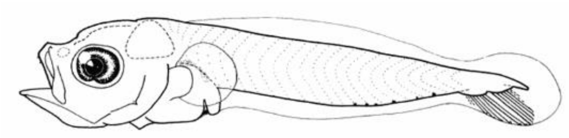


Figure 2.4 *Pelates quadrilineatus* in preflexion larvae stage (3.6 mm). Figure was after Leis and Carson-Ewart (2000).

3.2.2 Postflexion larvae as in Figure 2.5 showed that the body was somewhat more elongated than *Terapon jarbua*. Opercular spine was long and strong but did not extend beyond margin of opercular lobe and preopercular spine was serrated (Jeyaseelan & Vannucci, 1998).

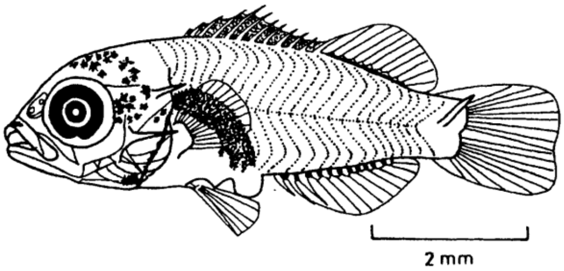


Figure 2.5 *Pelates quadrilineatus* in postflexion larvae stage (7.0 mm). Figure was after Jeyaseelan and Vannucci (1998).

3.2.3 Juvenile had moderate body depth and laterally compressed jaw equal, gape oblique and posterior margin of upper jaw extend to the vertical line through posterior nostril. Opercular spine is very long and strong, but not extending beyond margin of opercular lobe. Posttemporal bone not expanded or exposed. Color was generally silver with 4-6 narrow dark brown or black horizontal stripes on body. Dorsal fin had a black blotch dorsally between 3rd and 7th spines. A blotch was present on the shoulder. The caudal fin was without bands or stripes (Jeyaseelan & Vannucci, 1998).

C. Materials and Methods

1. Fish Sample

In this study, specimens of both species were collected from two sources. The planktonic larvae of both species (*T. jarbua* N=8 and *P. quadrilineatus* N=6) were sampled from offshore area of Rajamangala Beach, Sikao Bay, Trang Province. These planktonic larvae were used for the description of the preflexion, flexion and postflexion stages. The area is 2 km from the shore with depth of 8-10 meter (Figure 2.6). The bottom sediment was mainly sand. Samples were collected by using surface tow plankton net (0.5 m mouth diameter; 330 μm mesh size) by low speed boat tow in 3 min. All samples collected by this method were fixed and preserved in 4% neutral buffered formalin. The samples were collected monthly from January to December 2013.

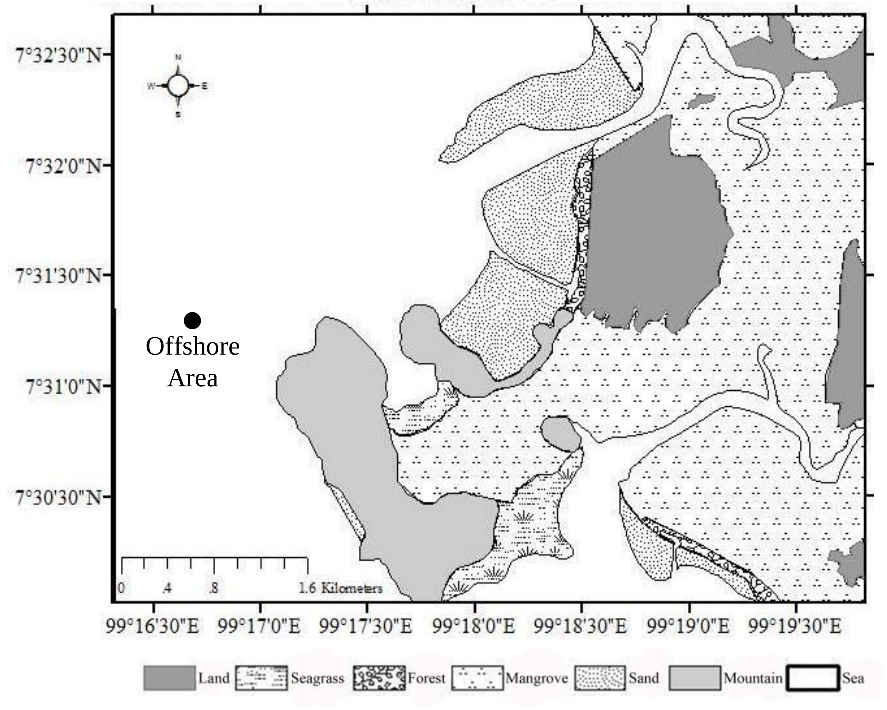


Figure 2.6 Offshore area approximately 2 km from the coastline of Sikao Bay of Trang Province.

Another group of specimens used for this study was from the collection of Tongnunui *et al*. (2010) (*T. jarbua* N=358 and *P. quadrilineatus* N=308). These specimens were sampled by small beach seine (4.5 m wide and 2.5 mm mesh size, with 7.5 m long central purse-bag) from Rajamangala coastal swamp and natural seagrass beach at Libong Island, in Trang Province. The sediment bottom was mainly sand. A variety of plants such as, *Casuarina equisetifalia*, *Rhizophora apiculata* and *Pandanus tectorius* was found around the coastal swamp. On the other hand, the seagrass bed at Libong Island was the natural seagrass bed. The sediment was soft mud. *Cymodocea serrulata* was the dominant species. All specimens were preserved in 10% neutral buffered formalin. Specimens from both sources were sorted and identified on the basis of the identification guide of (Jeyaseelan & Vannucci, 1998; Leis & Carson-Ewart, 2000; Leis & Rennis, 1983; Okiyama, 1988).

2. Developmental Patterns of Terapon jarbua and Pelates quadrilineatus

All samples of 366 *T. jarbua* and 314 *P. quadrilineatus* were examined. Terminology and methods for the classification of developmental stages followed those of Okiyama (1988), Leis and Rennis (1983), Leis and Carson-Ewart (2000), Jeyaseelan and Vannucci (1998), Miller and Kendall (2009).

Fifteen morphometric characters, 12 meristic characters and pattern of pigmentation were measured and counted. The morphometric characters in Table 2.1 and Figure 2.7 are as follows: total length, standard length, body depth, head length, eye diameter, snout length, jaw length, mouth gape, mouth diameter, predorsal length, length of base of dorsal fin, length of longest dorsal fin spine, length of longest dorsal fin ray, length of longest anal fin spine and length of longest anal fin ray, were measured with a micrometer attached to a binocular microscope and vernier caliper.

All measurements were measured to ± 0.001 mm. Larvae and juvenile size was reported as SL measurement in millimeter. The meristic characters included dorsal fin spine, dorsal fin ray, anal fin spine, anal fin ray, pectoral fin, pelvic fin spine, pelvic fin ray, postemporal spine, opercular spine, preopercular spine, interopercular spine and maxilla spine were counted using a phase contrast microscope. The illustrations were carried out under stereomicroscope with camera lucida and optical micromerter attached.

Table 2.1 Morphometric characters measured in the representative developmental stage of *Terapon jarbua* and *Pelates quadrilineatus*.

Character	**Description**
Total length	From tip of snout to posterior margin of the body
Standard length	From tip of snout to posterior tip of the caudal peduncle
Body depth	Dorsal to the anus
Head length	From tip of snout to the margin of gill cover
Eye diameter	Parallel to the longitudinal axis of the body
Snout length	From tip of the upper jaw to anterior margin of the orbit
Jaw length	From anterior tip of lower jaw to posterior tip of the lower jaw
Mouth gape	From tip of the upper jaw to tip of the lower jaw
Mouth diameter	From posterior tip of left jaw to posterior tip of right jaw
Predorsal length	From tip of the snout to the base of the anterior dorsal fin spine
Length of base of dorsal fin	From the first dorsal fin spine to the last dorsal fin ray
Length of longest dorsal fin spine	From base to tip of longest dorsal fin spine
Length of longest dorsal fin ray	From base to tip of longest dorsal fin ray
Length of longest anal fin spine	From base to tip of longest anal fin spine
Length of longest anal fin ray	From base to tip of longest anal fin ray

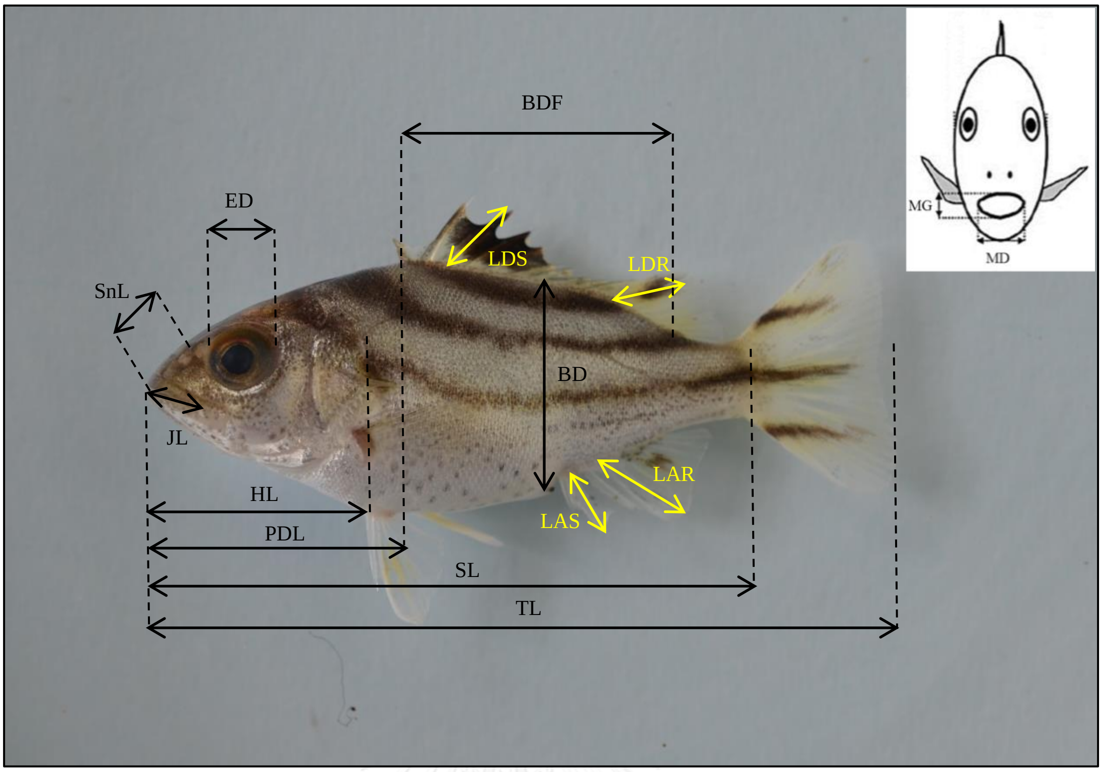


Figure 2.7 Morphometric characters measured in both terapontid fish, *Terapon jarbua* and *Pelates quadrilineatus* (total length = TL, SL = standard length, BD = body depth, HL = head length, ED = eye diameter, SnL = snout length, JL = jaw length, MG = mouth gape, MD = mouth diameter, PDL = predorsal length, BDF = length of base of dorsal fin, LDS = length of longest dorsal fin spine, LDR = length of longest dorsal fin ray, LAS = length of longest anal fin spine, LAR = length of longest anal fin ray).

3. Defining Length at Juvenile by Multivariate Morphometric Analysis

Defining the transition phase in particular defining length-at-juvenile in the two terapontid fish followed the multi-character approaches and technique developed by Nikolioudakis *et al.* (2010) and Nikolioudakis *et al.* (2014).

A total of 666 specimens (*T. jarbua*, n=358, 7.99-48.24 mm in SL and *P. quadrilineatus*, n=308, 9.01-54.13 mm in SL) were used for morphometric analysis. Raw measurements of the 13 morphometric characters (except TL and 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 larvae and juvenile stages of both species were compared by using Mann-Whitney U test: IBM SPSS statistics 21.

4. Allometric Relationships of Morphological Character and Size

Raw measurements of the 13 morphometric characters (except TL and SL) were regressed against the SL on a logarithmic scale (log10). This produced simple linear regressions described by the equation

$$\mathrm{Log}(y) = \log(a) + b \times \log(x)$$

A scaling relationship was considered allometric if the 95% confidence interval for its slope failed to overlap the slope predicted for isometry (a slope = 1.0). If slope did not significantly differ from 1,variables showed isometric growth. Significant values of $b > 1$ indicated positive allometric growth, whereas values of $b < 1$ indicated negative allometry (Fuiman, 1983). All regression procedures were conducted using IBM SPSS statistics 21.

D. Results and Discussions

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. The developmental stages of both species which related to size can be divided into 5 developmental stages follows: (1) preflexion larvae, (2) flexion larvae, (3) postflexion larvae, (4) transforming larvae, and (5) juvenile.

1. Developmental Patterns of *Terapon jarbua*

1.1 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. The pigment also formed series of dot along the base of anal fin (15-16 dots) (Figure 2.8A).

1.2 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 2 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 a series of 3 dots along base of anal fin (Figure 2.8B).

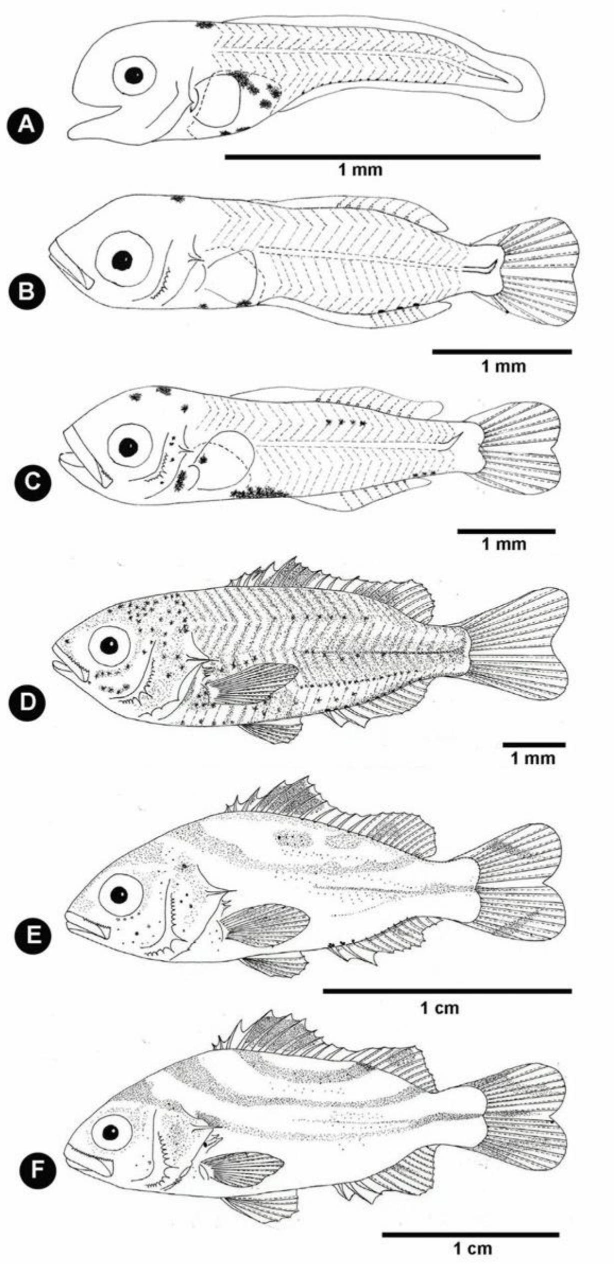


Figure 2.8 Development series of *Terapon jarbua* from the coastal area of Trang Province. (A) 1.49 mm in SL preflexion larvae; (B) 3.71 mm in SL flexion larvae; (C) 4.92 mm in SL postflexion larvae; (D) 9.02 mm in SL and (E) 14.97 mm in SL transforming larvae; (F) 24.98 mm in SL juvenile.

1.3 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 3 types of spines on head, opercular spine, preopercular spine, and maxilla spine. At this stage, the dot 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 from the flexion larvae stage. A series of 3 dots along base of anal fin still remained in this stage (Figure 2.8C).

1.4 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 (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 5 types of spines on head: opercular spine, preopercular spine, interopercular spine, maxilla spine and postemperal spine. Fins were 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 2.8D, 2.8E).

1.5 Juvenile (n=51; 23.16-48.24 mm): 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, maxilla spine, postemperal spine (Figure 2.9). Fin rays compliment was completed. Pigment formed in 3 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 2.8F). The presence of meristic character of *T. jarbua* as related to standard length was shown in Table 2.2

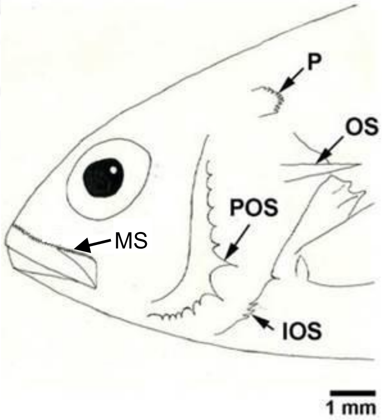


Figure 2.9 Head spines of juvenile *Terapon jarbua* from the coastal area of Trang Province (24.50 mm in SL) (OS = Opercular spine, P = Posttemporal spine, POS = Preopercular spine, IOS = Interopercular spine, MS = maxilla spine).

Table 2.2 Meristic character of *Terapon jarbua* (N=358) as related to size from the coastal area of Trang Province (+ = found).

Characteristic	**Standard length (mm)**																			
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Fin																				
Dorsal fin spine (XI-XII)		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Dorsal fin ray (9-11)					+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Anal fin spine (III)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Anal fin ray (7-10)				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pecteral fin (13-15)					+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Plevic fin spine (I)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Plevic fin ray (5)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Head spine																				
Postemporal spine	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Opercular spine	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Preopercular spine	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Interopercular spine	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Maxilla spine	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pigmentation																				
Black dots spread over head and body	+	+	+	+	+	+	+	+	+	+	+	+	+	+						
Black dots on dorsal fin spine	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Black dots on dorsal fin ray	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Black dots on anal fin									+	+	+	+								
2 horizontal downwardly curved								+	+	+	+	+	+	+	+					
3 horizontal downwardly curved stripes along head and body													+	+	+	+	+	+	+	+
Three transverse bands on cadul fin								+	+	+	+	+	+	+	+	+	+	+	+	+

2. Development Patterns of *Pelates quadrilineatus*

2.1 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. The pigment also formed series of dot along the base of anal fin but number of dot is less than *T. jarbua* (9-10 dots) (Figure 2.10A).

2.2 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 2 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 edge. Pigments were found on head, ventral side of gut and a series of 6 dots along base of anal fin (Figure 2.10B).

2.3 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 2 types of spines on head, opercular spine and preopercular spine. Pigments were found on head, ventral side of gut and a series of 4 dots along base of anal fin (Figure 2.10C).

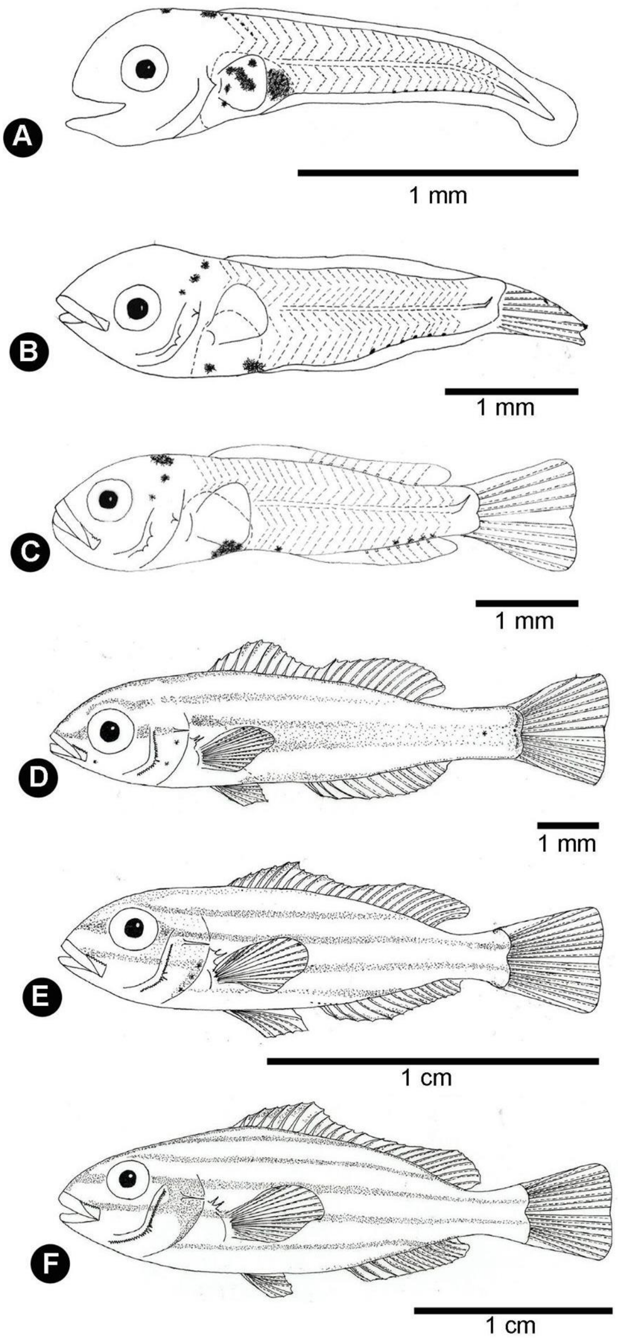


Figure 2.10 Development series of *Pelates quadrilineatus* from the coastal area of Trang Province (A) 1.64 mm in SL preflexion larvae; (B) 3.81 mm in SL flexion larvae; (C) 5.12 mm in SL postflexion larvae; (D) 9.01 mm in SL and (E) 13.97 mm in SL transforming larvae; (F) 24.95 mm in SL juvenile.

2.4 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 3 types of spines on head: opercular spine, preopercular spine and maxilla spine which found in13.00 mm in SL. Fin rays were 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 2.10D, 2.10E).

2.5 Juvenile (n=168; SL=18.24-54.13 mm): 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 3 types of spines on head: opercular spine, preopercular spine and maxilla spine (Figure 2.11). Fin rays compliment was completed. Pigment was formed in 5 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 2.10F). The presence of meristic character of *P. quadrilineatus* as related to standard length was shown in Table 2.3.

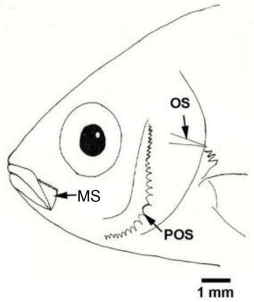


Figure 2.11 Head spines of juvenile *Pelates quadrilineatus* from the coastal area of Trang Province (23.02 mm in SL) (OS = Opercular spine, POS = Preopercular spine, MS = maxilla spine).

Table 2.3 Meristic character of *Pelates quadrilineatus* (N=308) as related to size from the coastal area of Trang Province (+ = found).

Characteristic	**Standard length (mm)**																			
Fin	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Dorsal fin spine (XI-XIII)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Dorsal fin ray (9-11)						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Anal fin spine (III)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Anal fin ray (9-11)						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pecteral fin (13-16)						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Plevic fin spine (I)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Plevic fin ray (5)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Head spine																				
Opercular spine	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Preopercular spine	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Maxilla spine						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pigmentation																				
Three horizontal stripes extending along head and body	+	+	+	+																
Four horizontal stripes extending along head and body					+	+	+	+	+	+										
Five horizontal stripes extending along head and body									+	+	+	+	+	+	+	+	+	+	+	+
Black dots on dorsal fin spine	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

3. Defining Length of Juvenile Stage in *Terapon jarbua* and *Pelates quadrilineatus*

The result of multivariate morphometric analysis for estimating length at juvenile of *T. jarbua* and *P. quadrilineatus* were 23.16 and 18.24 mm, respectively (Figure 2.12 and 2.13). Predorsal length and eye diameter of *T. jarbua* show high factor loading (>0.3) on the PC2 as in Table 2.4. These characters were important factors that changes between developing stage and influence the identification between the transforming larval and the juvenile of *T. jarbua*. Predorsal length, eye diameter, longest dorsal fin spine and longest dorsal fin ray of *P. quadrilineatus* show high factor loading (> 0.3 and < -0.3) on the PC2. These four characters undergoes through changes during the developmental stages and can be used to distinguish the transforming larval and the juvenile of *P. quadrilineatus*.

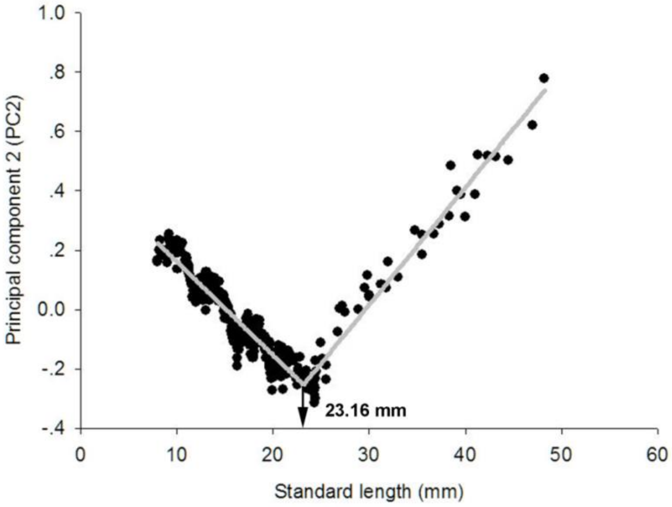


Figure 2.12 Piecewise regression of principal component 2 scores from PCA of 13 morphometric characters on standard length for estimating length at juvenile in *Terapon jarbua* (n=358; r=0.925). Arrow indicated transition point between larvae and juvenile of *Terapon jarbua*.

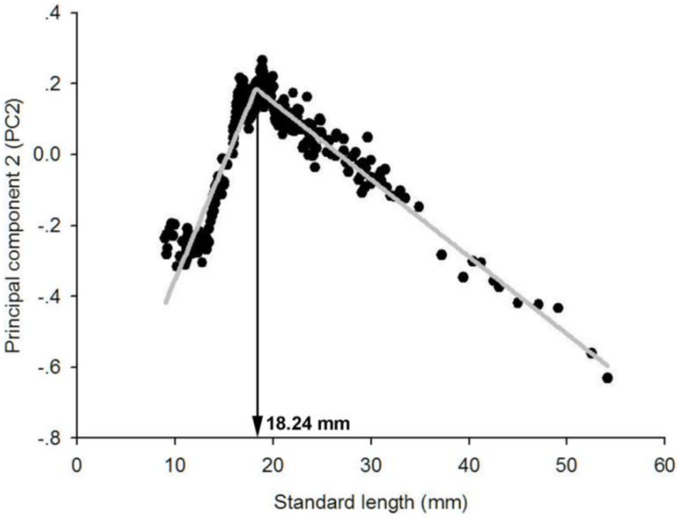


Figure 2.13 Piecewise regression of principal component 2 scores from PCA of 13 morphometric characters on standard length for estimating length at juvenile in *Pelates quadrilineatus* (n=308; r=0.975). Arrow indicated transition point between larvae and juvenile of *Pelates quadrilineatus*.

Table 2.4 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) study.

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

All morphometric measurements as in Table 2.5 were significant different ($p < 0.05$) between transforming larvae and juvenile stage in both species. Juvenile had deeper body, larger head with larger mouth gape and broader mouth diameter as compared to transforming larvae. The juvenile stage also possessed the longer predorsal length and longer base of dorsal fin. The snout length in juvenile was long as well as eye diameter and jaw length. All the dorsal and anal fin spine and ray also longer in juvenile stage as compared to the transforming larvae.

Table 2.5 Ratios of morphometric character to standard length or head length of *Terapon jarbua* (N=358) and *Pelates quadrilineatus* (N=308) from the coastal area of Trang Province.

Morphometric character	***Terapon jarbua***		***Pelates quadrilineatus***	
	Transforming larvae	**Juvenile**	**Transforming larvae**	**Juvenile**
Body depth /Standard length	0.34	0.35	0.28	0.31
Head length/Standard length	0.34	0.35	0.33	0.34
Mouth gape/Head length	0.31	0.35	0.33	0.36
Mouth diameter/Head length	0.26	0.27	0.31	0.36
Predorsal length/Standard length	0.38	0.35	0.36	0.34
Base of dorsal fin/Standard length	0.44	0.46	0.46	0.48
Snout length/Head length	0.41	0.42	0.32	0.35
Eye diameter/Head length	0.33	0.29	0.30	0.28
Jaw length/Head length	0.37	0.38	0.37	0.39
Longest dorsal fin spine/Standard length	0.14	0.16	0.12	0.15
Longest dorsal fin ray/Standard length	0.14	0.14	0.12	0.14
Longest anal fin spine/Standard length	0.13	0.13	0.10	0.11
Longest anal fin ray/Standard length	0.14	0.15	0.14	0.15

There are many criteria for defining the end of the larval period or the beginning of the juvenile period such as, the formation of fins, squamation, body pigmentation, development of sensory features, behavioral development and habitat shift (Koumoundouros *et al.*, 1999; Miller & Kendall, 2009). However, the use of only one character for identifying the length at juvenile of fish is often inadequate for a unified, unambiguous definition of size/age at metamorphosis (Ditty *et al.*, 2003; Urho, 2002). In addition, the length at juvenile defined by each characters can varies.

The transition timing to juvenile for individual characters was different. Different morphological characters, such as the characters of external morphology examined here (formation of fins, squamation, head spination and body pigmentation), may start transformation from larval to juvenile state at different ontogenetic times and with different rates (L. A. Fuiman *et al.*, 1998) (Table 2.6).

Table 2.6 The transition timing from larval to juvenile period for the formation of fin, squamation, head spination and body pigmentation in *Terapon jarbua* and *Pelates quadrilineatus* from the coastal area of Trang Province.

Species	**Method**	**Character**	**Length at Juvenile (mm)**
Terapon jarbua	Univariate morphometric analysis	Scales completed	14.00
		Fins completed	12.00
		Head spination completed	20.00
		Pigmentation completed	23.00
	Multivariate morphometric analysis		23.16
Pelates quadrilineatus	Univariate morphometric analysis	Scales completed	14.00
		Fins completed	13.00
		Head spination completed	13.00
		Pigmentation completed	18.00
	Multivariate morphometric analysis		18.24

Multivariate morphometric analysis can largely help in identifying thresholds (Shea, 1985). The larger number of characters used to delimit intervals, the better the resolution and the likelihood of delimiting ontogenetic intervals in natural processes

(Ditty *et al.*, 2003). The close agreement between sizes at allometric and morphological changes in white sea-bream, estimated in Nikolioudakis *et al.* (2010) after adopting a multivariate morphometric analysis, implies that such approaches can be very effective in identifying thresholds in fish ontogeny like metamorphosis. 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 completed pigmentation development of *T. jarbua* and *P. quadrilineatus* were 23.00 mm and 18.00 mm, respectively as in Table 2.6 while length at juvenile of *T. jarbua* and *P. quadrilineatus* from multivariate morphometric analysis were 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 reported by Jeyaseelan and Vannucci (1998). Jeyaseelan and Vannucci (1998) studied fish egg and larvae in mangrove forest of Ranong Province on Andaman coastline, Southern Thailand. He found that early juvenile of *T. jarbua* in this area was 22.50 mm. However, the use of multivariate morphometric analysis for defining length at juvenile of fish was limited by temperature. Nikolioudakis *et al.* (2014) found that *Oblada melanura* is a species that was recruited during the warmest period of month. They showed close estimation between mean length-at-metamorphosis and border between intermediate and juvenile stage. On the other hand, the mean length-at-metamorphosis and border between intermediate and juvenile stage in species that was recruited during the cold period of month were not in close proximity. Therefore, the defining length at juvenile of fish by multivariate morphometric analysis is more appropriate in fish which was recruited in warm temperature than in cool temperature.

4. Allometric Relationships of Morphological Character and Size in *Terapon jarbua* and *Pelates quadrilineatus*

A variety of significant allometric relationships were evident in the growth of terapontid morphological characters (Davis *et al.*, 2012b). Summary results of regression analyses are outline in Table 2.7. Positive allometric growth was observed during ontogeny for both species except for the predorsal length and eye diameter. Significant negative allometric in eye diameter was identified in all terapontid species (Davis *et al.*, 2012b). This indicated that eye diameter become disproportionately smaller in most species of terapontid species as they increased in size.

Table 2.7 Allometric relationships in *Terapon jarbua* and *Pelates quadrilineatus* among standard length and other 13 morphometric characters (+ = positive allometric growth, - = negative allometric growth).

Morphological variable	**Species**	
	Terapon jarbua	***Pelates quadrilineatus***
Body depth	+ (r = 0.998)	+ (r = 0.885)
Head length	+ (r = 0.987)	+ (r = 0.999)
Mouth gape	+ (r = 0.999)	+ (r = 0.950)
Mouth diameter	+ (r = 0.925)	+ (r = 0.998)
Predorsal length	- (r = 0.925)	- (r = 0.913)
Base of dorsal fin	+ (r = 0.999)	+ (r = 0.999)
Snout length	+ (r = 0.915)	+ (r = 0.950)
Eye diameter	- (r = 0.825)	- (r = 0.952)
Jaw length	+ (r = 0.821)	+ (r = 0.875)
Longest dorsal fin spine	+ (r = 0.895)	+ (r = 0.993)
Longest dorsal fin ray	+ (r = 0.995)	+ (r = 0.827)
Longest anal fin spine	+ (r = 0.915)	+ (r = 0.994)
Longest anal fin ray	+ (r = 0.998)	+ (r = 0.995)

5. Morphological Development of *Terapon jarbua* and *Pelates quadrilineatus* as Related to Ontogenetic Niche Shift

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 as similar to previous studies (Jeyaseelan & Vannucci, 1998; Leis & Carson-Ewart, 2000; Okiyama, 1988). There are changes in morphometric characters, meristic characters and pigmentation pattern during the development. The change of all characters can be used to identify or compare the morphological development of fish (Ditty *et al.*, 2003). In addition, it also identifies ontogenetic niche shifts in resource use of fish (Boglione *et al.*, 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 find food, gain better mobility, avoid predators and find suitable habitat for survival. The main character of larvae is that they are adapted to make use of resources not normally used by adults (Urho, 2002). The end of larval period or beginning of the juvenile period is important usually associated with habitat shift as well as the extreme changes in the morphological and meristic characters. The changes in the transformation stage listed by Kendall (1984) are pigmentation pattern, body shape, fin migration, photophore formation, loss of elongate fin rays and head spines, eye migration and scale formation. These indicate the change from larval body form and characters to juvenile-adult body form and characters. These changes were evidences in the developmental patterns of the two terapontid fishes.

There were some used distinguish between *T. jarbua* and *P. quadrilineatus* in each stage as in Figure 2.14. In planktonic larvae stages, the number of dot pigments along the base of anal fin and the length of opercular spine showed the different pattern between *T. jarbua* and *P. quadrilineatus*. **In preflexion larvae,** the pigment formed series of dot along the base of anal fin (15-16 dots) in *T. jarbua*. The pigment also formed series of dot along the base of anal in *P. quadrilineatus* fin but the number of dot (9-10 dots) was less than *T. jarbua*. **In flexion larvae,** the series of dot along the base of anal fin was found only to 3 dots in *T. jarbua* and 6 dots in *P. quadrilineatus*. Opercular spine was apparent. The opercular spine of *T. jarbua* was long and strong, extending beyond margin of opercular lobe. The opercular spine of *P. quadrilineatus* was also long and strong however not extending beyond margin of opercular lobe. The difference in the length of opercular spine in both species persisted until they became adult fish. **In postflexion larvae,** the series of dot along the base of anal fin remained to 3 dots in *T. jarbua* and to 4 dots in *P. quadrilineatus*.

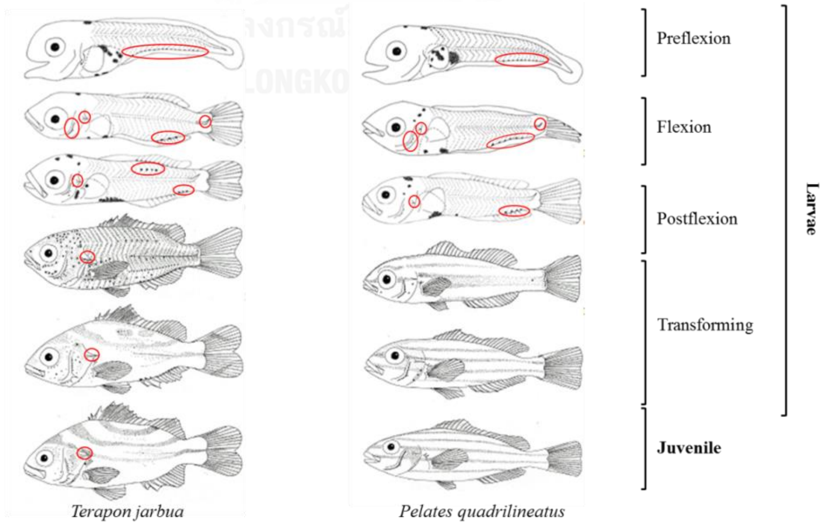


Figure 2.14 Important morphological characters for the discrimination different between *Terapon jarbua* and *Pelates quadrilineatus* in each developmental stage.

Preflexion larvae, flexion larvae and postflexion larvae were planktonic stage. Many previous studies reported that planktonic larvae of both species were found offshore (Horinouchi *et al.*, 2012; Horinouchi *et al.*, 2009; Ikejima *et al.*, 2003; Matsuura *et al.*, 2005). At these stages, fishes 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 mainly zooplankton which is the exogenous factor highly affected their survival. Their body and fin were transparent. This convergence trait help fish camouflage from predator.

Pigment patterns on the body, body depth and head spination were important characters used to distinguish between *T. jarbua* and *P. quadrilineatus* in the transforming larvae and juvenile stages. In the beginning phase of **transforming larvae**, pigmentation changed rapidly with growth by spreading to cover the head and the body of *T. jarbua*. Later during this stage, two bands of pigment developed as the discontinuous blackish-brown downwardly curved longitudinal strips on the body. In *Pelates quadrilineatus*, pigments formed in 1-4 horizontal stripes extending along the head and the body. Pigments formed in 3 horizontal downwardly curved bands extending along lateral side of the body of juvenile *T. jarbua*. Pigments were formed as 5 horizontal stripes extending along the head and the body of juvenile *P. quadrilineatus*. *Terapon jarbua* showed deeper body depth than *P. quadrilineatus* during transformation phase. In addition, during these stage *T. jarbua* developed 5 types of spines on the head namely opercular spine, preopercular spine, interopercular spine, maxilla spine and postemperal spine while *P. quadrilineatus* only developed 3 types of spines on the head namely opercular spine, preopercular spine and maxilla spine.

In transforming larvae of both *T. jarbua* and *P. quadrilineatus* moved to shallow nearshore habitats. 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 (Matsuura *et al.*, 2005; Tongnunui *et al.*, 2010). 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 allows 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 (Horinouchi *et al.*, 2012; Horinouchi *et al.*, 2009; Tongnunui *et al.*, 2010). 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, which mouth gape and jaw size 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 corresponded 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 *et al.*, 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 *et al.*, 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.

E. Conclusion

Using all morphometric character, meristic character and pigmentation pattern, the developmental pattern of *T. jarbua* and *P. quadrilineatus* can be divided into 5 development stages as follows: (1) preflexion larvae, (2) flexion larvae, (3) postflexion larvae, (4) transforming larvae, and (5) juvenile. The development of pigmentation along the base of anal fin and and the length of opercular spine were the important characters used to distinguish between the planktonic larvae stages of *T. jarbua* and *P. quadrilineatus*. Pigment pattern of the body, body depth and head supination were the important characters used to distinguish between *T. jarbua* and *P. quadrilineatus* in transforming larvae and juvenile stages. The length at juvenile of *T. jarbua* and *P. quadrilineatus* were 23.16 and 18.24 mm estimated by multivariate morphometric analysis. The morphology development of both species demonstrates their ontogenetic niche shift. Positive allometric growth was observed during ontogeny for both species except for the predorsal length and eye diameter. Important characters in this study that showed relationship between morphological development and ontogenetic niche shifts were mouth gape, jaws, body shape, fin and pigment patterns.

CHAPTER 3

HABITAT UTILIZATION AS SPAWNING AND NURSERY AREAS IN TERAPONTID FISHES, *Terapon jarbua* AND *Pelates quadrilineatus*

A. Introduction

Estuaries have well-defined roles as spawning areas, nursery areas, feeding areas and areas of migration routes for spawning for many fishes (Elliott *et al.*, 2002). When evaluating fish habitat use in estuaries, these four important functions that estuarine habitats may fulfill for fish should be considered (Pihl *et al.*, 2002). It is difficult to define the estuarine habitat as a refuge from predation alone. The refuge function of estuarine habitat usually is an integral part of the nursery function of a habitat. Adult fish may also seek predation refuge in estuaries as well as feeding grounds. The understanding of the life cycle in fish may help explaining the habitat utilization of fish in each stage (Whitfield, 1990). The choosing of habitats for spawning and nursery areas in fish is important for the survival of their offspring. To deposit or release their eggs and to mate, fish may select specific areas to optimize the survival of the eggs or of the early larval stages. Some fish utilize estuarine for only certain part of their life cycle such as marine migrant species return to the sea or the freshwater species move into freshwater habitats for spawning. Estuarine resident species use the estuarine habitats for spawning, while a large proportion of marine and freshwater species also uses the estuary for spawning. Sediment characteristics, currents, water depth and vegetation may all have an impact on the survival and retention of the earliest life stages in the estuary and thus determine the likelihood that a fish species will spawn in a habitat (Pihl *et al.*, 2002). The presence of matured adults and their eggs and larvae can be the indicative of spawning grounds (Elliott *et al.*, 2002).

Mature fish of the same species gather on spawning grounds to lay eggs at a certain time of the year as one of the basic form of parental care. Spawning sites are usually restricted in size that there is insufficient food supply for hatching larvae. The progeny of most species have to disperse after hatching particularly those with pelagic eggs start early and others after a short inactive phase. The search for food for tiny fish always involves predation risk. Minimising visibility to predators is therefore an advantage. There are special areas or habitats where larvae can feed and attain the size that are large enough or developed to be competitive enough in the feeding areas of juveniles and adults. Larval morphology and behavior after hatching, together with environmental cues, determine the tactics which larvae may use to reach the nursery area where they can find food, avoid predators and developed into the individuals that are competitive enough to share the feeding areas with the juveniles and the adults. Most fish larvae change habitat in the course of the ontogeny and extend their feeding areas (Urho, 2002). Juveniles migrate passively or actively to estuarine nursery grounds and concentrate in specific habitats to spend their early lives. Nurseries are defined as areas where juveniles aggregate, are spatially or temporally separated from the adults. Nursery areas also enhance the juvenile survival through better feeding conditions, optimal growth and/or refuge-opportunities. After attaining a well-defined length class, recruitment to the adult or subadult populations follows the emigration from the nursery areas (Pihl *et al.*, 2002). Heupel *et al.* (2007) work’s on shark nusery area corresponded to the definition of nursery areas as defined by Pihl *et al.* (2002). They found that all sharks have nursery areas which provide the most advantageous habitat from growth and survival of young sharks by being in productive area and having an abundant supply of food. Natural mortality rates of shark juveniles within the nursery areas are low compared to rates in non-nursery areas. Moreover sharks are more commonly encountered in the area and have a tendency to remain or return for extended period. They emphasized that these shark nursery areas or habitats should be repeatedly used across years.

Nursery role of mangrove and seagrass beds for fishes is widely accepted (Blaber, 1997, 2000; Horinouchi, 2007; Horinouchi *et al.*, 2009; Ikejima *et al.*, 2003; Laegdsgaard & Johnson, 1995; Nagelkerken *et al.*, 2000; Robertson & Blaber, 1993). Several hypotheses have been proposed to explain the high abundance of juvenile fishes in the mangroves and seagrass beds 1) the structural complexity, such as prop roots, pneumatophores, branch and debris in mangroves as well as seagrass height/shoot density or plant biomass, provide excellent shelters against predators; 2) these biotopes are often located at a distance from offshore area and are therefore less frequent visited by predators; 3) turbid water reduce the effectiveness of large predators on fish; 4) these biotopes provide a great abundance of food for fishes and 5) these biotopes often cover extensive areas and may intercept planktonic fish larvae more effectively.

Another reasons why estuarine habitat utilization as feeding ground is important, not only for adult fish but also to support the larvae and juveniles. The importance of estuaries for fish ranked by average number of fish species in selected European estuarine system as follows: feeding > nursery > spawning > route of migration (Pihl *et al.*, 2002). Habitat utilization as feeding ground will be discussed in details in separate chapter. Habitat utilization as well as environmental parameter played the important role in the distribute and abundance of larvae, juvenile and adult fish in the estuarine area (Laegdsgaard & Johnson, 1995; Nanami & Endo, 2007; Phinrub *et al.*, 2015).

Terapon jarbua and *Pelates quadrilineatus* have been reported to be a marine migrant fish which spawn at sea and often enter estuaries in large numbers as juveniles (Elliott *et al.*, 2007; Vari, 2001; Vidthayanon & Premcharoen, 2002; Whitfield, 1990). The adult are sympatric offshore area. Their eggs and larvae drift with the coastal current to estuaries where they become juveniles as estuarine dependent for nursery area (Munro, 1967; Robertson & Blaber, 1993; Smith & Heemstra, 1986). These two fish species found to coexist in the coastal area of Trang Province on the southwest coast of Thailand. Many previous studies reported that planktonic larvae and adult of both species were found at offshore area (Ikejima (Horinouchi *et al.*, 2012; Horinouchi *et al.*, 2009; Ikejima *et al.*, 2003; Matsuura *et al.*, 2005). Transforming larvae and juveniles of *T. jarbua* were found distributed in the coastal swamps and mangrove forests while the transforming larvae and juveniles of *P. quadrilineatus* were found distributed in seagrass beds (Duangdee, 1995; Horinouchi *et al.*, 2012; Horinouchi *et al.*, 2009; Ikejima *et al.*, 2003; Tongnunui *et al.*, 2002; Tongnunui *et al.*, 2001; Tongnunui *et al.*, 2010). Habitat utilization as spawning and nursery area by these two coexisting terapontid fishes needs to be investigated in order to understand the spatial and temporal resource partitioning in each stage of their life cycle. To answer these research questions, specific aims of the study involved: (1) the distribution and abundance pattern of *T. jarbua* and *P. quadrilineatus* in each stage in the coastal area of Trang Province throughout the year (2) the reproductive biology of adult *T. jarbua* and *P. quadrilineatus* in particular the gonadal development, Gonadosomatic index, fecundity and size at first sexual maturity in order to identify the spawning periods in both species (3) to ascertain the spawning and nursery areas in the coastal area of Trang Province for the coexisting terapontid fishes and how these habitats fulfill the functions for the fish in question.

B. Literature Reviews

1. Life History Pattern of Fish

Estuaries have well-defined roles as nursery area, feeding area, area of refuge and migration routes of fishes (Elliott *et al.*, 2002; Elliott *et al.*, 2007). Many marine species are entering estuaries mainly as juveniles and return to the sea prior to maturity. Breeding strategies are often geared towards minimizing the distance between marine spawning grounds and nursery area, although not all species follow this pattern. This had led to a number classification systems for life history pattern of fish by Elliott *et al.* (2007), based mainly on how they utilize estuaries and where they spawn (Table 3.1). The following classification scheme is similar, but emphasized on the importance of spawning behavior (Blaber, 2000). The understanding of the life cycle of fish may help in explaining the habitat utilization of fish in each stage. This should be used in conjunction with the feeding and reproduction of fish (Whitfield, 1990). This study focused on life history of marine migrant species. This group usually characterized as marine spawners. This is a large group of fishes in subtropical and tropical estuaries such as, *Chanos chanos*, Chanidae; *Liza macrolepis*, Mugilidae; *Valamugil cunnesius*, Mugilidae and *Eucinostomus gula*, Gerreidae (Elliott *et al.*, 2007). *Terapon jarbua* and *P. quadrilineatus* were also classified as marine migrants. Adult of both species live in offshore area where they spawn while juvenile seek shallow coastal water of estuaries (Munro, 1967; Smith & Heemstra, 1986; Whitfield, 1998).

Table 3.1 Life cycle categories of estuarine fishes modified from Elliott *et al.* (2007).

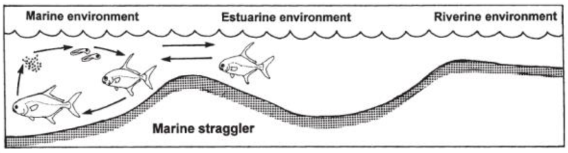
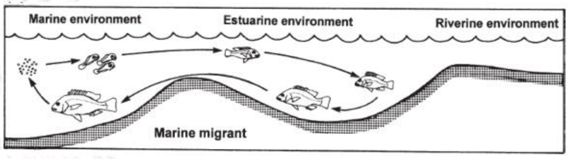
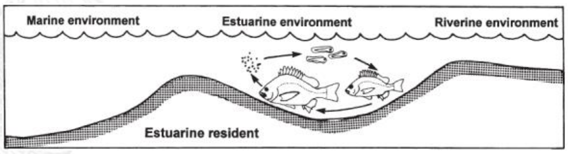
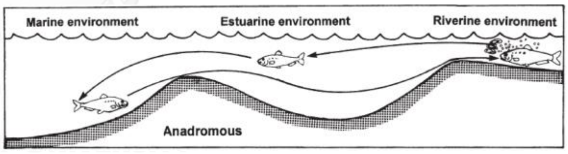
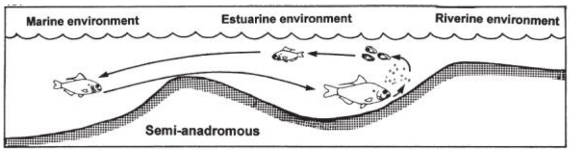
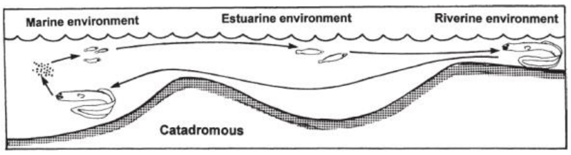
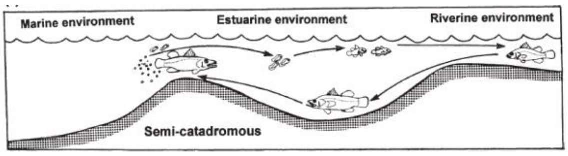
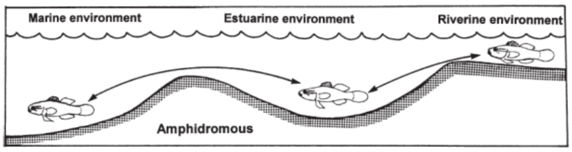
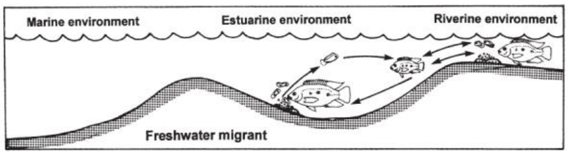
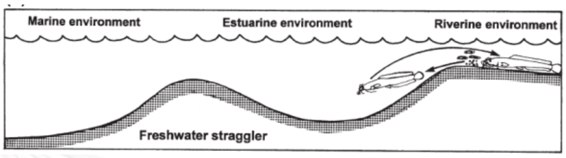
Categories	**Definition**	**Life cycle**
Marine stragglers	Species that spawn at sea and typically enter estuaries only in low numbers and occur most frequently in the lower reaches where salinities are approximately 35 PSU.	
Marine migrant	Species that spawn at sea and often enter estuaries in large numbers, particularly as juvenile and move throughout the full length of the estuary	
Estuarine species	Species that capable of completing their entire life cycle within the estuarine environment	
Anadromous	Species that undergo their greatest growth at sea and which, prior to the attainment of maturity, migrate into rivers where spawning subsequently occurs	
Semi-anadromous	Species whose spawning run from the sea extends only as far as the upper estuary rather than going into freshwater	
Catadromous	Species that spend all of their trophic life in freshwater and which subsequently migrate out to sea to spawn	
Semi-catadromous	Species whose spawning run extends only to estuarine areas rather than the marine environment	

Table 3.1 Continued.

Categories	Definition	Life cycle
Amphidromous	Species which migrate between the sea and freshwater and in which the migration in neither direction is related to reproduction	
Freshwater migrant	Freshwater species found regularly and in moderate numbers in estuaries and whose distribution can extend beyond the oligohaline sections of these systems	
Freshwater stragglers	Freshwater species found in low numbers in estuaries and whose distribution is usually limited to the low salinity, upper reaches of estuaries	

2. Habitat Utilization in Estuarine Fishes

Estuary is ecologically dynamic and productive areas used by larvae, juveniles and adults of many estuarine dependent fish for foraging, reproduction and refuges. Distribution and abundance of fish in each stage in different habitat demonstrate the habitat utilization of fish in life cycle. Elliott *et al.* (2002) classify the habitat utilization of fish in estuary into 4 groups.

(1) Spawning ground: The presence of eggs, larvae of broadcast spawners and mature fish with running eggs or sperm can be used as the indicators of spawning grounds, although it should be noted that later larval stages may migrate actively or passively from the spawning site (Elliott *et al.*, 2002). Estuary is the important spawning habitat for estuarine fish that capable in completing their entire life cycle within the estuarine environment. Spawning in estuary help to reduce the larval mortality during the dispersion from spawning ground to nursery grounds. In addition, some fish demonstrate the parental care behavior by producing fewer

demersal eggs in the area where they select the environmental conditions necessary for developing egg and larvae. These reproductive strategies must ensure the maintenance of viable populations and adequate dispersal of larvae to suitable habitats. On the other hand, many marine migrant species choose to spawn offshore area and utilize estuary for nursery ground. High predation pressure in shallow waters renders them unusually hazardous for pelagic eggs and larvae of the resident fishes. As an apparent consequence a number of strategies have been evolved for minimizing this predation. Many larger species (>25 cm total length) migrate toward deeper water to spawn. The eggs that they released and the larvae usually drift near the surface over deep water and are thus out of range of the benthic and demersal predators in their adult habitats. Small species (< 25 cm total length) are more susceptible to predation as adults than are larger species. They typically remain near the refuges in their normal habitat to spawn. This increases their chances of recruiting to parent populations (Miller & Kendall, 2009).

(2) Nursery grounds: The areas where juveniles are found are termed nursery grounds. It has been suggested that nursery grounds are those sites where juveniles aggregate in higher densities, have reduced rates of predation and have faster growth rates than in other habitats, which should result in nursery grounds providing a greater relative contribution to adult recruitment in comparison to non-nursery ground habitats (Beck *et al.*, 2003; Heupel *et al.*, 2007; Pihl *et al.*, 2002). Coastal habitats and estuaries are known in many parts of the world as nursery grounds for several fishes in particular mangrove forests, seagrass beds and mudflats (Horinouchi, 2007; Horinouchi *et al.*, 2009; Ikejima *et al.*, 2003; Laegdsgaard & Johnson, 1995; Lugendo *et al.*, 2007; MacDonald *et al.*, 2009; Nagelkerken *et al.*,

2000; Parrish, 1989; Pihl *et al.*, 2002; Robertson & Blaber, 1993). Several species of fishes reproduce in the offshore areas but their larvae and post-larvae may be found to develop nearshore, before returning to estuarine systems where they develop into adults. Several hypotheses that support the high abundance of larva and juvenile fishes in estuarine area including (i) high abundance and diversity of food items, (ii) avoidance of predators by turbid waters (iii) the complexity of micro habitat structures and (iv) cover the extensive area for the interception of planktonic fish larvae. Laegdsgaard and Johnson (2001) reported that juvenile fish living in mangroves were with stomach fullness and survival rates higher than those living in non-mangrove habitats.

(3) Feeding ground, Estuary is the important feeding habitat for many fish. However, the quantity and type of food may differ among estuaries and different parts of estuary. The presence of mangroves and seagrass beds in estuaries increases the quantity and diversity of food item to fish (Blaber, 2000; Horinouchi, 2007; Nagelkerken *et al.*, 2000). The density of zooplankton in mangroves increase during the late of dry to mid wet season corresponding to the recruitment period of fishes (Robertson & Blaber, 1993). In addition, adult fish increase in abundance seasonally when they enter estuaries to feed (Wallace *et al.*, 1984). From the foregoing it is obvious the estuarine is important both direct and indirect for fish in particular the benefits from the rich feeding grounds provided by estuaries.

(4) Migration route for breeding of fresh water fish and marine fish. However, there are larval and juvenile migrations of many marine migrant species into estuaries which also tend to be seasonal (Elliott *et al.*, 1990; McHugh, 1967);The migration of fish larvae enter estuaries occur during late winter, spring and early

summer when high temperatures and rich food supply for rapid growth. They are also protected from most marine predators. Juveniles spend varying lengths of time in estuaries. Sub-adult fish tend to inhabit marine inshore areas, where they join the adult spawning populations once they become matured.

Terapon jarbua and *Pelates quadrilineatus* generally classified as marine migrant, constitute the dominant components in estuarine fish assemblages from tropic to temperate zones (Blaber, 2000). Most of them spawn offshore area, their larvae then drifting with the tidal currents, the juveniles enter the estuaries to feed and find shelter until they reach sexual maturity. Estuarine use by fish has been inferred indirectly from changes in their spatio-temporal occurrence (Bruton *et al.*, 1987; Harrison & Whitfield, 2006), or they were tracked directly by means of mark-recapture (Funicelli *et al.*, 1989). Inferences from these studies, which provide instantaneous patterns of movement, might be strengthened by examining the entire-life migratory history as revealed by the fish's own chronological and environmental recorder, the otolith. The otolith is a biomineralized calcium carbonate ($CaCO_3$) crystalline structure within the membranous labyrinth of the inner ear of the fish. Strontium (Sr) content in the otolith has been found to differ between freshwater and seawater life history phases (Arai *et al.*, 2003; C. Chang *et al.*, 2004; Suzuki *et al.*, 2011). This difference corresponds to the ambient Sr concentration, which is higher in seawater than freshwater. Accordingly, Sr content in fish otoliths offers the potential to distinguish between time spent in seawater and freshwater and can provide information regarding the environmental history of individual fishes.

3. Reproductive Patterns and Spawning Pattern in Terapontid Fish

Terapon jarbua and *Pelates quadrilineatus* are marine migrant fish which spawn at sea. The eggs are fertilized and developed in the environment outside the female as pelagic egg and juvenile move to the estuary (Veerappan *et al.*, 2009). They share the same reproductive and spawning patterns. However, previous studies showed differences in the spawning season of both species. Size at first maturity of male and female in *T. jarbua* in Taiwanese waters were 143 and 148 mm, respectively (Miu *et al.*, 1990). This was corresponding to Prabhu (1956) which reported that mature adult of *T. jarbua* from Indian waters was 145-162 mm. The ovary of *T. jarbua* was assigned into 5 maturity stages followed Miu *et al.* (1990) (Table 3.2). Their batch fecundity ranged 37,083-480,400 eggs. The gonad investigation indicated spawning season of *T. jarbua* in Taiwanese waters was during April and October which corresponded to the occurrence of their larvae and juvenile during May and November (Miu *et al.*, 1990).

Table 3.2 Ovary development of female *Terapon jarbua* from Taiwanese waters modified from Miu *et al.* (1990).

Stage	Ovary development
Stage I	Small ovary, egg size varies from 0.1-0.2 mm and GSI not exceeding 2
Stage II	Eggs was growing (0.3-0.4 mm) and GSI about 2.5-7.8
Stage IIIa	Two modes of egg were formed, advanced eggs (0.4 mm) and normal eggs (0.2 mm) and GSI about 10-12
Stage IIIb	No change of egg size but GSI increased (13-21)
Stage IV	Two clearly separated modes of eggs were recognized (0.6 and 0.3 mm)
Stage V	Spent condition

The mature adult in *P. quadrilineatus* from Indian waters was 121-132 mm. The ovary was assigned into 4 maturity stages (Table 3.3). The gonad investigation indicated spawning season of *P. quadrilineatus* during February to April (Prabhu, 1956).

Table 3.3 Ovary development of female *Pelates quadrilineatus* from Indian waters modified from Prabhu (1956).

Stage	**Ovary development**
Stage I	Transparent ovary and could be distinctly recognized as possessing a nucleus and a protoplasmic layer
Stage II	Yolk begin form in ovary
Stage III	Ovary full of yolk and with distinct yolk spherules, but still contained within the follicle
Stage IV	Partly transparent eggs have burst from the follicles

As mentioned above, the study on the reproductive biology of adult *T. jarbua* and *P. quadrilineatus* in coastal area of Trang Province in particular gonadal development, gonadosomatic index, fecundity and size at first sexual maturity can identify spawning season of both species. It can be hypothesize that difference spawning periods between the two terapontid fishes can reduce the interspecific competition when coexist in the same area.

4. Distribution of *Terapon jarbua* and *Pelates quadrilineatus* in Thailand

Terapon jarbua and *P. quadrilineatus* were commonly found along coastal area both of Gulf of Thailand and Andaman Sea. They can be found distributed in various habitat types, such as, coral reefs, mangroves, sandy beaches, coastal swamps, seagrass beds and offshore area. The distribution of *T. jarbua* and *P. quadrilineatus* in Thailand were showed in Table 3.4. However, both species showed difference in pattern of distribution between Gulf of Thailand and Andaman Sea. On the Gulf of Thailand, larvae and adult of *T. jarbua* were co-occurring and distributed in coral reefs, mangroves and sandy beaches (Chayakul, 2007; Paphavasit *et al.*, 2006; Paphavasit *et al.*, 2004; Somkleeb *et al.*, 2002). Larvae of *P. quadrilineatus* were found only in sandy beaches at Ban Krut beach, Prachuabkhirikhan and found coexist with larvae of *T. jarbua* (Chayakul, 2007)

On Andaman Sea, especially coastal area of Trang Province, differences in the distribution pattern of both fish in each stage were found. Larvae of *T. jarbua* were found distributed offshore area, coastal swamps and seagrass beds (Duangdee, 1995; Tongnunui *et al.*, 2010; Yoknoi, 2012). Juvenile of *T. jarbua* were distributed in mangroves, sandy beaches and coastal swamps (Macintosh *et al.*, 2002; Pimoljinda, 1998; Tongnunui *et al.*, 2010; Yoknoi, 2012). Adult of *T. jarbua* were found at the offshore area and the seagrass beds (Matsuura *et al.*, 2005; Yoknoi, 2012). Larvae and adult of *P. quadrilineatus* were found at the offshore area and the seagrass beds (Duangdee, 1995; Matsuura *et al.*, 2005; Yoknoi, 2012). Juvenile of *P. quadrilineatus* limited their distribution only in seagrass beds (Horinouchi *et al.*, 2012; Horinouchi *et al.*, 2009; Yoknoi, 2012). Adult of *P. quadrilineatus* were found offshore area and seagrass beds (Matsuura *et al.*, 2005; Yoknoi, 2012). The distribution of the two terapontid fishes in coastal area of Trang Province can be hypothesized that *T. jarbua* use the mangroves, sandy beaches and coastal swamps as nursery ground and feeding ground during the larval and juvenile stages. *Pelates quadrilineatus* on the other hand use the seagrass beds as nursery ground and feeding ground during the larval and juvenile stages. Adults of both species are found offshore area as spawning ground and feeding ground.

Table 3.4 Distribution of *Terapon jarbua* and *Pelates quadrilineatus* in Thailand (L = Larvae, J = Juvenile, A = Adult, M =Mangrove, CS = Coastal Swamp, S = Sandy Beach, SG = Seageass Bed, C = Coral Reef, OS = Offshore area, P = Plankton net, V = Velon, SS = Small seine net, G = Gill net).

Region	***T. jarbua***			***P.quadrilineatus***			**Habitat**	**Equipment**	**Reference**
	L	J	A	L	J	A			
Gulf of Thailand									
Kang Kao Island, Chonburi	✓		✓				C	P	Somkleeb, *et al*. (2002)
Bangpakong River, Chachengchao			✓				M	P / V	Paphavasit, *et al*. (2006)
Ban Khun Samut Chin, Samut Prakarn			✓				M	P / V	Paphavasit, *et al*. (2006)
Ban Krasa Khao, Samut Sakhon			✓				M	P / V	Paphavasit, *et al*. (2006)
Ban Bang Yaphrak, Samut Sakhon			✓				M	P / V	Paphavasit, *et al*. (2006)
Phan Thai Norasing, Samut Sakhon	✓		✓				M	P / V	Paphavasit, *et al*. (2006)
Tha chin river, Samut Sakhon			✓				M	P / V	Paphavasit, *et al*. (2006)
Ban Bangkaew, Samut Songkhram.	✓						M	P / V	Paphavasit, *et al*. (2006)

Table 3.4 Continued.

Region	***T. jarbua***			***P.quadrilineatus***			**Habitat**	**Equipment**	**Reference**
	L	J	A	L	J	A			
Ban laemphakbia, Phetchaburi			✓				M	P / V	Paphavasit, *et al*. (2006)
Sirinath Rajini Mangrove Ecosystem Learning Center, Phetchaburi			✓				M	P / V	Paphavasit, *et al*. (2006)
Ban Krut, Prachuabkhirikhan	✓			✓			S	P	Chayakul (2007)
Pak Phanang Estuary, Nakhon Si Thammarat			✓				M	P / V	Paphavasit, *et al*. (2004)
Andaman Sea									
Ban Ngao, Ranong		✓					M	P	Macintosh *et al*. (2002)
Phangnga Bay Phangnga		✓					S	P	Pimoljinda (1998)
Rajamangala Swamp, Trang	✓	✓					CS	SS	Tongnunui *et al*. (2010); Yoknoi (2012)
Rajamangala Beach, Trang	✓		✓	✓		✓	OS	P/G	Yoknoi (2012)
Rajamangala Beach, Trang		✓					S	SS	Yoknoi (2012)
Boonkong Bay, Trang					✓		SG	SS	Yoknoi (2012)
Makham Bay, Trang				✓	✓		SG	SS	Yoknoi (2012)
Chao Mai Beach, Trang	✓			✓			SG	P	Duangdee (1995)
Ban Khuan Tung Ku, Trang					✓		SG	SS	Horinouchi *et al*. (2009); Horinouchi *et al*. (2012)
Had Yao Beach, Trang					✓		SG	SS	Horinouchi *et al*. (2009); Horinouchi *et al*. (2012)
Libong Island, Trang			✓	✓		✓	SG	SS	Matsuura and Kimura (2005)

C. Materials and Methods

1. Description of Study Area and Sampling Period

The study area is part of 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 dry season is usually accompanied by light winds from the northeast monsoon while strong winds associated with the southwest monsoon occurred during the wet season. The study area consists of 8 sampling stations as shown in Figure 3.1 and Table 3.5. The two terapontid fishes, *T. jarbua* and *P. quadrilineatus* are distributed among these sampling stations. The samples were collected monthly during January to December 2013.

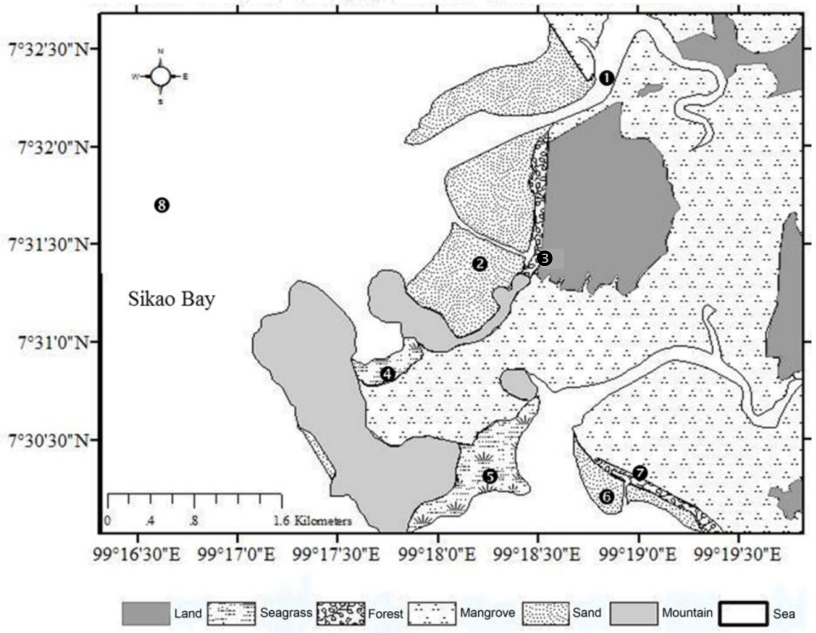


Figure 3.1 Study area located in the coastal area of Trang Province on the southwest coast of Thailand (❶: Sikao Creek, ❷: Rajamangala Beach, ❸: Rajamangala Coastal Swamp, ❹: Boonkong Bay, ❺: Makham Bay, ❻: Pakmeng Beach, ❼: Pakmeng Coastal Swamp and ❽: Offshore area).

Table 3.5 Sampling stations and environmental parameters during dry season (January - April 2013) and wet season (May - December 2013) in the coastal area of Trang Province.

Station	**Site description**	**Water depth (m)**		**Temperature (^{o}C)**		**Salinity (psu)**	
		Dry	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**
1 Sikao Creek	This area was the part of Sikao creek opening into Sikao bay. The width of the creek was approximately 25 meters. The bottom consisted of sand and soft mud sediment. Sikao creek was lined by the natural *Rhizophora apiculata* mangrove forest. This area was always under tidal influence.	0.69 ±0.11	0.72 ±0.19	28.88 ±0.63	27.61 ±0.36	27.20 ±0.24	27.43 ±0.90
2 Rajamangala Beach	This area located in the intertidal zone of Rajamangala beach. The coastline was 2.2 kilometers in the length. The bottom sediment was mainly sand	1.00 ±0.13	0.92 ±0.19	29.38 ±0.48	27.94 ±0.50	29.88 ±0.63	28.88 ±0.79
3 Rajamangala Coastal Swamp	Natural coastal swamp, Rajamangala coastal swamp, was connecting to the Rajamangala Beach. The area of this natural coastal swamp was 18 meters in length and 3.5 meters in width. The catchment area of this coastal swamp was about 30 m^3. The bottom sediment was mainly sand. Small forest lined the coastal swamp with dominant trees of *Casuarina equisetifalia*, *Rhizophora apiculata* and *Pandanus tectorius*. During the year 2013, this coastal swamp dried up during March to April.	0.51 ±0.08	0.55 ±0.15	28.25 ±0.35	27.64 ±0.56	29.65 ±0.21	28.38 ±0.88
4 Boonkong Bay	This station located in the natural seagrass bed of Boonkong Bay. This seagrass bed consisted of *Halophila ovalis* (71.47%), *Cymodocea serrulata* (23.23%), *Thalassia hemprichii* (5.04%) and *Enhalus acoroides* (0.26%). The bay was 750 meters in length and 525 meters in width. The bottom sediment was soft mud.	0.98 ±0.25	0.90 ±0.14	29.25 ±0.65	28.06 ±0.34	30.35 ±0.72	29.25 ±0.65

Table 3.5 Continued.

Station	**Site description**	**Water depth (m)**		**Temperature (^oC)**		**Salinity (psu)**	
		Dry	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**
5 Makham Bay	This station was located in the natural seagrass bed of Makham Bay. Makham Bay seagrass bed was dominented by *Cymodocea serrulata* (87.0%), *Enhalus acoroides* (9.0%), *Halophila ovalis* (1.0%) and *Thalassia hemprichii* (1.0%). The bay was 720 meters in length and 550 meters in width. The bottom sediment was soft mud**.**	0.77 ±0.26	0.80 ±0.71	29.00 ±0.41	28.08 ±0.33	29.88 ±0.63	29.25 ±0.80
6 Pakmeng Beach	This sampling station was located in the sandy intertidal zone of Pakmeng beach. The total coastline was 4.7 kilometers in length.	0.85 ±0.25	0.88 ±0.20	28.75 ±0.65	28.03 ±0.56	30.25 ±0.65	29.66 ±0.71
7 Pakmeng Coastal Swamp	Natural coastal swamp, Pakmeng Coastal Swamp, was connected to Pakmeng Beach. The coastal swamp was 15 meters in length and 2 meters in width. The catchment area of this coastal swamp was approximately 15 m^3. The bottom sediment was mainly sand. The coastal swamp was dominanted by various plants such as, *Casuarina equisetifalia*, *Rhizophora apiculata* and *Pandanus tectorius*.	0.48 ±0.12	0.95 ±0.15	28.13 ±0.25	27.90 ±0.46	30.20 ±0.40	28.43 ±0.35
8 Offshore Area	The sampling station representing the offshore area was in front of Rajamangala Beach being 2 km from the coastline.	12.25 ±2.06	11.75 ±2.19	28.63 ±0.75	28.04 ±0.29	30.38 ±0.48	30.21 ±0.51

2. Environmental Parameter

Salinity, temperature and water depth were recorded monthly at each station. Salinity and temperature were measured by salinity and temperature meter AZ8371. Depth of water was measured by depth measuring rope. One-way ANOVA: IBM SPSS statistics 21 was used to determine whether or not the environmental parameters differed significantly among stations and seasons.

3. Fishery Survey

Preflexion, flexion and postflexion larvae stages of fish were collected by surface tows using plankton net (0.5 m mouth diameter; 330 µm mesh size). The plankton net was towed by the low-speed boat (3 min) at each station except for station 3 and station 5. At these two stations, fish larvae were sampled by filtering 100 L of seawater through the plankton net of 330 µm mesh size. Three replicates samples were taken for each station. Samples were preserved in 4% neutral formalin.

Transforming larvae and juvenile fish were collected by small seine net with two 5 m long x 0.5 m high wings and a 2.5 m long cod end of 2.5 mm stretched mesh size. Three replicates were taken at each station. For each tow, the net was initially laid out at the randomly established starting point in order for the net mouth opening to be 5 m and afterward the net being pulled by two persons at the distance of 20 meters. Samples were preserved in 10% neutral formalin.

Adult fish were collected from gill nets (30 m long, mesh size of 30 mm) used by fisherman at the fishery landings. All samples were kept on ice and preserved in the refrigerator at 4^{o}C in the laboratory.

4. Reproductive Biology of *Terapon jarbua* and *Pelates quadrilineatus*

4.1 Histological study of gonad

In the laboratory, total length, standard length and body weight were measured for each specimen (to the nearest 1.0 mm and 0.01 g, respectively). For the adult fish sample, the abdomen was cut open to remove the gonad, weighed to nearest 0.01 g and preserved in 10% buffered formalin. All gonad specimens were processed using standard histological techniques (Humason, 1979). The middle part of gonad was cut about 5 mm. The gonad tissues were dehydrated in a series of ethanol (70%, 70%, 80%, 95%, 95% and100%) for about 1 hour in each solution. Then the tissues were cleared in 2 changes of xylene and then embed in 2 changes of 50^{o}C paraffin for about 1 hour in each solution. The paraffin blocks of gonadal tissue were serially sectioned at 6 µm thickness and stained. Deparaffinize the tissue section by 3 changes of xylene for about 5 min in each solution, 2 changes of 100% ethanol for about 2 min in each solution, 2 changes of 95% ethanol for about 1 min in each solution and distill water for about 1 min. Stain tissue for 3 min with Mayer hematoxylin. Rinse with water to remove excess reagent for about 10 min. Stain tissue for 2 min with 1% Eosin G Aqueous solution. Dehydrate in 2 changes each of reagent 95% alcohol, absolute alcohol and xylene for 3 minutes each solution then mount the slide. Light microscope was used to observe the histological structure of gonad. Developmental stages of gonad were categorized according to Brown-Peterson *et al.* (2011) Sex was determined by examination of the gonads.

4.2 Gonadosomatic Index

The gonadosomatic index (GSI) of males and females were calculated as the proportion of the weight of the gonad to the weight of eviscerated body in percent. The gonadosomatic index (GSI) was calculated for each fish as followed Cailliet *et al.* (1986):

$$GSI = \text{gonad weight} \times 100 / \text{body weight}$$

4.3 Fecundity

The fecundity of gravid females was estimated individually using the gravimetric method as reported in Cailliet *et al.* (1986).

$$F = (p / P) \times n$$

Where p is the total weight (g) of the gonad

n is a sub-sample of the gonad (fixed as 100 oocytes)

P is the weight (g) of n

4.4 First Sexual Maturity

The data of standard length and reproductive phase from gonads were used to calculated proportion of reproductive males or females for each size class. Logistic equations are used to estimate the first sexual maturity. Parameter estimations were performed using the Non Linear Regression routine of IBM SPSS 21.0 (Cailliet *et al.*, 1986).

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5. Movement Patterns in *Terapon jarbua* and *Pelates quadrilineatus* from Sr:Ca Ratio in Otoliths

Sagittal otoliths were extracted from each fish. Otolith of 5 adult *T. jarbua* and 5 adult *P. quadrilineatus* were used for measurement of Sr and Ca concentrations. The otolith were extracted, cleaned and embedded in epoxy resin. The otoliths were polished along the frontal plane. After polishing, the otoliths were rinsed with deionized water, air-dried and coated with carbon. Concentrations of Sr and Ca in the otoliths were measured with a wave-length dispersive X-ray electron probe microanalyzer (EPMA) from core to edge of otolith. The beam currents, beam sizes, intervals and peak counting time were 5 nA, 10 µm, 20 µm and 90 s, respectively. The mean of Sr:Ca ratio were plot against the distance from the core to otolith edge (µm) (C. Chang *et al.*, 2004).

D. Results and Discussions

1. Environmental Parameters Affecting the Distribution and Abundance of *Terapon jarbua* and *Pelates quadrilineatus*

Temperature, water depth and salinity were the environmental parameters investigated in this study. Seasonal variations in temperature, water depth and salinity in Table 3.5 were minimal among stations in the coastal area of Trang Province ($p > 0.05$). The temperature among stations in the dry season were slightly higher than those recorded during the wet season. According to mangrove habitats and coastal swamp, the Sikao Creek, Rajamangala Coastal Swamp and Pakmeng Coastal Swamp, the temperature were in the range of 28.0-29.5 ^{o}C during the dry season and in the range of 27.0-28.5 ^{o}C during the wet season as in Figure 3.2. The seagrass beds habitat, Boonkong Bay and Makham Bay showed the similar trend. The temperature during the dry season was in the range of 28.5-30.0 ^{o}C while the temperature of 27.5-28.5 ^{o}C was found during the wet season. The two sandy beaches, Rajamangala Beach and Pakmeng Beach, also showed the similar trend. No significant seasonal variations in the temperature in the offshore station.

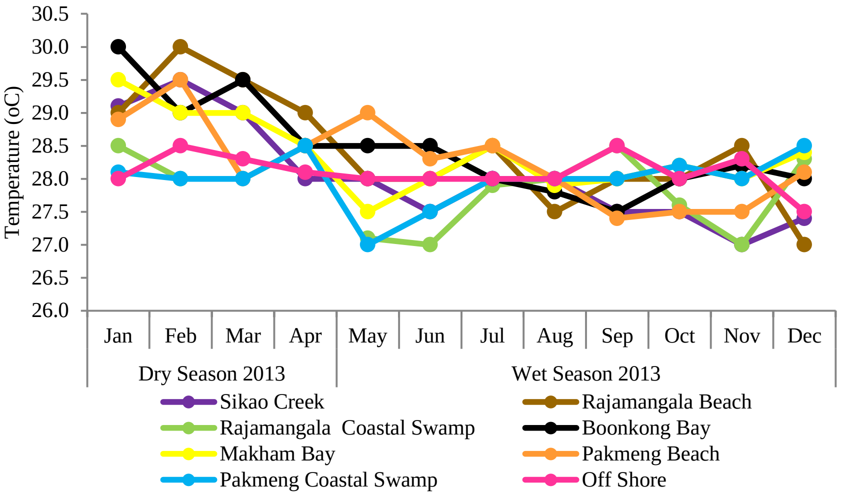


Figure 3.2 Monthly variations of water temperature in the coastal area of Trang Province.

The water depth in the mangrove habitat showed minimal seasonal variations except for Rajamangala Coastal Swamp as in Figure 3.3. The water depth recorded for the Sikao Creek and Pakmeng Coastal Swamp was in the range of 0.34-0.78 m in the dry season and 0.35-1.00 m in the wet season. At the Rajamangala Coastal Swamp, during the months of March and April, the coastal swamp dried up. The water depth recorded for the seagrass beds, Boonkong Bay and Makham Bay were in the range of 0.43 and 1.25 m during the dry season and in the range of 0.55 and 1.15 m during the wet season respectively. The water depth at sandy beaches, Rajamangala Beach and Pakmeng Beach, were in the range of 0.54-1.15 m during the dry season and in the range of 0.57-1.20 m during the wet season. The depth at the offshore station ranged from 10.00-15.00 m.

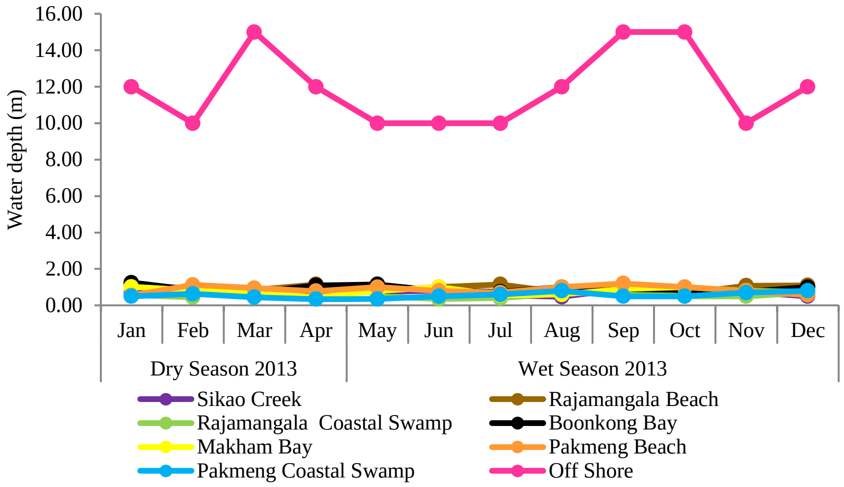


Figure 3.3 Monthly variations of water depth in the coastal area of Trang Province.

Seasonal variations in salinity were not detected in most study areas of the mangrove habitat, seagrass beds, sandy beaches and offshore area except for the coastal swamp. High salinity during the dry season in the coastal swamps, Rajamangala Coastal Swamp and Pakmeng Coastal Swamp, was in the range of 29.0-30.8 psu as compared to the salinity range of 28.0-29.0 psu observed in the wet season ($p<0.05$) as in Figure 3.4. Being small enclosed, the salinity fluations were easily detected. At the beginning of the dry season in January, toward the late dry season in April, high salinity were observed at both stations. In the early wet season in May, the low salinity observed due to the rainfall from the Southwest Monsoon. Daily fluctuations in the coastal swamps were observed under the tidal influences.

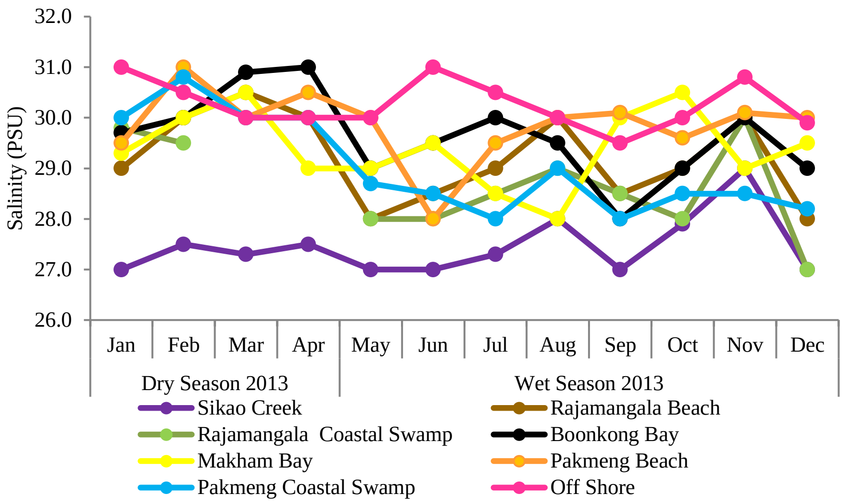


Figure 3.4 Monthly variations of salinity in the coastal area of Trang Province.

The environmental parameters temperature, water depth and salinity did not showed the significant relationships with the density of the two terapontid fishes, *T. jarbua* and *P. quadrilineatus* found distributed in the coastal area in Trang Province (p>0.05).

2. Distribution and Abundance in *Terapon jarbua*

Terapon jarbua showed the clear habitat utilization in coastal area of Trang Province between developmental stages. They have separate habitat distribution in each developmental stage. The distribution and abundance of planktonic larvae (preflexion larvae, flexion larvae, and postflexion larvae), were found only in the offshore area station. The abundance of planktonic larvae in each stage showed no statistically significant difference ($p > 0.05$) between the dry season and wet season. Abundance and distribution of the Preflexion larvae of *T. jarbua* in the coastal area, Trang Province was shown in Figure 3.5. Abundance and distribution of the flexion and postflexion larvae were shown in Figure 3.6 and Figure 3.7, respectively.

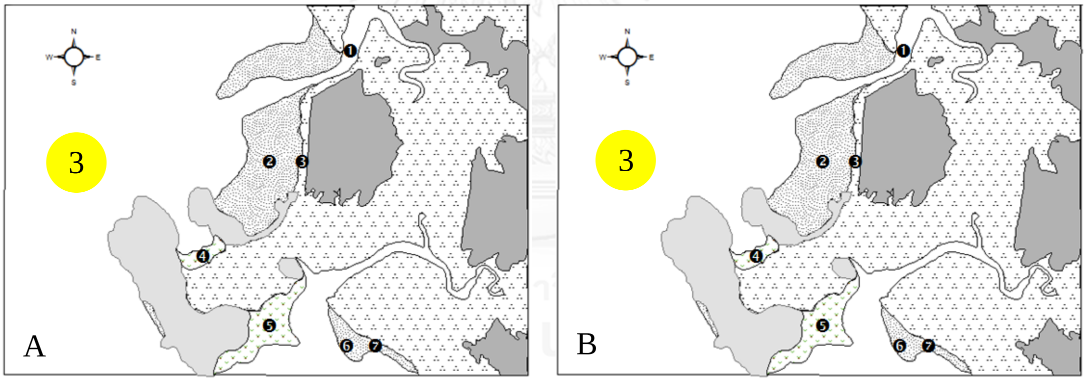


Figure 3.5 Abundance (individual/1000 m^3) and distribution of preflexion larvae of *Terapon jarbua* between dry season (A) and wet season (B) from the coastal area of Trang Province.

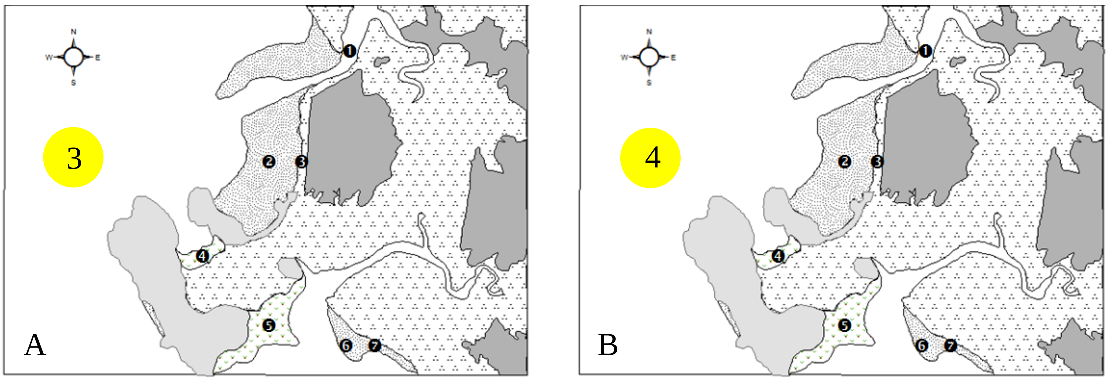


Figure 3.6 Abundance (individual/1000 m^3) and distribution of flexion larvae of *Terapon jarbua* between dry season (A) and wet season (B) from the coastal area of Trang Province.

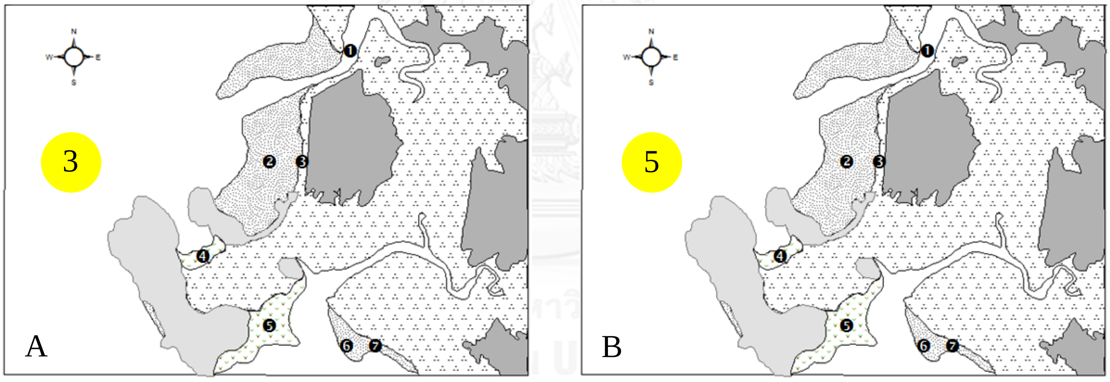


Figure 3.7 Abundance (individual/1000 m^3) and distribution of postflexion larvae of *Terapon jarbua* between dry season (A) and wet season (B) from the coastal area of Trang Province.

Transforming larvae and juveniles were found distributed in the coastal swamp habitat under the tidal influences of Rajamangala Coastal Swamp and Pakmeng Coastal Swamp. The abundance of transforming larvae and juveniles showed significantly differences between the dry and wet season ($p<0.05$). Transforming larvae of *T. jarbua* were found in highest density in Pakmeng Coastal Swamp during the month of May and October in the wet season. The transforming larvae were found in respective order of density in the Rajamangala Coastal Swamp as in Figure 3.8.

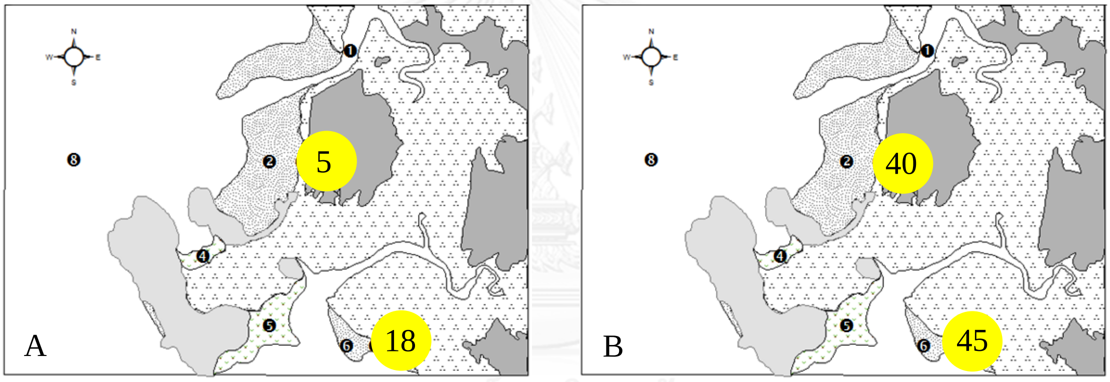


Figure 3.8 Abundance (individual/1000 m^3) and distribution of transforming larvae of *Terapon jarbua* between dry season (A) and wet season (B) from the coastal area of Trang Province.

Juveniles of *T. jarbua* also found in high abundant during the wet season, in particular May and October, in Pakmeng Coastal Swamp as in Figure 3.9. Juveniles also distributed in the sandy beach of Pakmeng Beach, the transitional area between the coastal swamp and the offshore area. High density of juveniles at Pakmeng Beach was observed during the wet season.

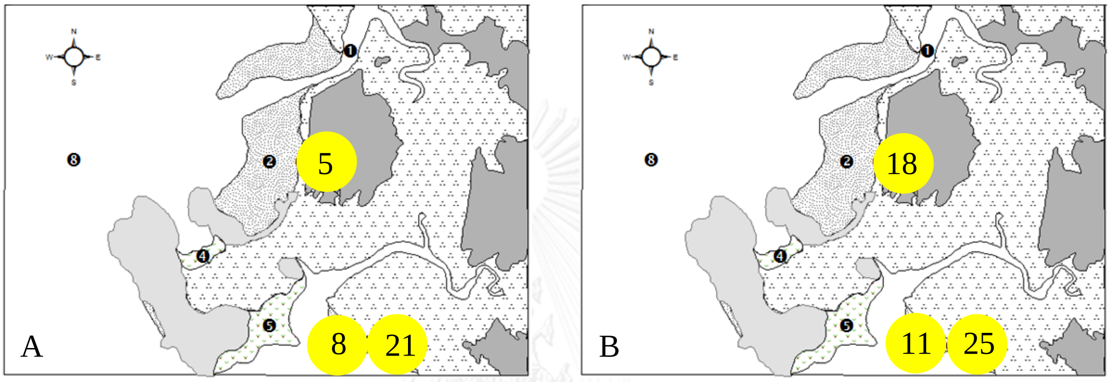


Figure 3.9 Abundance (individual/1000 m^3) and distribution of juvenile of *Terapon jarbua* between dry season (A) and wet season (B) from the coastal area of Trang Province.

The distribution and abundance of adult fish were found only offshore area along with the planktonic larvae (Figure 3.10). The abundance of adult fish during the dry season was not statistically significant difference ($p > 0.05$) from the abundance of adult fish during the wet season.

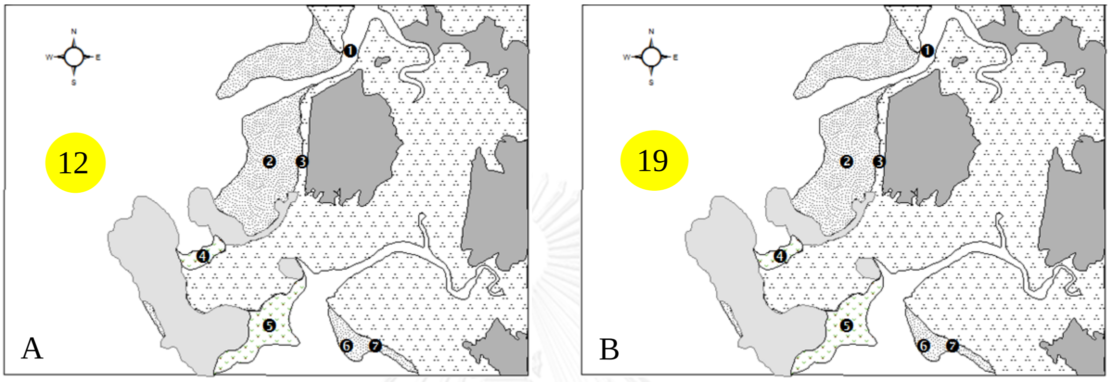


Figure 3.10 Abundance (individual/1000 m^3) and distribution of adult of *Terapon jarbua* between dry season (A) and wet season (B) from the coastal area of Trang Province.

3. Distribution and Abundance in *Pelates quadrilineatus*

Pelates quadrilineatus also showed the clear habitat utilization in coastal area of Trang Province between developmental stages as observed in *T. jarbua*. All stages of planktonic larvae, preflexion larvae, flexion larvae, and postflexion larvae, were found offshore area. The abundance of planktonic larvae showed no statistically significant difference ($p > 0.05$) between the dry season and wet season. The preflexion larvae abundance and distribution was shown in Figure 3.11.

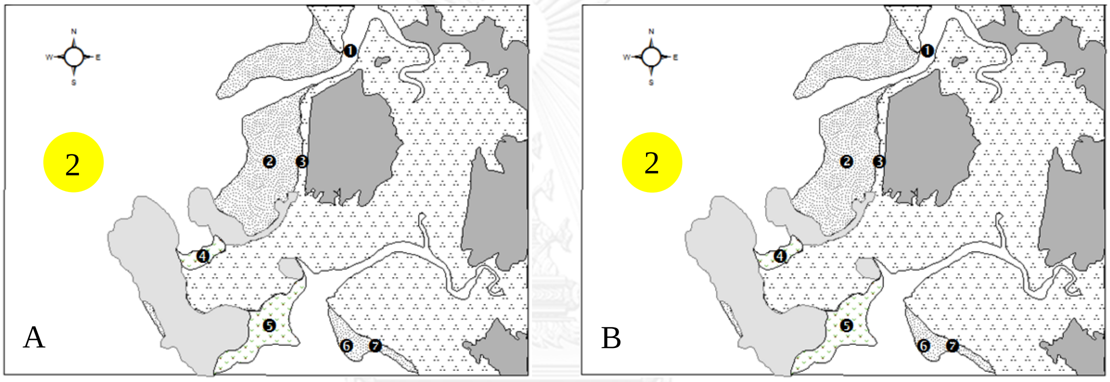


Figure 3.11 Abundance (individual/1000 m^3) and distribution of preflexion larvae of *Pelates quadrilineatus* between dry season (A) and wet season (B) from the coastal area of Trang Province.

The abundance and distribution of flexion larvae of *P. quadrilineatus* in coastal area of Trang Province was shown in Figure 3.12, while the abundance and distribution of postflexion larvae was shown in Figure 3.13.

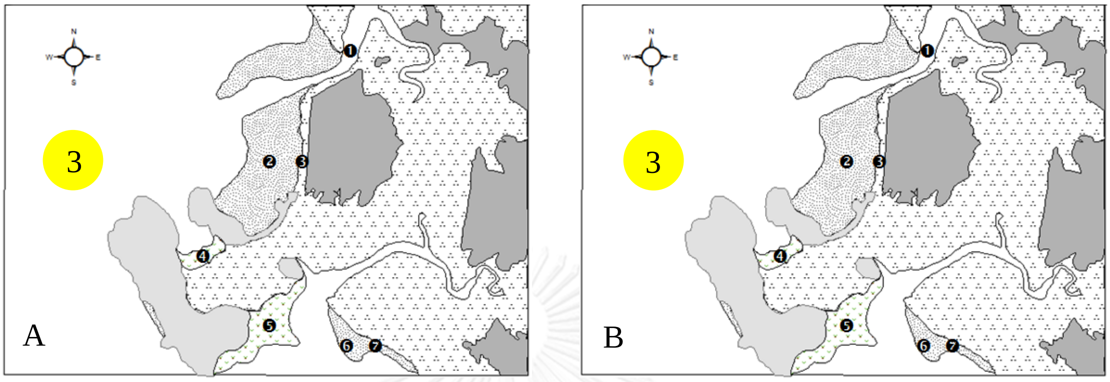


Figure 3.12 Abundance (individual/1000 m^3) and distribution of flexion larvae of *Pelates quadrilineatus* between dry season (A) and wet season (B) from the coastal area of Trang Province.

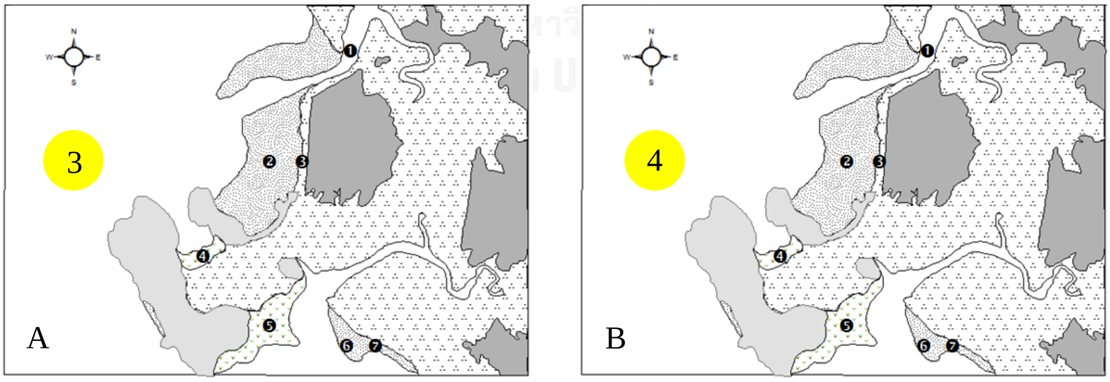


Figure 3.13 Abundance (individual/1000 m^3) and distribution of postflexion larvae of *Pelates quadrilineatus* between dry season (A) and wet season (B) from the coastal area of Trang Province.

Transforming larvae and juveniles of *P. quadrilineatus* were found distributed in seagrass beds of Boonkong Bay and Makham Bay. They were also found distributed in the transitional area of the sandy beach, Pakmeng Beach, connecting the seagrass beds and the open sea. Makham bay showed the highest density of transforming larvae as compared to the seagrass bed at Boonkong Bay. The abundance of transforming larvae showed significantly differences between the dry and wet season ($p<0.05$). The density of transforming larvae was high during the dry season as in Figure 3.14.

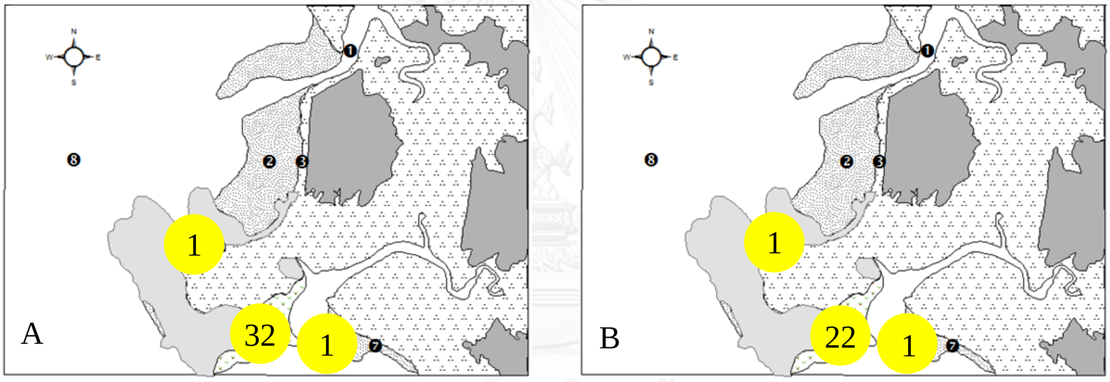


Figure 3.14 Abundance (individual/1000 m^3) and distribution of transforming larvae of *Pelates quadrilineatus* between dry season (A) and wet season (B) from the coastal area of Trang Province.

Juveniles of *P. quadrilineatus* (Figure 3.15) showed similar trend of distribution and abundance as in the transforming larvae. The abundance of juveniles showed significantly differences between the dry and wet season ($p<0.05$). Makham Bay showed the highest density of juveniles during the dry season.

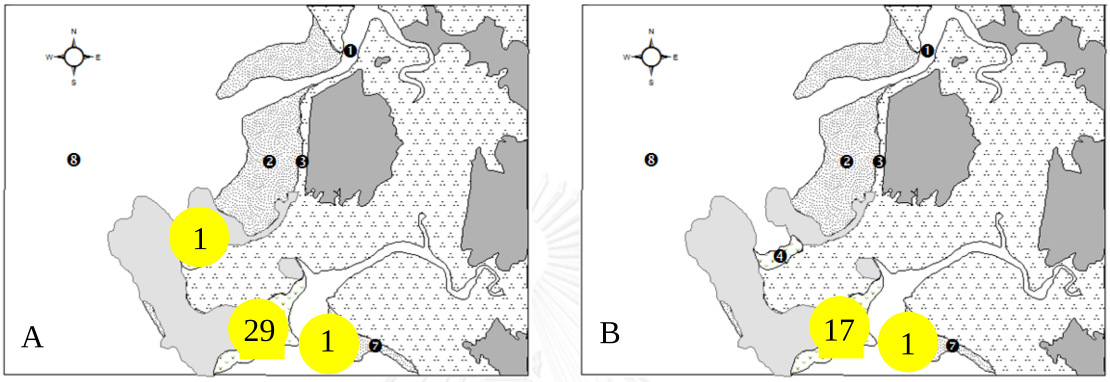


Figure 3.15 Abundance (individual / 1000 m^3) and distribution of juvenile of *Pelates quadrilineatus* between dry season (A) and wet season (B) from the coastal area of Trang Province.

The distribution and abundance of adult fish were found only offshore area (Figure 3.16). The abundance of adult showed no statistically significant difference ($p > 0.05$) between the dry season and wet season.

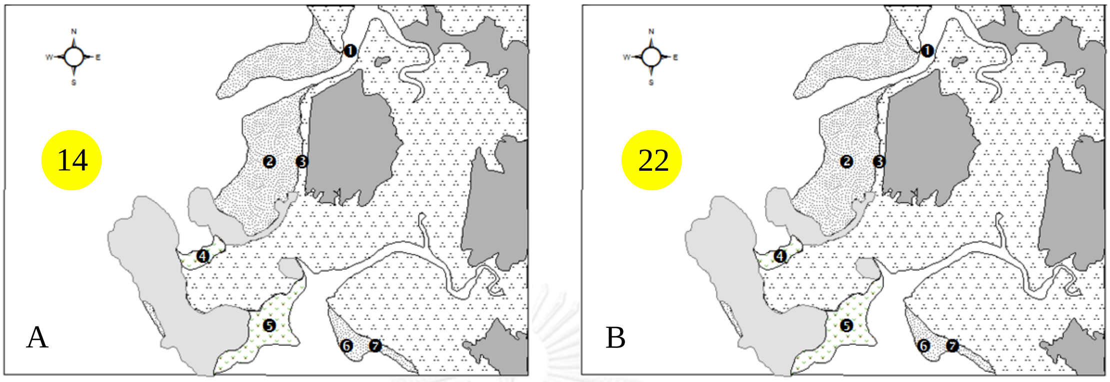


Figure 3.16 Abundance (individual/1000 m^3) and distribution of adult of *Pelates quadrilineatus* between dry season (A) and wet season (B) from the coastal area of Trang Province.

4. Reproductive biology and Spawning period in *Terapon jarbua*

4.1 Reproductive biology in male *Terapon jarbua*

1) Testis structure of male *Terapon jarbua*

The testes of *T. jarbua* are paired and elongate, organs located on dorsal part of the gut. The testis is covered with tunica albuginea which composed of connective tissue layer and blood vessels. The cross section of testes reveals a random distribution of various clusters of seminiferous lobule, which contains a specific stage of spermatogenic cells. Spermatogenic cells were classified based on the cell size, shape, nuclear characteristics, chromatin condensation, amount of cytoplasm and staining properties. The spermatogenic cells of *T. jarbua* are classified into 5 stages as follows: **(1) Spermatogonium (Sg)** is the largest of spermatogenic cells generally located close to the basement membrane of seminiferous lobule. This stage is characterized by the appearances of lightly basophilic nucleus, distinct nuclear membrane and moderate amount of light granular cytoplasm. **(2) Primary spermatocyte (Psc)** is smaller in size than spermatogonia. It is spherical in shape with basophilic nucleus. The nucleolus is still prominent and chromatins are condensed. Moderate amount of distinctive cytoplasm is found in this stage. **(3) Secondary spermatocyte (Ssc)** is smaller than primary spermatocytes. In this stage, dense basophilic nucleus contains perinucleolar chromatin without nucleolus. Amount of cytoplasm is found to decrease compared with the previous stage. **(4) Spermatid (St)** arises from secondary spermatocyte after second meiotic division. The spermatid is small and more condensed with intense basophilic nucleus and small amount of cytoplasm because they lose their cytoplasm during spermiogenesis. **(5) Spermatozoan (Sz)** is the smallest among spermatogenic cells. It is a mature cell consisting of 2 regions; head and tail. The spermatozoa are released into the lumen and vasa efferentia, respectively (Figure 3.17).

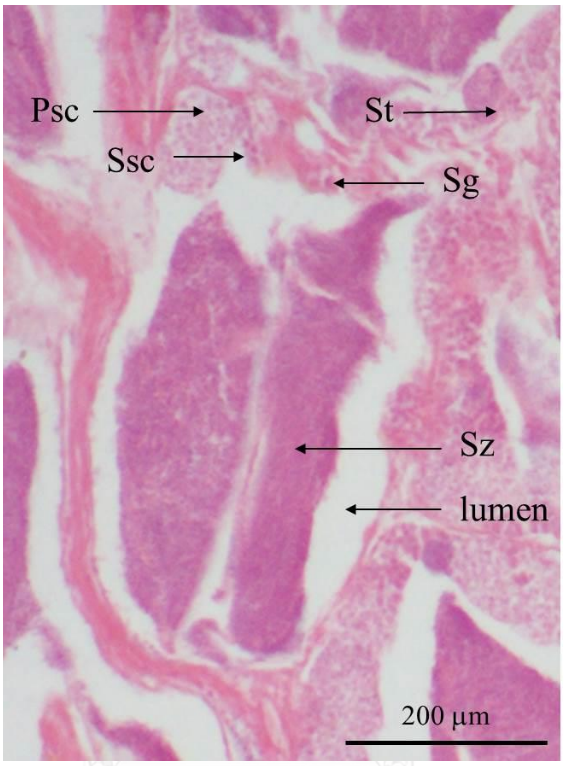


Figure 3.17 Spermatogenic cells in testis of male *Terapon jarbua* (155.41 mm in SL; GSI = 1.98) (Sg = Spermatogonium, Psc = Primary spermatocyte, Ssc = Secondary spermatocyte, St = Spermatid, Sz = Spermatozoan).

2) Reproductive phase of male *Terapon jarbua*

Testes of *T. jarbua* were assigned into five maturity stages:

Immature stage (Stage 0): The testis was very small, often clear, blood vessels indistinct. Only spermatogonium and primary spermatocyte presented. No lumen in lobules (Figure 3.18).

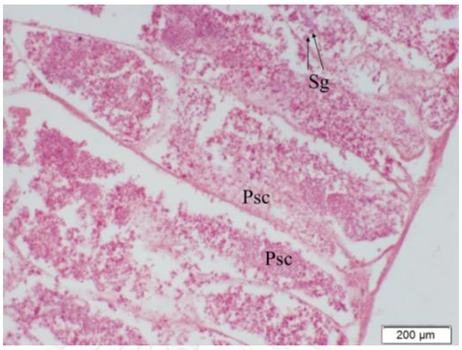


Figure 3.18 Immature reproductive phase of male *Terapon jarbua* (155.22 mm in SL; GSI = 0.85) (Sg = Spermatogonium, Psc = Primary spermatocyte).

Developing stage (Stage 1): The testis was small but easily identified. Secondary spermatocyte predominated. Spermatid and spermatozoa can be presented (Figure 3.19).

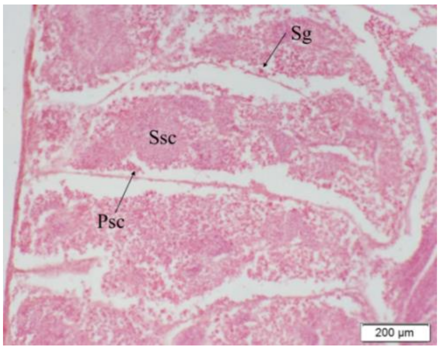


Figure 3.19 Developing reproductive phase of male *Terapon jarbua* (117.50 mm in SL; GSI = 1.08) (Sg = Spermatogonium, Psc = Primary spermatocyte, Ssc = Secondary spermatocyte).

Spawning capable stage (Stage 2): The testis was large and firm. Spermatid and spermatozoa presented in lumen of lobules and/or sperm ducts. Spermatocyte can be presented (Figure 3.20).

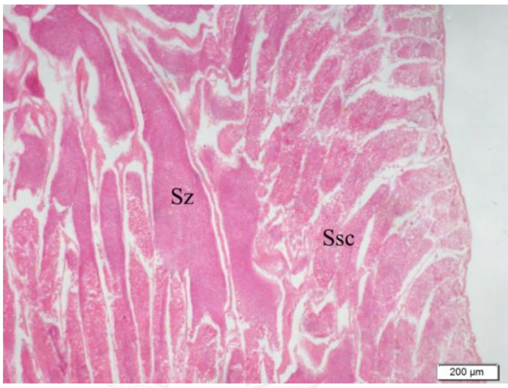


Figure 3.20 Spawning capable reproductive phase of male *Terapon jarbua* (147.30 mm in SL; GSI = 1.88) (Ssc = Secondary spermatocyte; Sz = Spermatozoan).

Regressing stage (Stage 3): The testis was small and flaccid. Residual spermatozoa presented in lumen of lobules and in sperm ducts. Secondary spermatocyte and spermatid were scattered near periphery (Figure 3.21).

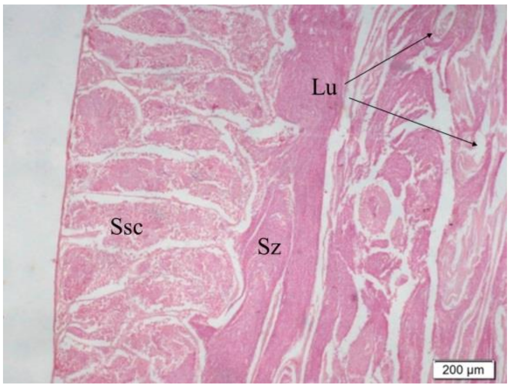


Figure 3.21 Regressing reproductive phase of male *Terapon jarbua* (155.95 mm in SL; GSI = 1.25) (Ssc = Secondary spermatocyte, Sz = Spermatozoan, Lu = Lumen).

Regenerating stage (Stage 4): The testis was small and often threadlike. Testes were possessing new crypts of spermatogonium and primary spermatocytes. Moreover, testes also had empty lumen and some residual spermatozoa (Figure 3.22).

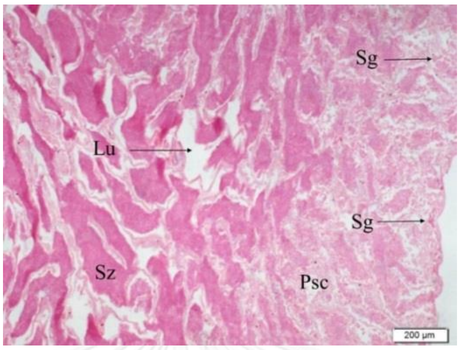


Figure 3.22 Regenerating phase of male *Terapon jarbua* (153.50 mm in SL; GSI = 1.33) (Sg = Spermatogonium, Psc = Primary spermatocyte, Sz = Spermatozoan, Lu = Lumen).

The monthly percentage of gonadal maturity stage indicated that, *T. jarbua* with testes at spawning stages occurred high percentage in two phases were April to June and September to October (Figure 3.23).

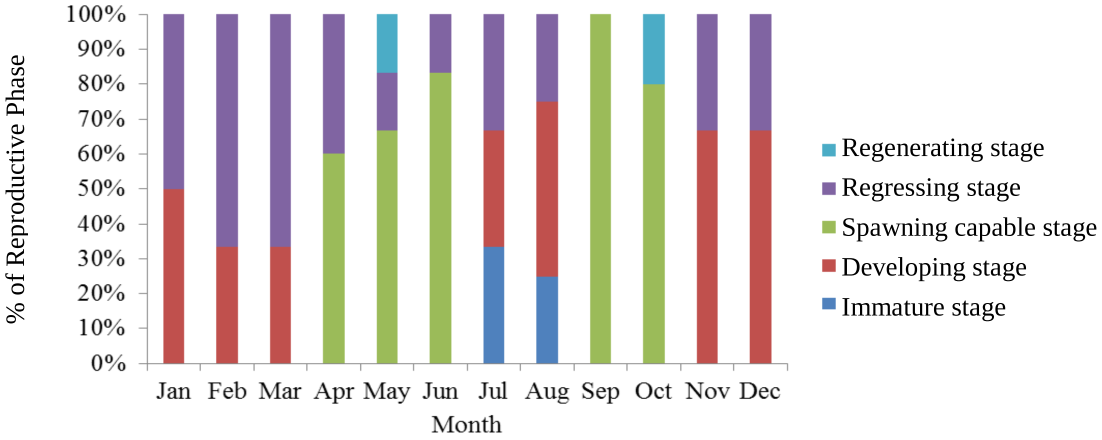


Figure 3.23 Monthly percentage frequencies of gonadal maturity stages of male *Terapon jarbua* (n=49) from the coastal area of Trang Province.

3) Gonadosomatic Index of male *Terapon jarbua*

Monthly changes of gonadosomatic index showed, the gonadosomatic index of male *T. jarbua* high in two phases were May to June and September to October. The GSI increased from 0.75 in January to the peak of 2.19 in May, decreased thereafter to 0.97 in August and then gradually increased to the peak again of 1.85 in October (Figure 3.24).

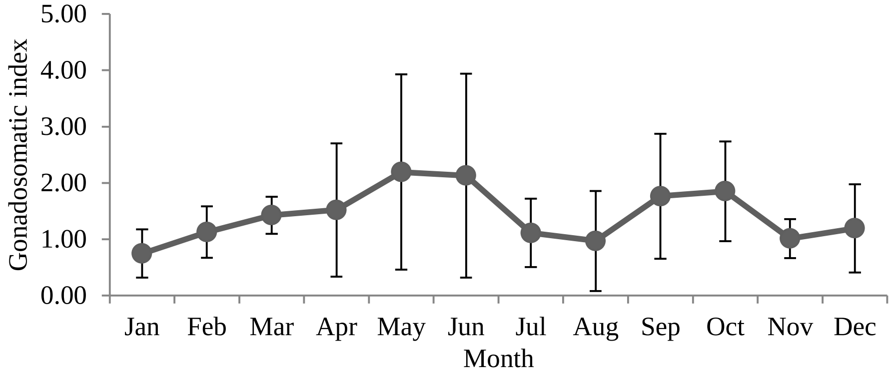


Figure 3.24 Monthly mean Gonadosomatic Index of male *Terapon jarbua* (n=49) from the coastal area of Trang Province.

4) Size at first sexual maturity

The size at first sexual maturity of male *T. jarbua* was 153.77 mm in SL (Figure 3.25).

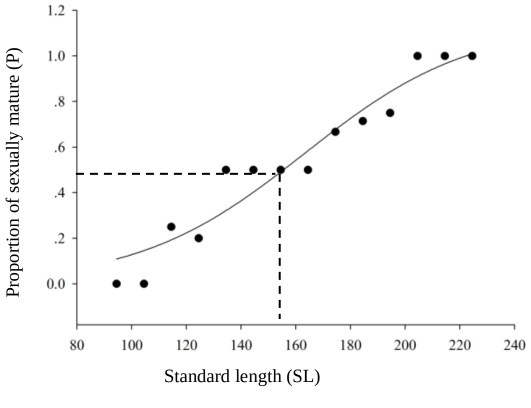


Figure 3.25 The size at first sexual maturity of male *Terapon jarbua* (n=49) from the coastal area of Trang Province.

4.2 Reproductive biology in female *Terapon jarbua*

1) Ovarian structure of female *Terapon jarbua*

Female *T. jarbua* has two ovarian sacs with situated on dorsal part of gut. The surface of ovary is surrounded by tunica albuginea which is a thin layer of connective tissue and numerous blood vessels. The cross section of ovary reveals a random distribution of various stages of oocyte. Developmental stages of oocyte have been classified based mainly on the cell size, shape, nuclear characteristics, amount and characteristics of cytoplasm and staining properties. The female germ cells are classified as follows: **(1) Perinucleolar stage oocyte (PG)** has multiple nucleoli appear at the periphery of nucleus. The cytoplasm increases in mass and appears basophilic (Figure 3.26A). **(2) Cortical alveolar stage oocyte (CA)** is larger than perinucleolar stage oocyte. The nucleus also contains many nucleoli at the periphery near the nuclear membrane. This stage is characterized by the presence of cortical alveoli or yolk vesicles accumulated in the peripheral region of the cytoplasm (Figure 3.26B). **(3) Vitellogenic stage oocyte (Vtg)** is also increased in size. The yolk vesicles are enlarged and still occur in the cytoplasm. In this stage, the oocyte is characterized by the appearance of numerous lipid droplets and yolk granules accumulated in the cytoplasm. Vitellogenic stage oocyte is subdivided in 3 different stages. Primary vitellogenic stage oocyte (Vtg1): Lipid droplets occupy more cytoplasmic area than yolk granules (Figure 3.26C). **(4) Secondary vitellogenic stage oocyte (Vtg2):** Lipid droplets occupy similar cytoplasmic area than yolk granules (Figure 3.26D). **(5) Tertiary vitellogenic stage oocyte (Vtg3):** Lipid droplets occupy less cytoplasmic area than yolk granules (Figure 3.26E). **(6) Mature stage oocyte (MO)** The nucleus could not be observed and the membrane of the nucleus dissolved.

The lipid and protein particles were fused and demonstrated a homogeneous appearance. Oil droplet is clearly evident at central part of the oocyte (Figure 3.26F). **(7) Atresia (A)** is breakdown of the ovarian follicles (Figure 3.26G). **(8) Post-ovulatory follicle (POF)** is polymorphic structures resulting from the collapse of the follicle at ovulation (Figure 3.26H).

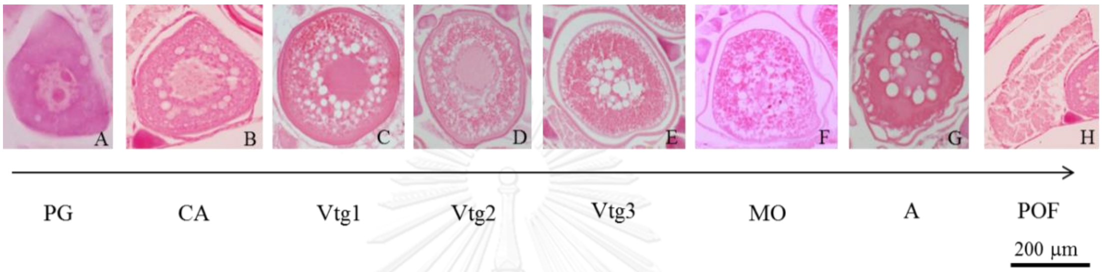


Figure 3.26 Oocyte developments of female *Terapon jarbua* (PG = Perinucleolar stage oocyte, CA = Cortical alveolar stage oocyte, Vtg1 = Primary vitellogenic stage oocyte, Vtg2 = Secondary vitellogenic stage oocyte, Vtg3 = Tertiary vitellogenic stage oocyte, MO = Mature stage oocyte, A = Atresia, POF = Post-ovulatory follicle).

2) Reproductive phase of female *Terapon jarbua*

Ovaries of *T. jarbua* were assigned into five maturity stages.

Immature stage (Stage 0): The ovary was very small, often clear, blood vessels indistinct. Only perinucleolar stage oocyte and cortical alveolar stage oocyte presented. No atresia or muscle bundles (Figure 3.27).

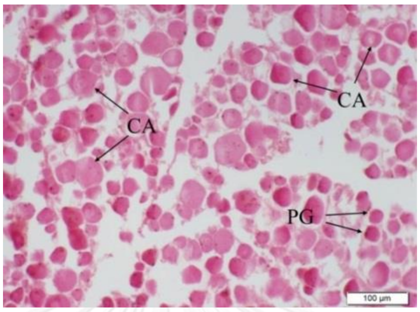


Figure 3.27 Immature reproductive phase of female *Terapon jarbua* (110.37 mm in SL; GSI = 1.25) (PG = Perinucleolar stage oocyte, CA = Cortical alveolar stage oocyte).

Developing stage (Stage 1): The ovary was beginning to grow and develop. Enlarging ovaries and blood vessels were becoming more distinct. Perinucleolar stage oocyte, cortical alveolar, primary vitellogenic, and secondary vitellogenic oocytes were dominant (Figure 3.28).

Figure 3.28 Developing reproductive phase of female *Terapon jarbua* (127.30 mm in SL; GSI = 2.58) (PG = Perinucleolar stage oocyte, Vtg1 = Primary vitellogenic stage oocyte, Vtg2 = Secondary vitellogenic stage oocyte, Vtg3 = Tertiary vitellogenic stage oocyte).

Spawning capable stage (Stage 2): The ovary was large and blood vessels prominent. Tertiary vitellogenic oocytes and mature stage oocyte were dominant. Atresia of vitellogenic may be presented (Figure 3.29).

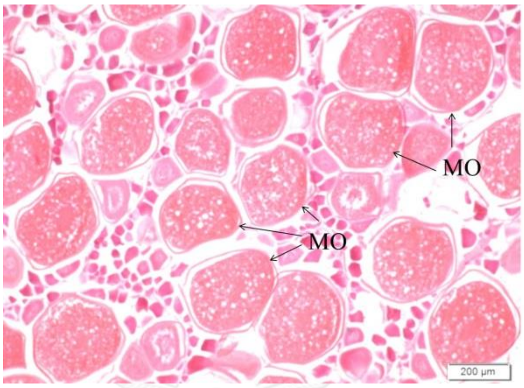


Figure 3.29 Spawning capable reproductive phase of female *Terapon jarbua* (165.60 mm in SL; GSI = 5.85) (MO = Mature stage oocyte).

Regressing stage (Stage 3): The ovary was flaccid and blood vessels prominent. Atresia and postovulatory follicle complex presented. Some cortical alveolar and/or vitellogenic oocytes presented (Figure 3.30).

Figure 3.30 Regressing reproductive phase of female *Terapon jarbua* (172.14 mm in SL; GSI = 3.15) (MO = Mature stage oocyte A = Atresia, POF = Post-ovulatory follicle).

Regenerating stage (Stage 4): The ovary was small and blood vessels reduced but presented. Perinucleolar stage oocyte and cortical alveolar stage oocyte presented. Atresia or degenerating postovulatory follicle complex may be present (Figure 3.31).

Figure 3.31 Regressing reproductive phase of female *Terapon jarbua* (152.95 mm in SL; GSI = 3.55) (PG = Perinucleolar stage oocyte, Vtg1 = Primary vitellogenic stage oocyte, A = Atresia, POF = Post-ovulatory follicle).

The monthly percentage of gonadal maturity stage indicated that, *T. jarbua* with ovaries at spawning stages occurred high percentage in two phases were April to June and September to October (Figure 3.32).

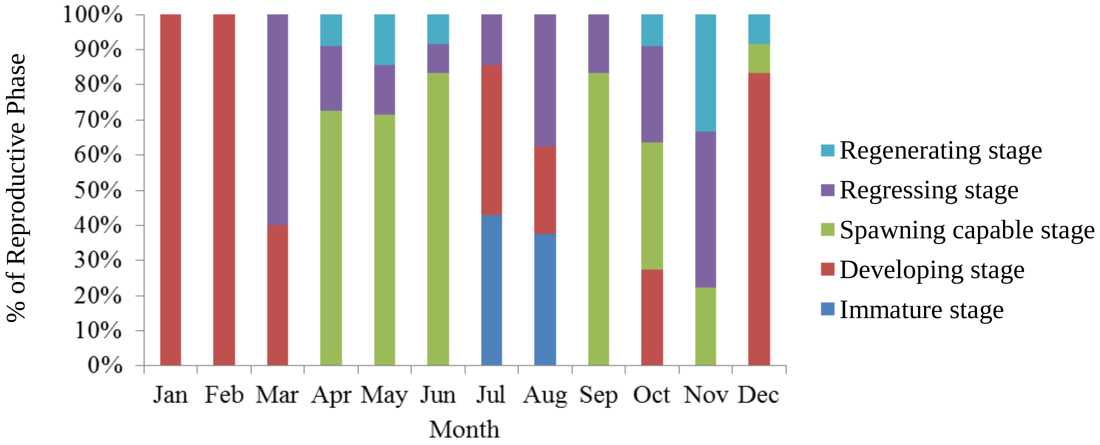


Figure 3.32 Monthly percentage frequencies of gonadal maturity stages of females *Terapon jarbua* (n =109) from the coastal area of Trang Province.

3) Gonadosomatic Index of female *Terapon jarbua*

Monthly changes of gonadosomatic index showed, the GSI of female *T. jarbua* high in two phases were March to June and September to October. The GSI of female increased from 1.55 in January to the peak of 5.34 in May, decreased thereafter to 1.72 in July and then gradually increased to the peak again of 4.42 in September (Figure 3.33).

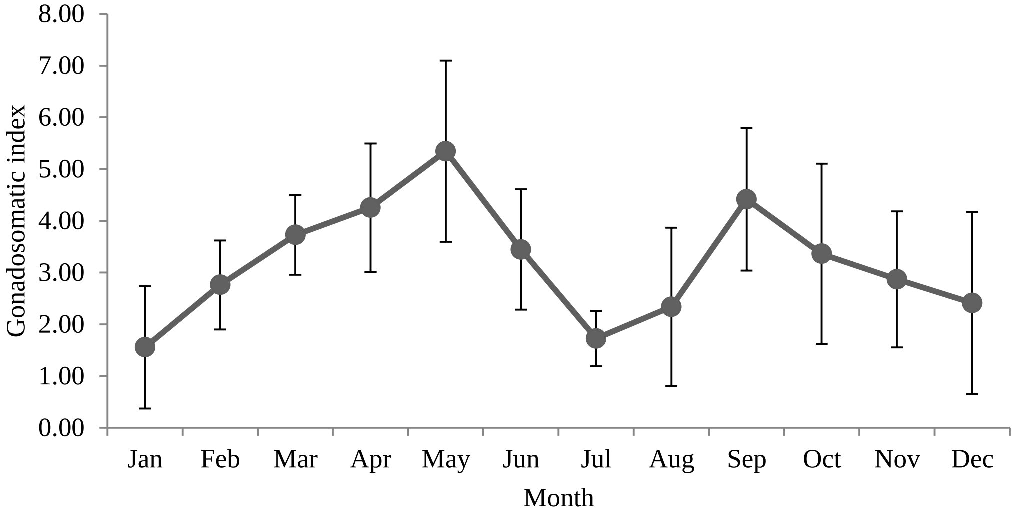


Figure 3.33 Monthly mean Gonadosomatic Index of female *Terapon jarbua* (n =109) from the coastal area of Trang Province.

4) Fecundity of female *Terapon jarbua*

The fecundity of *T. jarbua* was estimated to range from 228,150 to 763,600 eggs. The fecundity increased from 347,667 eggs in January to the peak of 763,600 eggs in March, relatively constant to September and then decreased to 357,895 eggs in October (Figure 3.34). Egg size in *T. jarbua* ranged from 0.08-0.77 mm with the average egg size of 0.31 mm.

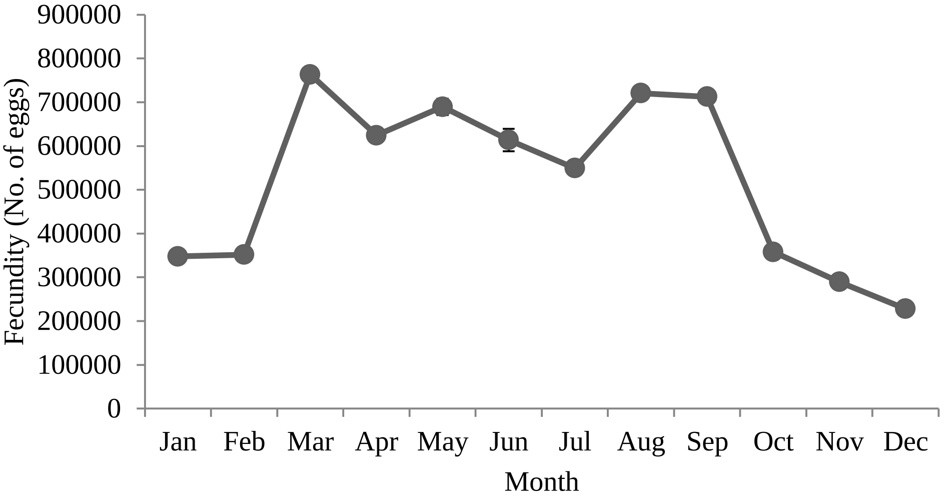


Figure 3.34 Monthly mean fecundity of females *Terapon jarbua* (n =98) from the coastal area of Trang Province.

5) Size at first sexual maturity of female *Terapon jarbua*

The Size at first sexual maturity of female *T. jarbua* was 156.92 mm (Figure 3.35).

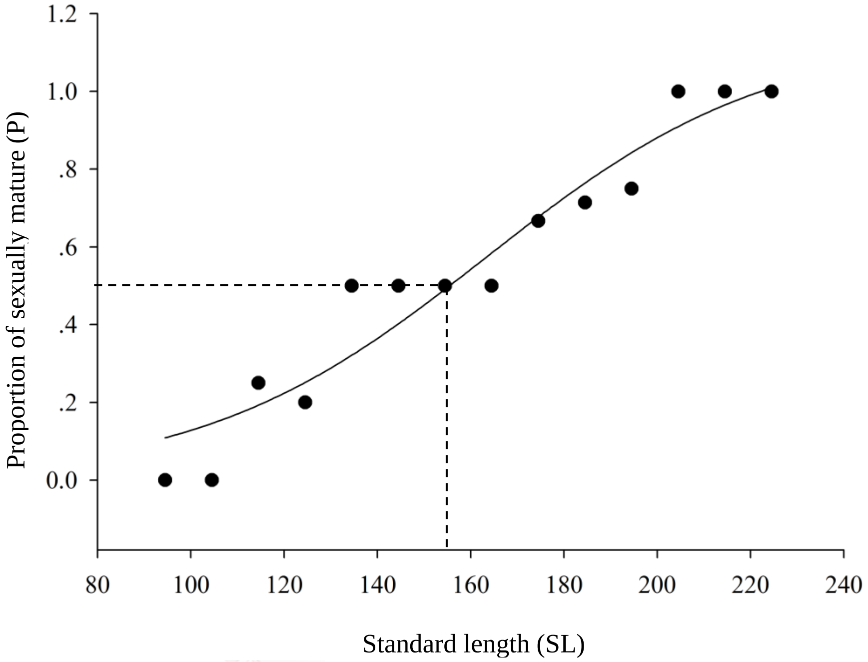


Figure 3.35 The size at first sexual maturity of female *Terapon jarbua* (n =109) from the coastal area of Trang Province.

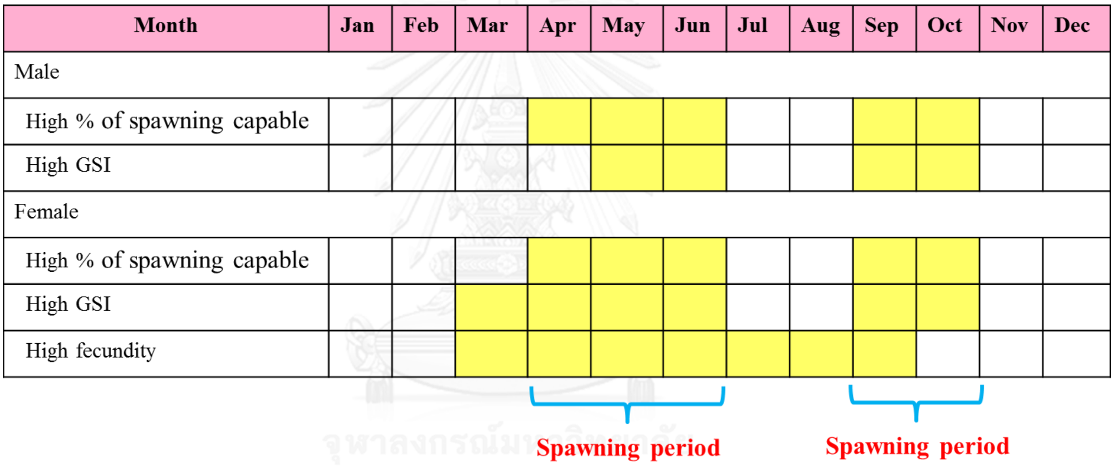
4.3 Spawning period in *Terapon jarbua*

From the histological study of gonad in *T. jarbua* reveled the immature adult 5.06% and the mature adult 94.94%. Five stages of gonadal development in male and female: immature, developing, spawning capable, regressing and regenerating stage, were identified for *T. jarbua* as in Table 3.6.

Table 3.6 Histological character and first initial size recorded in gonadal development stages of *Terapon jarbua* from the coastal area of Trang Province.

Gonadal stages	**First initial size (mm)**		**Histological characteristic**	
	Male	**Female**	**Male**	**Female**
Immature stage	102.39	105.53	• Only spermatogonium and primary spermatocyte presented. • No lumen in lobules.	• Only perinucleolar stage oocyte and cortical alveolar stage oocyte presented. • No atresia.
Developing stage	115.23	119.14	• Secondary spermatocyte predominated. • Spermatid and spermatozoa can be presented.	• Perinucleolar stage oocyte, cortical alveolar, primary vitellogenic, and secondary vitellogenic oocytes were dominant.
Spawning capable stage	120.93	125.77	• Spermatid and spermatozoa presented in lumen of lobules and/or sperm ducts.	• Tertiary vitellogenic oocytes and mature stage oocyte were dominant. • Atresia of vitellogenic may be presented.
Regressing stage	124.55	127.63	• Residual spermatozoa presented in lumen of lobules and in sperm ducts. • Secondary spermatocyte and spermatid were scattered near periphery.	• Atresia and postovulatory follicle complex presented. • Some cortical alveolar and/or vitellogenic oocytes presented.
Regenerating stage	125.53	127.11	• Testes were possessing new crypts of spermatogonium and primary spermatocytes. • Testes also had empty lumen and some residual spermatozoa.	• Perinucleolar stage oocyte and cortical alveolar stage oocyte presented. • Atresia or degenerating postovulatory follicle complex may be present.

Corresponding peaks among the gonadal maturity stage, gonadosomatic index and fecundity of *T. jarbua* were observed as in Figure 3.36. *Terapon jarbua* with testis and ovaries at spawning stages occurred in high percentage during two phases; April to June and September to October. This corresponded to the gonadosomatic index peaks of both male and female *T. jarbua* in June and September. Moreover, the fecundity in female was high during March to September. This indicated that *T. jarbua* have two peaks of spawning season; from April to June and from September to October. Adult population distribution was offshore area.



Month	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Male												
High % of spawning capable				🟨	🟨	🟨			🟨	🟨		
High GSI					🟨	🟨			🟨	🟨		
Female												
High % of spawning capable				🟨	🟨	🟨			🟨	🟨		
High GSI			🟨	🟨	🟨	🟨			🟨	🟨		
High fecundity			🟨	🟨	🟨	🟨	🟨	🟨	🟨			

Figure 3.36 Spawning period of *Terapon jarbua* from the coastal area of Trang Province.

This confirmed that *T. jarbua* used the offshore area for breeding and spawning ground (Miu *et al.*, 1990). Miu *et al.* (1990) reported that *T. jarbua* in Taiwanese waters had prolonged spawning period from February to October. L. Chang (2006) reported that *T. jarbua* in Taiwanese waters had spawning period during April to October and peak in April. The spawning period was corresponding to plankton bloom period for fish larvae feeding. The size at first sexual maturity of female and male of *T. jarbua* were 156.92 mm and 153.77 mm. The lengths at first sexual maturity of *T. jarbua* in the coastal area of Trang Province were larger when compared to other studies. The lengths at first sexual maturity of female and male *T. jarbua* in Taiwan were 148 mm and 143 mm (Miu *et al.*, 1990) while lengths at first sexual maturity *T. jarbua* in India were in the range of 145-162 mm (Prabhu, 1956). Differences in the spawning period and length at sexual first maturity of fish depend upon various environmental stimuli (King, 2013).

5. Reproductive biology and Spawning period in *Pelates quadrilineatus*

5.1 Reproductive biology in male *Pelates quadrilineatus*

1) Testis structure of male *Pelates quadrilineatus*

The testes structure of *P. quadrilineatus* was similar to those of *T. jarbua*. The testes are paired and elongate, organs located on dorsal part of gut. The testis is covered with tunica albuginea which composed of connective tissue layer and blood vessels. The cross section of testes reveals a random distribution of various clusters of seminiferous lobule, which contains a specific stage of spermatogenic cells. The spermatogenic cells of *P. quadrilineatus* also classified into 5 stages as in *T. jarbua* as follows: Spermatogonium, Primary spermatocyte, Secondary spermatocyte, Spermatid and Spermatozoan.

2) Reproductive phase of male *Pelates quadrilineatus*

Testes of *P. quadrilineatus* were assigned into five maturity stages.

Immature stage (Stage 0): The testis was very small, often clear, blood vessels indistinct. Only spermatogonium and primary spermatocyte presented. No lumen in lobules (Figure 3.37).

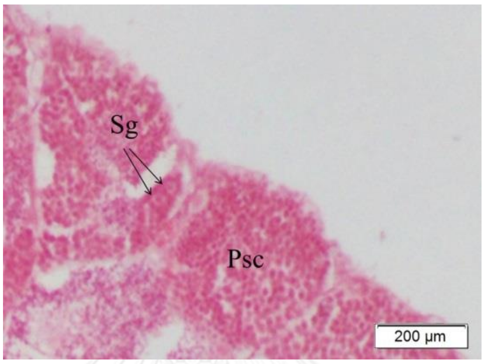


Figure 3.37 Immature reproductive phase of male *Pelates quadrilineatus* (90.00 mm in SL; GSI =1.55) (Psc = primary spermatocyte, Sg = Spermatogonium).

Developing stage (Stage 1): The testis was small but easily identified. Secondary spermatocyte predominated. Spermatid and spermatozoa can be presented (Figure 3.38).

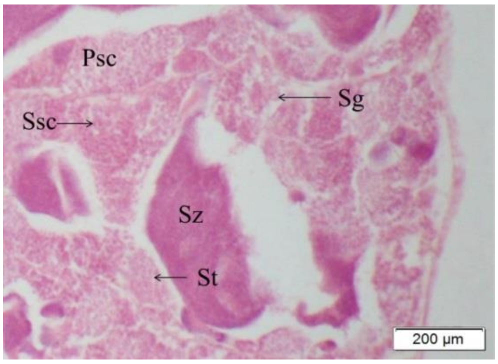


Figure 3.38 Developing reproductive phase of male *Pelates quadrilineatus* (102.55 mm in SL; GSI = 1.58) (Psc = primary spermatocyte, Ssc = Secondary spermatocyte Sg = Spermatogonium, St = Spermatid, Sz = Spermatozoan)

Spawning capable stage (Stage 2): The testis was large and firm. Spermatid and spermatozoa presented in lumen of lobules and/or sperm ducts. Spermatocyte can be presented (Figure 3.39).

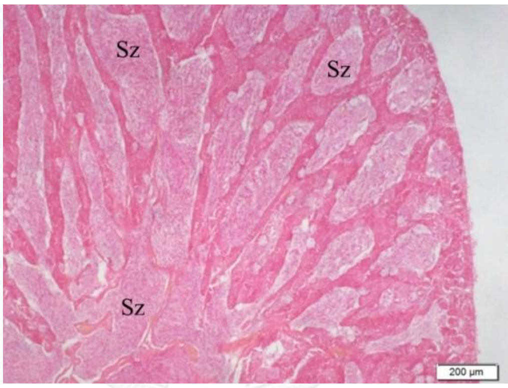


Figure 3.39 Spawning capable reproductive phase of male *Pelates quadrilineatus* (Sz = Spermatozoan).

Regressing stage (Stage 3): The testis was small and flaccid. Residual spermatozoa presented in lumen of lobules and in sperm ducts. Secondary spermatocyte and spermatid were scattered near periphery (Figure 3.40).

Figure 3.40 Regressing reproductive phase of male *Pelates quadrilineatus* (135.55 mm in SL; GSI = 3.23) (Ssc = Secondary spermatocyte, Sz = Spermatozoan, Lu = Lumen).

Regenerating stage (Stage 4): The testis was small and often threadlike. Testes were possessing new crypts of spermatogonium and primary spermatocytes. Moreover, testes also had empty lumen and some residual spermatozoa (Figure 3.41).

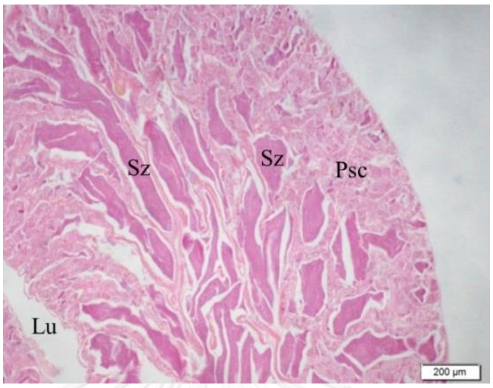


Figure 3.41 Regenerating reproductive phase of male *Pelates quadrilineatus* (132.45 mm in SL; GSI = 3.08) (Lu = Lumen, Psc = primary spermatocyte, Sz = Spermatozoan,).

The monthly percentage of gonadal maturity stage indicated that, *P. quadrilineatus* with testes at spawning stages occurred high percentage in one phase was November to April (Figure 3.42).

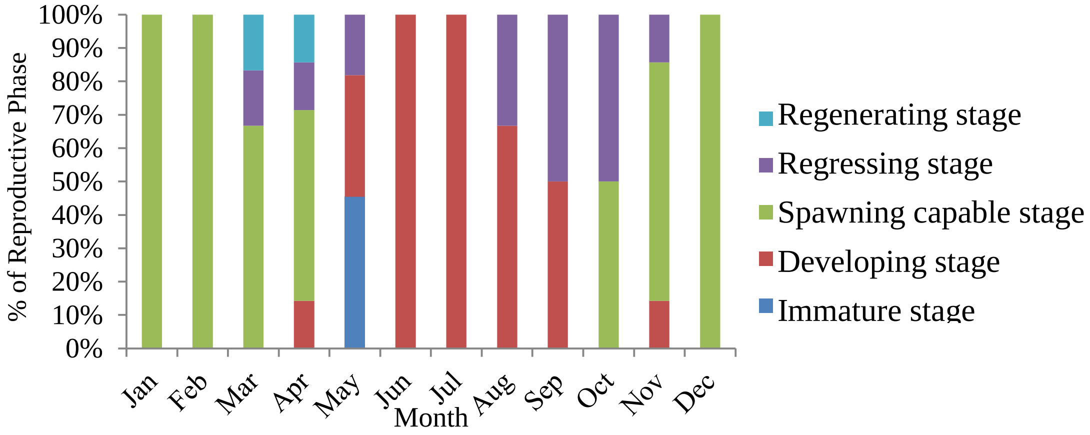


Figure 3.42 Monthly percentage frequencies of gonadal maturity stages of male *Pelates quadrilineatus* (n=53) from the coastal area of Trang Province.

3) Gonadosomatic Index of male *Pelates quadrilineatus*

The gonadosomatic Index of male *P. quadrilineatus* high only one phase but long period between November to April. The highest GSI of male were 2.71 shown in December too (Figure 3.43).

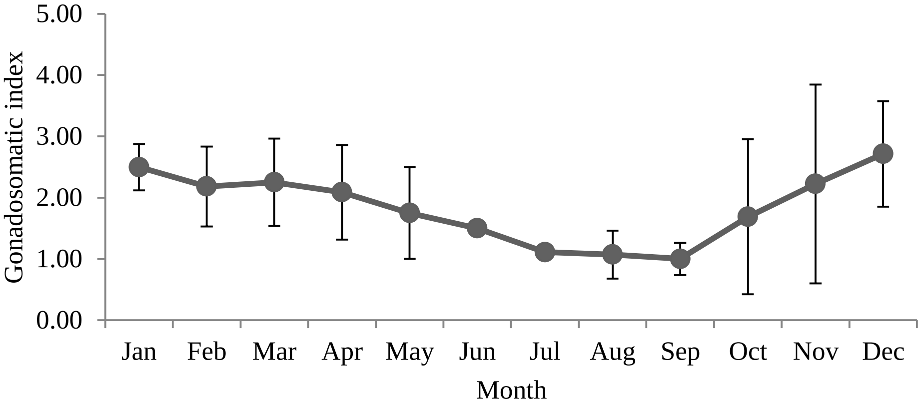


Figure 3.43 Monthly mean Gonadosomatic Index of male *Pelates quadrilineatus* (n = 53) from the coastal area, Trang Province.

4) Size at first sexual maturity of male *Pelates quadrilineatus*

The size at first sexual maturity of male *P. quadrilineatus* was 124.02 mm in SL (Figure 3.44).

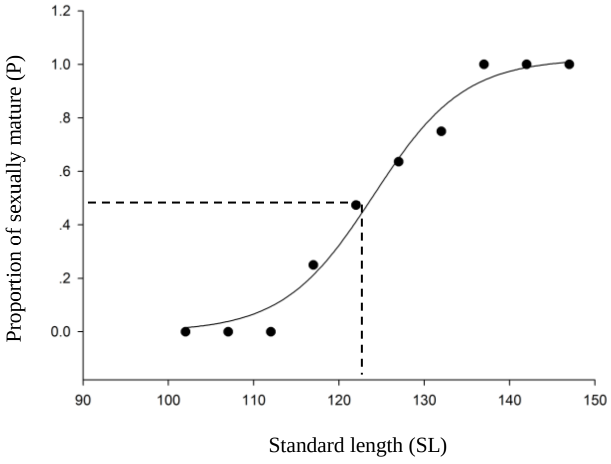


Figure 3.44 The size at first sexual maturity of male *P. quadrilineatus* (n = 53) from the coastal area of Trang Province.

5.2 Reproductive biology in female *Pelates quadrilineatus*

1) Ovarian structure of female *Pelates quadrilineatus*

The ovarian structure of *P. quadrilineatus* had same pattern in *T. jarbua*. *Pelates quadrilineatus* has two ovarian sacs with situated on dorsal part of gut. The surface of ovary is surrounded by tunica albuginea which is a thin layer of connective tissue and numerous blood vessels. The cross section of ovary reveals a random distribution of various stages of oocyte. The female germ cells are classified as follows: Perinucleolar stage oocyte, Cortical alveolar stage oocyte, Vitellogenic stage oocyte (Vtg1, Vtg2 and Vtg3), Mature stage oocyte, Atresia and Post-ovulatory follicle.

2) Reproductive phase of female *Pelates quadrilineatus*

Ovaries of *P. quadrilineatus* were assigned into five maturity stages same as *T. jarbua*.

Immature stage (Stage 0): The ovary was very small, often clear, blood vessels indistinct. Only perinucleolar stage oocyte and cortical alveolar stage oocyte presented. No atresia or muscle bundles (Figure 3.45).

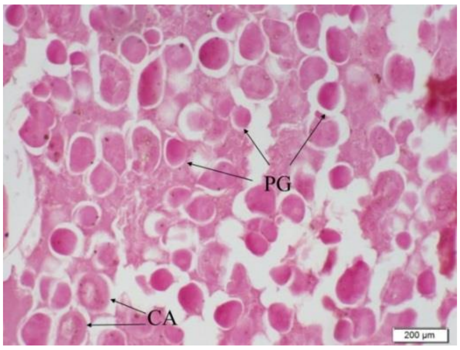


Figure 3.45 Immature reproductive phase of female *Pelates quadrilineatus* (95.45 mm in SL; GSI = 1.95) (CA = Cortical alveolar stage oocyte, PG = Perinucleolar stage oocyte).

Developing stage (Stage 1): The ovary was beginning to grow and develop. Enlarging ovaries and blood vessels were becoming more distinct. Perinucleolar stage oocyte, cortical alveolar, primary vitellogenic, and secondary vitellogenic oocytes were dominant (Figure 3.46).

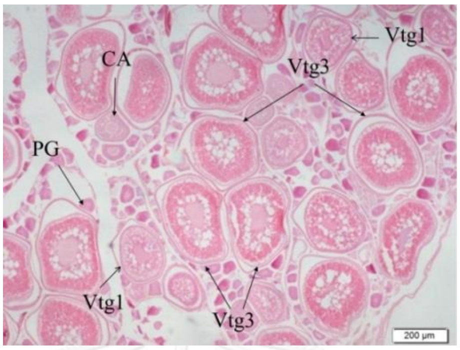


Figure 3.46 Developing reproductive phase of female *Pelates quadrilineatus* (124.50 mm in SL; GSI = 3.10) (CA = Cortical alveolar stage oocyte, PG = Perinucleolar stage oocyte, Vtg1 = Primary vitellogenic stage oocyte, Vtg3 = Secondary vitellogenic stage oocyte).

Spawning capable stage (Stage 2): The ovary was large and blood vessels prominent. Tertiary vitellogenic oocytes and mature stage oocyte were dominant. Atresia of vitellogenic may be presented (Figure 3.47).

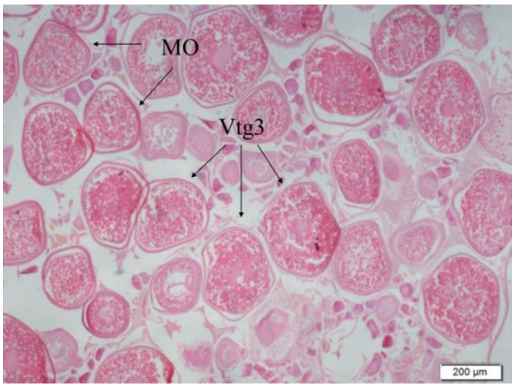


Figure 3.47 Spawning capable reproductive phase of female *Pelates quadrilineatus* (155.45 mm in SL; GSI = 5.85) (Vtg3 = Tertiary vitellogenic stage oocyte, MO = Mature stage oocyte).

Regressing stage (Stage 3): The ovary was flaccid and blood vessels prominent. Atresia and postovulatory follicle complex presented. Some cortical alveolar and/or vitellogenic oocytes presented (Figure 3.48).

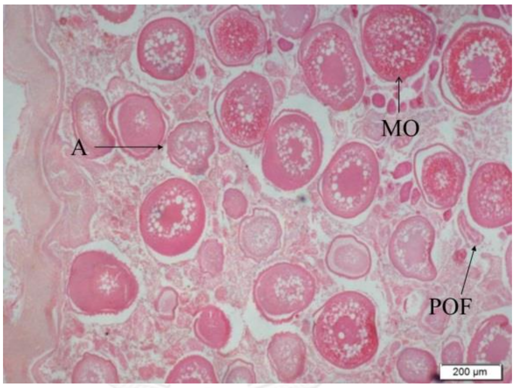


Figure 3.48 Regressing reproductive phase of female *Pelates quadrilineatus* (142.50 mm in SL; GSI = 4.78) (MO = Mature stage oocyte A = Atresia, POF = Post-ovulatory follicle).

Regenerating stage (Stage 4): The ovary was small and blood vessels reduced but presented. Perinucleolar stage oocyte and cortical alveolar stage oocyte presented. Atresia or degenerating postovulatory follicle complex may be present (Figure 3.49).

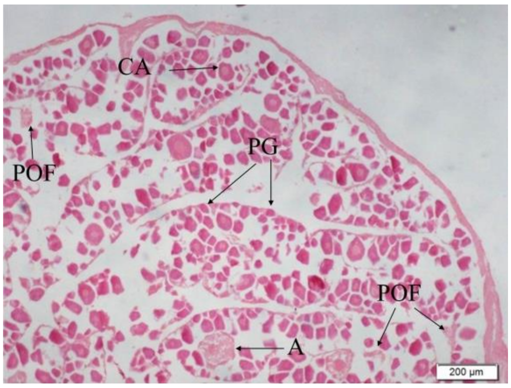


Figure 3.49 Regenerating reproductive phase of female *Pelates quadrilineatus* (152.15 mm in SL; GSI = 3.75) (CA = Cortical alveolar stage oocyte, PG = Perinucleolar stage oocyte, A = Atresia, POF = Post-ovulatory follicle).

The monthly percentage of gonadal maturity stage indicated that, *P. quadrilineatus* with ovaries at spawning stages occurred high percentage in one phase was November to April (Figure 3.50).

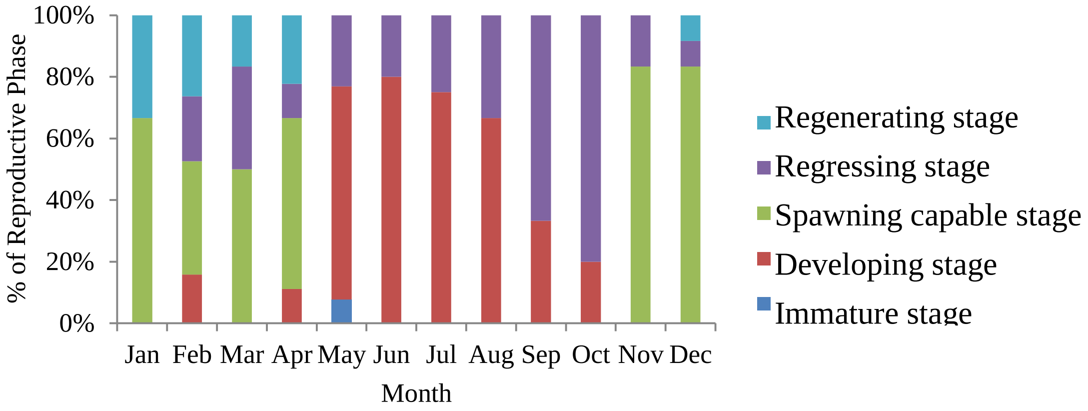


Figure 3.50 Monthly percentage frequencies of gonadal maturity stages of female *Pelates quadrilineatus* (n=97) from the coastal area of Trang Province.

3) Gonadosomatic Index of female *Pelates quadrilineatus*

Gonadosomatic Index of female *P. quadrilineatus* high only one phase but long period between November to April. The highest GSI of female were 5.15 shown in December (Figure 3.51)

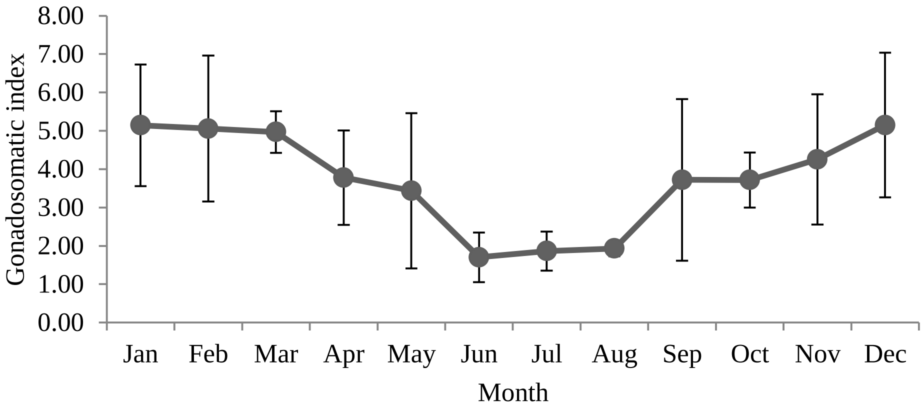


Figure 3.51 Monthly mean Gonadosomatic Index of female *Pelates quadrilineatus* (n = 97) from the coastal area of Trang Province.

4) Fecundity of female *Pelates quadrilineatus*

The fecundity of *P. quadrilineatus* was estimated to range from 134,037 to 472,575 eggs. The fecundity gradually increased from 135,166 eggs in January to the peak of 472,575 eggs in October, and then decreased (Figure 3.52). The average egg size was 0.78 mm. The egg size ranged from 0.11-0.86 mm.

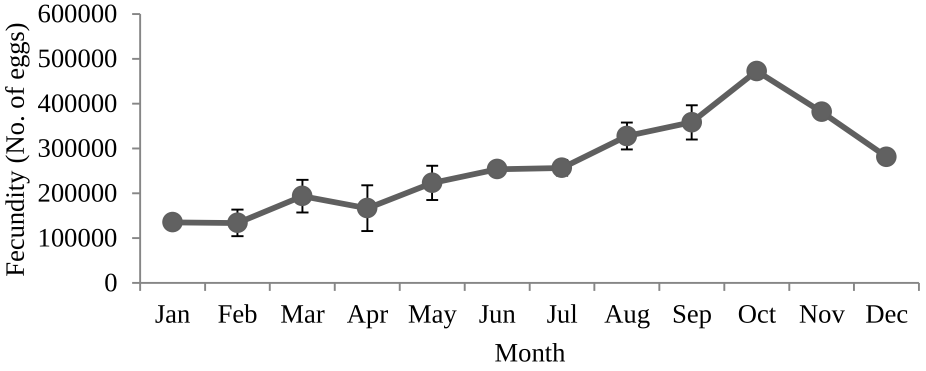


Figure 3.52 Monthly mean fecundity of females *Pelates quadrilineatus* (n = 93) from the coastal area of Trang Province.

5) Size at first sexual maturity of female *Pelates quadrilineatus*

The Size at first sexual maturity of female *P. quadrilineatus* was 120.31 mm (Figure 3.53).

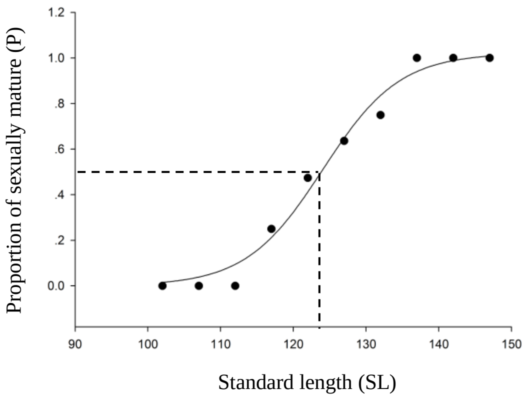


Figure 3.53 Size at first sexual maturity of female *Pelates quadrilineatus* (n = 97) from the coastal area of Trang Province.

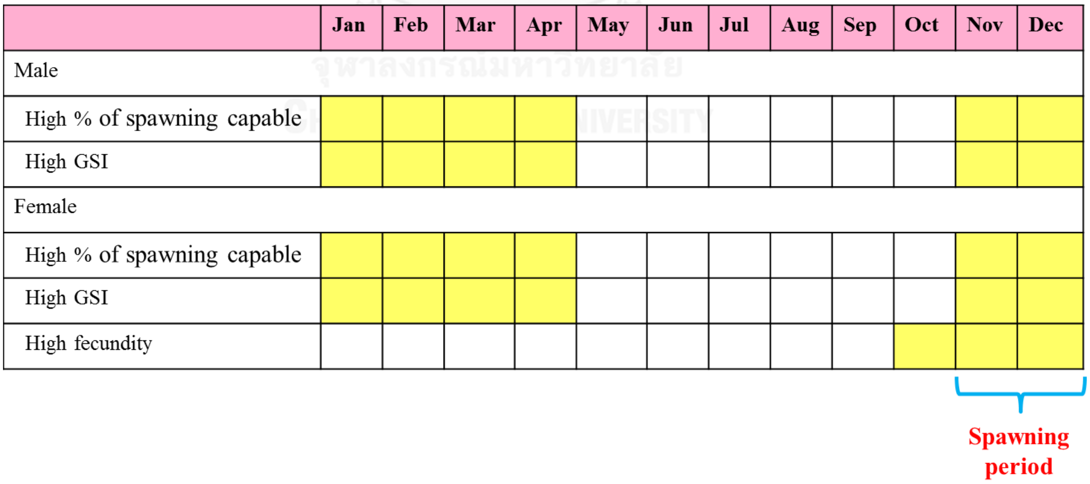
5.3 Spawning period in *Pelates quadrilineatus*

Immature adult and mature adult of *P. quadrilineatus* as revealed from histological study were 4.03% and 95.97%, respectively. Five stages of gonadal development in male and female: immature, developing, spawning capable, regressing and regenerating stage, were identified for *P. quadrilineatus* as in Table 3.7.

Table 3.7 Histological character and first initial size recorded in gonadal development stages of *Pelates quadrilineatus* from the coastal area of Trang Province.

Gonadal stages	**First initial size (mm)**		**Histological characteristic**	
	Male	**Female**	**Male**	**Female**
Immature stage	88.35	90.50	• Only spermatogonium and primary spermatocyte presented. • No lumen in lobules.	• Only perinucleolar stage oocyte and cortical alveolar stage oocyte presented. • No atresia.
Developing stage	95.85	100.00	• Secondary spermatocyte predominated. • Spermatid and spermatozoa can be presented.	• Perinucleolar stage oocyte, cortical alveolar, primary vitellogenic, and secondary vitellogenic oocytes were dominant.
Spawning capable stage	105.23	103.25	• Spermatid and spermatozoa presented in lumen of lobules and/or sperm ducts.	• Tertiary vitellogenic oocytes and mature stage oocyte were dominant. • Atresia of vitellogenic may be presented.
Regressing stage	110.55	104.50	• Residual spermatozoa presented in lumen of lobules and in sperm ducts. • Secondary spermatocyte and spermatid were scattered near periphery.	• Atresia and postovulatory follicle complex presented. • Some cortical alveolar and/or vitellogenic oocytes presented.
Regenerating stage	107.67	105.12	• Testes were possessing new crypts of spermatogonium and primary spermatocytes. • Testes also had empty lumen and some residual spermatozoa.	• Perinucleolar stage oocyte and cortical alveolar stage oocyte presented. • Atresia or degenerating postovulatory follicle complex may be present

Corresponding peaks among the gonadal maturity stage, gonadosomatic index and fecundity of *P. quadrilineatus* as in Figure 3.54 were observed as in *T. jarbua*. *Pelates quadrilineatus* with ovaries and testis at spawning stages occur in high percentage during November to December. This also corresponded to the high gonadosomatic index of both male and female *P. quadrilineatus* in December. The fecundity in female were high from October to December. This indicated that the spawning season in *P. quadrilineatus* was during November to December. Adult population of *P. quadrilineatus* was found offshore area. This confirmed that the offshore area was their breeding and spawning ground (Prabhu, 1956). The size at first sexual maturity of female and male *Pelates quadrilineatus* was 120.31 mm and 124.02 mm, respectively. This result corresponded to Prabhu (1956) which reported the lengths at sexual maturity of female and female *P. quadrilineatus* in India were in the range of 121-132 mm.



	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Male												
High % of spawning capable	🟨	🟨	🟨	🟨							🟨	🟨
High GSI	🟨	🟨	🟨	🟨							🟨	🟨
Female												
High % of spawning capable	🟨	🟨	🟨	🟨							🟨	🟨
High GSI	🟨	🟨	🟨	🟨							🟨	🟨
High fecundity										🟨	🟨	🟨

Figure 3.54 Spawning period of *Pelates quadrilineatus* from the coastal area of Trang Province.

6. Movement Patterns in Terapon jarbua and Pelates quadrilineatus

This study used a X-ray electron probe microanalyzer (EPMA) to determine the movement pattern of *T. jarbua* and *P. quadrilineatus* from the Sr:Ca ratios in otoliths of 10 adults fish (*T. jarbua* n = 5 and *P. quadrilineatus* n = 5) collected from offshore area, in coastal area of Trang Province. The mean Sr:Ca ratios increased significantly from the core to the otolith edge ($p < 0.05$) ($2.11 \times 10^{-3} \pm 1.35$ to $8.40 \times 10^{-3} \pm 2.46$ in *T. jarbua* as in Figure 3.55 and $5.33 \times 10^{-3} \pm 2.70$ to $8.25 \times 10^{-3} \pm 1.06$ in *P. quadrilineatus* as in Figure 3.56). The Sr:Ca ratios in otoliths of adult *T. jarbua* and *P. quadrilineatus* were positively correlated with the salinities of the sampling sites. Secor and Rooker (2000) found relationship between otolith Sr:Ca ratios and environmental salinity. They divided estuarine fishes into freshwater (salinity range of 0 to 5‰; mean Sr:Ca ratios of 1.97×10^{-3}), estuarine (5 to 25‰; 5.03×10^{-3}) and marine (>25‰; 7.43×10^{-3}) habitats. The increase in Sr:Ca ratios from core to edge of the otolith was consistent with fish dispersal from the low-salinity estuaries to the high-salinity offshore area. A life-history scan of the otolith Sr:Ca ratios indicated that the migratory environmental history of *T. jarbua* and *P. quadrilineatus* indicating that they migrated between estuary and offshore area. In juvenile stage, they utilized estuary for feeding and nursery grounds while in adult stage, they utilized offshore area for feeding, breeding and spawning grounds. However, this study did not detected the decreased of Sr:Ca ratios in the beginning phase which help to confirmed the migration between offshore area and estuary of planktonic larvae. Because both species have short period in planktonic phase, the changed of Sr:Ca ratios on otolith were short and/or may be error in determined the core of the otolith.

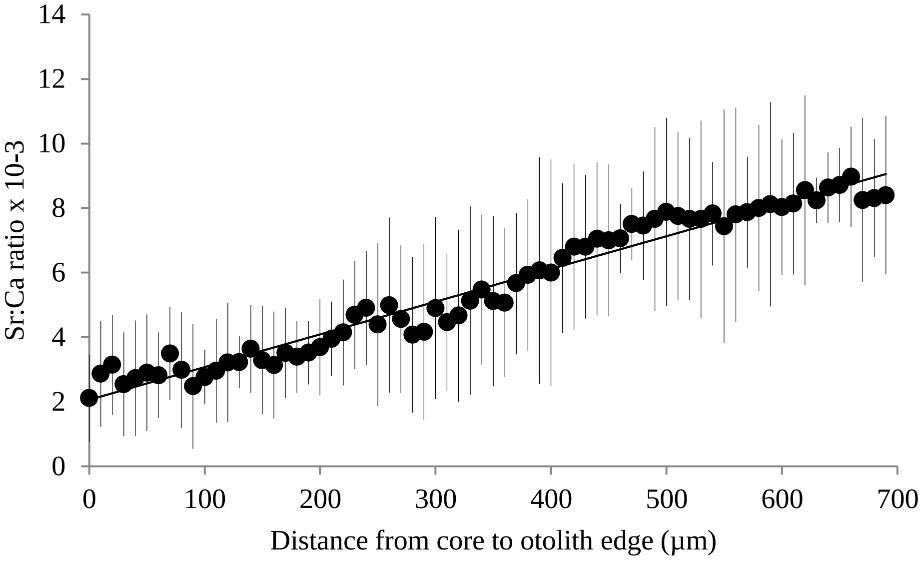


Figure 3.55 Changes in mean otolith Sr:Ca ratios from core to otolith edge of 5 adults *Terapon jarbua* from the coastal area of Trang Province.

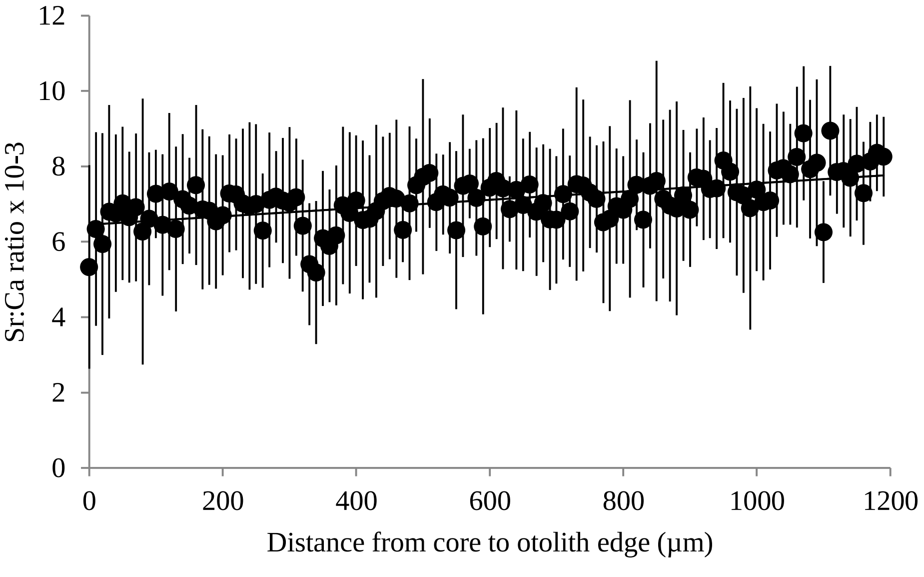


Figure 3.56 Changes in mean otolith Sr:Ca ratios from core to otolith edge of 5 adults *Pelates quadrilineatus* from the coastal area of Trang Province.

7. Habitat Utilization as Spawning and Nursery Areas in *Terapon jarbua* and *Pelates quadrilineatus*

From the reproductive biology and distribution patterns in different stages of the two terapontid fishes, *T. jarbua* and *P. quadrilineatus* in the coastal area in Trang Province reveled that both species are marine migrant species spawning at sea and often enter estuaries in large numbers as juveniles. Adults of both species were found distributed in offshore area of 10.00-15.00 m depth. High density were found during the wet season. The salinity ranged 28.0-29.0 psu. Five stages of gonadal development in male and female: immature, developing, spawning capable, regressing and regenerating stage, were identified for both *T. jarbua* and *P. quadrilineatus* as in Table 3.6 and Table 3.7. Although adults of *T. jarbua* and *P. quadrilineatus* shared the same breeding and spawning ground in the offshore area, they showed the temporal resource partitioning due to the differences in spawning season as in Figure 3.57. Both fishes were broadcast spawners with pelagic eggs. Both species showed the differences in their size at first sexual maturity, fecundity and egg size. *Terapon jarbua* was the medium size fish with small size egg of 0.31 mm. This species spawned twice a year with the spawning period during April to June and September to October. Size at first sexual maturity in the male and female were 153.77 and 156.92 mm, respectively. Prabhu (1956) found that *T. jarbua* in Indian water was also the medium size fish with small size egg of 4.0 mm. This species spawned once a year during the month of February to March. The first sexual maturity size was 124 mm. However, *T. puta*, another medium size fish with medium size egg of 0.50 mm, spawned twice a year in February to March and August to September (Prabhu, 1956). Miu *et al.* (1990) reported that *T. jarbua* in the Tamshui estuary in Taiwan showed the prolonged spawning during April and October. Size at first maturation in the male and female were 143 and 148 mm in fork length, respectively. Fecundity size in *T. jarbua* in the coastal area of Trang Province was 228,150 to 763,600 eggs with the peak in March. The fecundity size in this study was higher than those reported by Miu *et al.* (1990) in the range of 37,083-480,400 eggs. Larger size as in the size at first sexual maturity in *T. jarbua* found in the coastal area in Trang Province resulted in the high fecundity size.

Pelates quadrilineatus, on the other hand, was the medium size fish with medium size egg ranging from 0.11-0.86 mm with the average size of 0.78 mm. The size at first sexual maturity for male and female were 124.02 and 120.31 mm which were smaller than those *T. jarbua*. The differences in size between the two terapontid fishes were observed during the transforming larvae and juvenile stages. The average total length in *T. jarbua* and *P. quadrilineatus* transforming larvae were 18.66 and 17.21 mm, respectively. The average total length in the juvenile of *T. jarbua* and *P. quadrilineatus* were 37.29 and 28.74 mm, respectively. The planktonic larvae of the two terapontid fishes were in the same size range of 1.49-5.65 mm. The fecundity of *P. quadrilineatus* was in the range of 134,037-472,575 eggs with the peak in October. *Pelates quadrilineatus* in the coastal area in Trang Province spawned once a year with short definite period from November to December. This finding corresponded with Prabhu (1956) that *P. quadrilineatus* in Indian waters spawned once a year during February to April. First sexual maturity size in *P. quadrilineatus* from Indian waters was in the range of 121-132 mm.

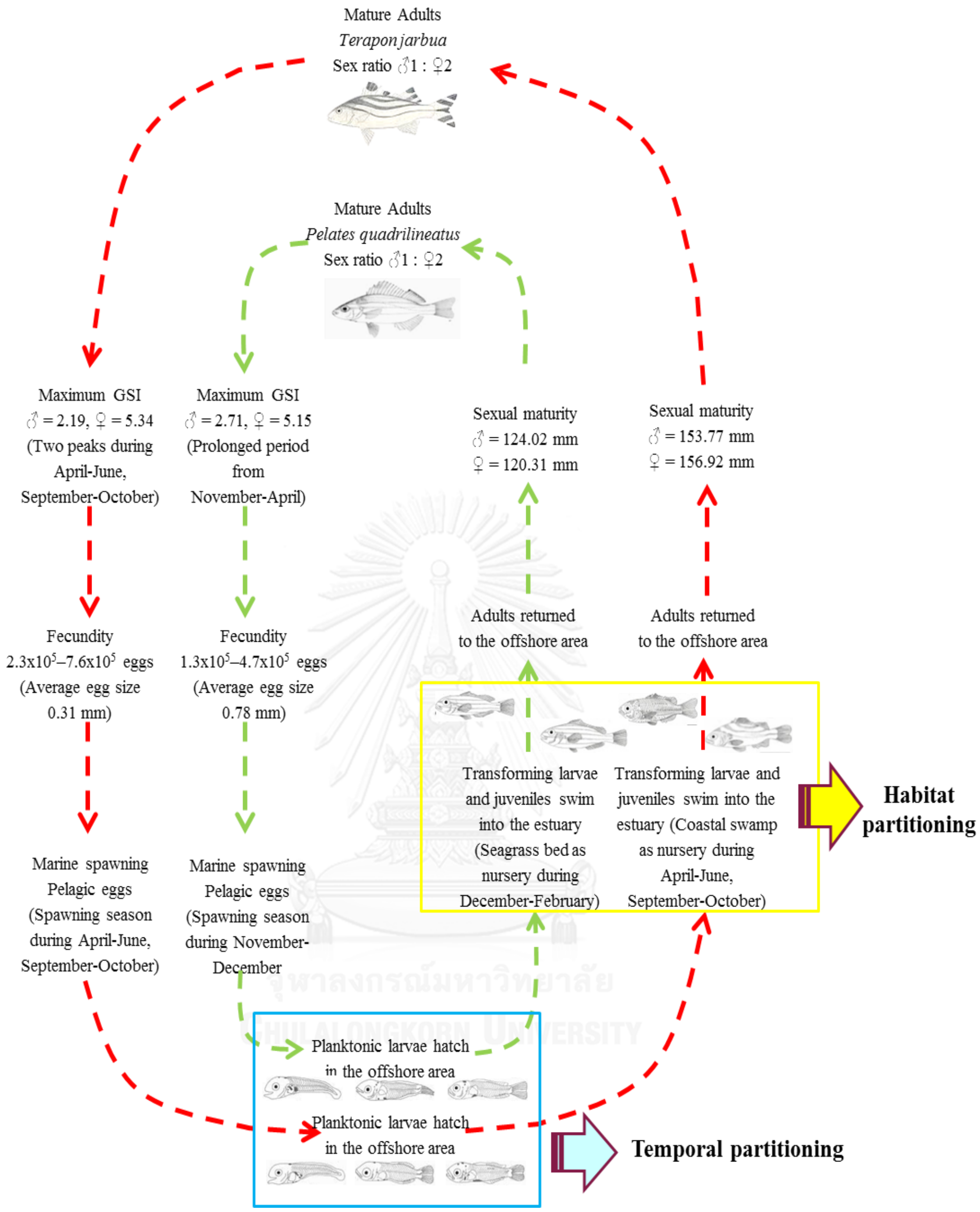


Figure 3.57 Habitat utilization as spawning and nursery areas in *Terapon jarbua* and *Pelates quadrilineatus* from the coastal area of Trang Province.

The planktonic larvae (preflexion, flexion and postflexion) were found to coexist in the offshore area. High density of planktonic stage of *T. jarbua* was found during April to June and during September to October. High density of planktonic larvae in *P. quadrilineatus* was found offshore area during November to December. Both adult and planktonic stages of the two terapontid fishes inhabited offshore area indicating offshore as the breeding and spawning ground. As high predation pressure in the shallow waters determine the survival of pelagic eggs and larvae. Most of the tropical species in particular larger species migrate offshore area to deeper water to spawn. Seasonal variations in salinity, temperature and water depth were minimal in the offshore area. The planktonic larvae can easily avoid the predation risks by their transparent bodies and fins. At this stage, the swimming ability was poor. The development of mouth, jaw, eyes, body, fins and pigmentation were not completed. The eggs and competent larvae commonly drift near the surface water over the deep water and are thus out of range of the benthic predators in their adult habitats. A strategy that is usually adopted by the marine migrants that use estuaries as juvenile nursery areas is to released their eggs in the coastal waters or in the vicinity of the estuary mouth, so that the distance between the larval and juvenile habitats is reduced. This increase the chances of recruitment to parent populations (Elliott *et al.*, 2007; Miller & Kendall, 2009). This study confirmed the previous studies on the distribution of the planktonic larvae and adult of both terapontid fishes in the offshore area (Duangdee, 1995; Matsuura *et al.*, 2005; Yoknoi, 2012).

The coastal habitats of Trang Province has played the important roles as the nursery grounds for the two terapontid fishes. *Terapon jarbua* and *P. quadrilineatus* are the sympatric species in the offshore area of the Rajamangala Beach. Adults and planktonic larvae of both species utilized the offshore area as breeding and spawning grounds. Transforming larvae and juveniles can migrated passively or actively to the estuarine area to seek for specific suitable habitats to spend their early lives. Both species displayed habitat shift and showed preference for different habitat type for nursery ground. High abundance of transforming larvae and juvenile fishes in the mangroves and seagrass beds suggested these areas as nursery grounds. This was probably due to the structural complexity of microhabitats, abundance and diverse food sources, reduced predation risks due to turbid waters and less frequented by larger marine predators and the interception of fish larvae due to the extensive area coverage (Blaber, 2000; Horinouchi, 2007; Horinouchi *et al.*, 2009; Ikejima *et al.*, 2003; Laegdsgaard & Johnson, 1995; Nagelkerken *et al.*, 2000; Robertson & Blaber, 1993). Transforming larvae and juveniles of *T. jarbua* were found distributed in the coastal swamp habitat under the tidal influences of Rajamangala and Pakmeng coastal swamps. High density of transforming larvae and juveniles of *T. jarbua* were found at Pakmeng coastal swamp during the wet season in particularly the month of May and October. The timing corresponded to the two spawning peaks in this species during April to June and September to October. Although the Pakmeng coastal swamp was smaller in size as compared to Rajamangala coastal swamp, higher density of transforming larvae and juveniles of *T. jarbua* were found in the area. Juveniles also distributed in the sandy beach of Pakmeng beach, the transitional area between the coastal swamp and the offshore area. Differences in fish assemblages among sites through the years had been reported in mangroves (Laegdsgaard & Johnson, 1995). The Rajamangala coastal swamp was dried up during the months of March and April during the year 2013. Ikejima *et al.* (2003) also found that the wet season coincided with the period of greatest recruitment of juvenile fishes and is greatest zooplankton abundance in the mangrove estuary of Sikao Creek in Trang Province. The fluctuation in salinity was minimal due to seasonality and sites in the mangrove estuary of Sikao Creek. The estuary did not received a significant freshwater input from a large river system. This study did not supported that salinity played an important role in structuring fish assemblage in mangrove estuary. This was also the case in the distribution of *T. jarbua* in the coastal area of Trang Province. The morphological changes such as increase of body depth, fin length and eye size during the metamorphosis phase were important to the mobility of fish to move into the coastal swamps to avoid the predator and search for food. Fishes adapted for searching prey in structurally complex habitats tend to have a deep and laterally compressed body, extended fins and larger eye (Hobson, 1979; Norton, 1995; Urho, 2002; Webb, 1984). This character enhanced the controlled of the swimming ability and visual senses in the turbid coastal habitats of coastal swamps. The intensive pigmentation on the body in juvenile stage help fish to camouflage from predator in the turbid and structurally complex habitats.

The morphological changes in the transforming larvae and juveniles in *P. quadrilineatus* also occurred in the same pattern as *T. jarbua*. Transforming larvae and juveniles of *P. quadrilineatus* were distributed in the seagrass beds of Boonkong bay and Makham bay. They were also found distributed in the transitional area of the sandy beach, Pakmeng beach, connecting the seagrass beds and the open sea. Makham bay showed the highest density of transforming larvae and juveniles in *P. quadrilineatus* during dry season. This also corresponded to the spawning season in *P. quadrilineatus*. This study was consistent with the previous findings that

P. quadrilineatus juveniles limited distribution in the seagrass beds of Trang Province (Duangdee, 1995; Horinouchi, 2007; Horinouchi *et al.*, 2012; Horinouchi *et al.*, 2009; Yoknoi, 2012). Horinouchi (2007) concluded that seagrass height and/or density reduction or clearance may affect the abundance of seagrass fishes. Seagrass fishes also showed preference on within-patch scale structural complexity. For fishes that employ anti-predator tactics associated with seagrass leaves (e.g. cryptic body coloration, mimicking seagrass, higing behind seagrass and agile maneuverability within a complex space), seagrass structure may be essential. While small fishes, depend largely on group-forming as an anti-predator tactic, apparently find dense seagrass to be unfavorable. Dense seagrass prevents the formation of a larger group which in turn reduced the effectiveness of that tactics. In addition, dense seagrass may sometime obstruct views of predators. Prey animals generally increase their visual scanning rates with increasing predation risk. The size of the seagrass bed at Boonkong bay and Makham bay were similar. Soft mud was the sediment characteristic of the two seagrass beds. However, *Halophila ovalis* (71.47 %) dominated the seagrass bed at Boonkong bay, while *Cymodocea serrulata* (87.0 %) dominated the Makham bay seagrass bed (Kongwatmai, 2015).The structural complexity in the *C. serrulata* bed was higher than those in the *H. ovalis*. Horinouchi *et al.* (2012) demonstrated the effect of habitat fragmentation on a seagrass fish assemblage in the coastal area of Trang. Habitat fragmentation may provide mosaic of multiple habitat types of more diverse microhabitats. Greater numbers of small habitat patches may provid more refugia which further enhances their chances of survival and/or coexistence. However, habitat fragmentation caused by anthropogenic disturbance in the long run would result in the decreased of the abundance of seagrass which in turn would affect the fisheries. This study confirmed that the mangrove coastal swamps and seagrass beds played the important roles as the nursery grounds for the two terapontids. According to Heupel *et al.* (2007) concept of nursery ground that apart from being in productive area to support growth and survival of young fish, the nursery areas or habitats should be repeatedly used across years. Transforming larvae and juveniles of *T. jarbua* were found distributed in mangrove coastal swamps while the transforming larvae and juveniles of *P. quadrilineatus* were found distributed in seagrass beds (Duangdee, 1995; Horinouchi *et al.*, 2012; Ikejima *et al.*, 2003; Tongnunui *et al.*, 2002; Tongnunui *et al.*, 2010; Yoknoi, 2012).

The study on the movement patterns in *T. jarbua* and *P. quadrilineatus* confirmed their life history traits as marine migrant species. They migrated between estuary and offshore area. Adult and planktonic larvae of the two terapontid fishes were found at the offshore area which they use for feeding, breeding and spawning grounds. Transforming larvae and juveniles migrate into estuary into different habitats for nursery grounds. *Terapon jarbua* seeked the coastal swamps as nursery ground while *P. quadrilineatus* seeked seagrass beds as nursery ground.

E. Conclusion

Terapon jarbua and *P. quadrilineatus* showed the clear pattern of habitat utilization among different developmental stages. The reproductive biology revealed the gonadal development in male and female as follows; immature, developing, spawning capable, regressing and regenerating stage. Adult of *T. jarbua* and *P. quadrilineatus* were broadcast spawners with pelagic eggs in the offshore area. Although both species shared the same breeding and spawning ground, but they showed the temporal resource partitioning. Different spawning period is one of the important strategy for coexisting species to reduce food and habitat competition between their offspring. Both species showed the differences in their size at first sexual maturity, fecundity and eggs size. *Terapon jarbua,* a medium size fish with small size eggs, spawned twice a year during April to June and September to October. *Pelates quadrilineatus,* on the other hand, was the medium size fish with medium size eggs. This species spawned once a year with short definite period from November to December. Both adults and planktonic stages of the two terapontid fishes inhabited offshore area indicating the breeding and spawning ground. Both *T. jarbua* and *P. quadrilineatus* displayed habitat shift during transforming larvae and juvenile stages. They showed preferences for different habitat type for nursery ground. High density of transforming larvae and juveniles of *T. jarbua* were found at Pakmeng coastal swamp during the wet season, coincided with the spawning season. Transforming larvae and juveniles of *P. quadrilineatus* were distributed in the seagrass beds. Makham bay showed the highest density of transforming larvae and juveniles during the dry season. This also corresponded to the spawning season in *P. quadrilineatus*. The transforming larvae and juveniles of *T. jarbua* and *P. quadrilineatus* showed the resource partitioning in term of spatial and temporal habitat utilization.

CHAPTER 4

HABITAT UTILIZATION AS FEEDING GROUNDS IN TERAPONTID FISHES, *Terapon jarbua* AND *Pelates quadrilineatus*

A. Introduction

In assessing the importance of estuaries for fish, habitat use as feeding ground usually ranked first of the four important habitat uses i.e. feeding, nursery, spawning grounds and route of migration (Pihl *et al.*, 2002). Several studies demonstrated the importance of mangrove and seagrass beds in the tropical coastal ecosystem as feeding habitats for fish (Blaber, 2000; Cruz-Escalona *et al.*, 2000; Hajisamae *et al.*, 2003; Hajisamae & Ibrahim, 2008; Hajisamae *et al.*, 2006; Horinouchi, 2007; Horinouchi *et al.*, 2012; Horinouchi *et al.*, 2009; Ikejima *et al.*, 2003; Laegdsgaard & Johnson, 2001; Lugendo *et al.*, 2007; Robertson & Blaber, 1993; Tongnunui *et al.*, 2002). Differences in fish composition among microhabitats within mangrove estuaries and season have also been found. Mangrove setting influenced the extent to which the mangrove habitat can be utilized as a potential feeding ground by fish. Lugendo *et al.* (2007) concluded from their study that fishes feed more from the mangrove-lined creeks as compared to fringing mangroves which is probably related to differences in the degree of mangrove inundation. As fishes depend solely on the presence of water and must move with the ebb tide, the degree of mangrove inundation is one of the crucial determinant of the extent to which fishes can use a mangrove habitats as a feeding ground. The size of the mangrove forest itself is another critical factor that determine the importance of mangroves as major feeding grounds for fishes. In seagrass beds, difference in fish composition among microhabitat diversity and seasonal were also observed. Within-patch scale structural complexity such as seagrass height and/or density reduction or clearance may affect the abundance of seagrass fishes (Hajisamae & Ibrahim, 2008; Horinouchi, 2007; Horinouchi *et al.*, 2012; Horinouchi *et al.*, 2009). Habitat type is also one of the important factor 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 (Crowder & Cooper, 1982).

The study of feeding ecology of fish is useful and fundamental to understanding of their resource utilization and their functional role in the ecosystem (Blaber, 1997; Cruz-Escalona *et al.*, 2000; Hajisamae *et al.*, 2003). 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 segregating fish species in community. Thus coexistence of species can be obtained through the differentiation of their ecological niches (Ross, 1986). It is rare for fish to specialize on one particular prey category throughout their life cycle. The diets of most fish change with growth in order to achieve the maximum net gain from food according to the optimal foraging theory. The ultimate objective of dietary change is to maximize energy intake, enhance growth rate and minimize the risk of predation in competing for food with larger predators (Brown, 1985). Ontogenetic niche shift is one of the important process in niche partitioning with the shift of resources during development. Size imposes important constraints on the animal’s energetic requirement, potential for resource exploitation, its susceptibility to natural enemies and the competitive ability. During ontogeny, the growing consumers are expected to change their ecological niche with respect to prey type, prey size or habitat type to meet their increasing basic metabolic demands and optimize their ecological foraging performance (Persson *et al.*, 1998; Werner & Gilliam, 1984). Many fishes show distinct ontogenetic changes in feeding habits and prey selection (Jobling, 1995). The actual timing of switches in diet usually relates to larvae becoming juveniles or juveniles becoming adult (Blaber, 2000). The ontogenetic niche shifts were often detected as clear shifts in diet or habitat use with increasing body size. Ecomorphology in fishes often described the patterns of association between morphology and resource use. There is often a correlation between feeding structure and trophic role because morphology determines how fish can feed. Size-related of morphological change are important in relation to many aspects of the feeding structures of fish. These include position of mouth, mouth gape, jaw length, number of gill raker, dentition and intestinal length (Davis *et al.*, 2012b; Davis *et al.*, 2013; Eggold & Motta, 1992; McCormick, 1998; Mittelbach & Persson, 1998; Piet, 1998; Stoner & Livingston, 1984; Wainwright & Richard, 1995). Mouth gape has been shown as an important determinant of prey size (Mittelbach & Persson, 1998; Peterson & McIntyre, 1998). In the ontogeny of piscivory, maximum and mean prey size eaten increased with predator size in all species. Mouth gape size determined the maximum-sized prey a predator can ingest. Fish of different species living in the same habitat may partitioned their food by feeding on different food types. On the other hand, species that feed on the same diet may seek to live in different habitats in order to reduce competition when resources are restricted (Chakrabarty & Homechaudhuri, 2015). Difference in feeding structure morphology may also be the outcome of food partitioning. The result of food partitioning may be alternative process in reducing competition for fish sharing the same feeding ground (Blaber, 1997). As mentioned above, ontogenetic niche shift and feeding structure morphologies are internal factor in determining the feeding strategy of fishes. In addition, habitat type and seasonal change are also an important external factor in determining the feeding strategy of fishes by selectively foraging opportunities (Hajisamae *et al.*, 2003). A fish may have to choose among different habitats that provide different prey diversity and abundance to reduce food competition (Crowder & Cooper, 1982). Seasonal change is another feature that involves the life history pattern of prey or the feeding activity of fish (Lucena *et al.*, 2000; Snyder, 1984). Prey distribution patterns sometimes control those of predators (Bell & Westoby, 1986; Horinouchi, 2007).

The Terapontidae is one of the most tropically diverse of Australian's marine water fish families having feeding habitats that range from carnivorous, omnivorous and detritivorous modes (Davis *et al.*, 2011; Davis *et al.*, 2010). A number of species in the same family, primarily marine or estuarine, distributed in the Indo-Pacific region (Berra, 2001). Australian terapontid diet can be classified into 7 groups: lepidophagous carnivores, microphagous carnivores, meiophagous omnivores, macrophagous omnivores, herbivores, detritivores algivores and aquatic invertivores. Ontogenetic diet shifts are also a prominent feature of terapontid dietary ecology. Diets of all juvenile terapontids were similar, mainly comprising of aquatic insects and zooplankton. Larger size classes of terapontids diversed into a broad spectrum of feeding groups comprising of carnivorous dietary modes including piscivory and lepidophagy; omnivory modes including frugivory and consumption of allochthonous prey; herbivory and detritivory. The interactions between body size and allometric growth of particular morphological characters such as intestinal length, maxilla length and mouth width, played an important role in the dietary habits of terapontids.

Intestinal length was strongly positively associated with detritivory and, to a lesser extent, consumption of filamentous algae. Several species demonstrated the ontogenetic dietary shifts, transition from carnivory-omnivory in small size classes to specialized detritivory and herbivory in larger size classes based on the high rate of allometric increase in intestinal length. Morphometrics related to mouth gape have been repeatedly demonstrated the correlation with prey size and piscivorous feeding habits (Davis *et al.*, 2011; Davis *et al.*, 2012a, 2012b; Davis *et al.*, 2010; Davis *et al.*, 2013). In order to evaluate the degree of food partitioning of the two coexisting terapontid fishes, *T. jarbua* and *P. quadrilineatus* in the coastal area of Trang Province as feeding grounds, the following issues need to be address 1) ontogenetic dietary shifts and feeding habits in *T. jarbua* and *P. quadrilineatus*; 2) the role of the interaction of body size and allometric growth in morphological characters in particular feeding structure morphology in the dietary habits of the two coexisting terapontid fishes; 3) diet breadth and diet overlap in the diets of the two coexisting terapontid fishes.

B. Literature Reviews

1. Optimal Foraging Theory

Optimal foraging theory is the model of cost and benefit analysis that can give quantitative predictions on animal feeding behavior. Optimal foraging theory predicts how animals achieved the maximum net gain with the objective of maximizing lifetime reproductive success and fitness. The total energy that is consumed as food minus the energy cost of obtaining that food is the net energy gain. For predation, the energy costs in predator can include danger, loss of valuable time, and wasted energy. Benefits are usually counted in terms of net energy intake (consumed calories) per unit time. All foraging models consist of (1) energy (E) is the net number of calories obtained by consuming the prey item, (2) handling time (h) is the amount of time required to handle the prey between the time it is encountered to the time it is consumed. The profitability of a prey item is then defined as E/h. Additionally, (3) search time (s) is the mean expected time between encounters of prey of the same food type. Search time depends on the abundance of the prey and the ease of locating it. The model are based on the profitability, as the energy gained (Gerking, 1994).

Prey selection of fish may depend also on the availability and profitability of the prey. Optimal foraging theory has been used to predict the diet composition of fish on the basis of prey profitability. Prey selection by the optimal forager was based on three factors:

(1) prey size: the size of important prey items consumed was determined by mouth gape and jaw width of fish. An increase in predator size will widen the range of prey. Fish’s body size increases allometric growth results in their mouth and jaw is getting larger hence an ever increase prey size can be consume. The amount of energy and handling time also increase with prey size (Gill, 2003) (Figure 4.1). Horinouchi *et al.* (2012) studied food types and food size of *Terapon puta* in different size class. Smaller individuals (19.0–21.6 mm) consumed mainly copepods larvae and planktonic copepods. Larger individuals (34.9–78.4) consumed mostly harpacticoid copepods. A morphological examination of the feeding apparatus suggested that the size of important prey items consumed was determined by mouth gape and jaw width.

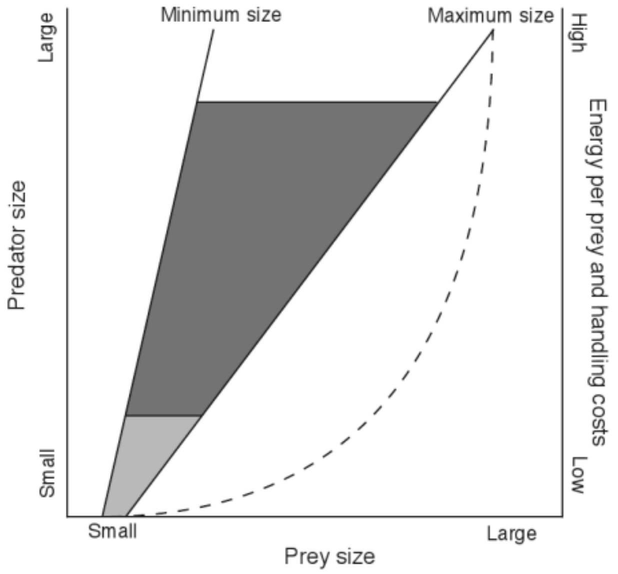


Figure 4.1 Prey selection based on prey-size availability, energy gain per prey item, and handling time. Small predators have a reduced size range of prey available to them as well as an overall smaller prey-size spectrum (light shading) compared to the prey-size range and prey-size spectrum (dark shading) of large predators. Energy gain per prey item and handling time are increasing with prey size (dashed line). Figures was after Gill (2003).

(2) food density: the amount of time that predator takes to search for a prey item depends on the density of the prey. Functional response curves show the rate of prey capture as a function of food density and can be used in conjunction with the optimal diet theory to predict foraging behavior of predators. There are three different types of functional response curves (Staddon, 1983) as in Figure 4.2.

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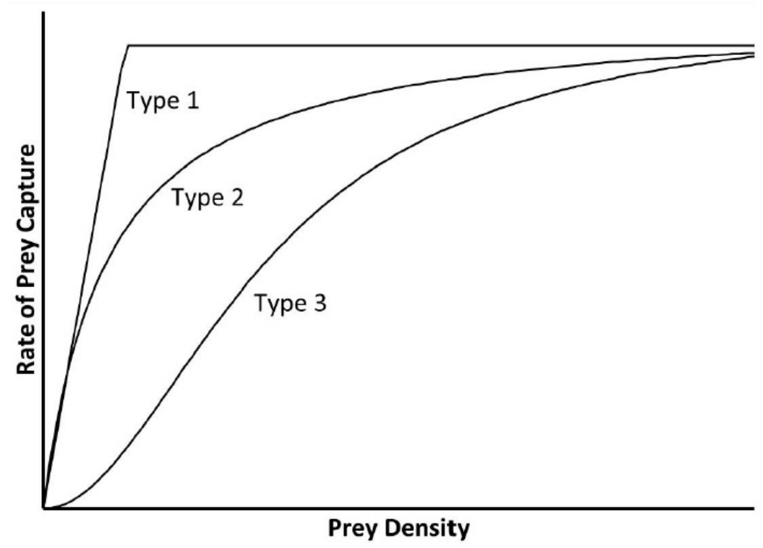


Figure 4.2 Three types of functional response curves. Figure was after Staddon (1983).

Type I, the rate of prey capture increases linearly with food density. At low prey densities, the search time is long. Since the predator spends most of its time searching, it eats every prey item it finds. As prey density increases, the predator is able to capture the prey faster. At a certain point, the rate of prey capture is so high, that the predator doesn’t have to eat every prey item it encounters. After this point, the predator should only choose the prey items with the highest E/h (Staddon, 1983).

Type II, the rate of prey capture negatively accelerates as it increases with food density. This is because it assumes that the predator is limited by its capacity to process food. In other words, as the food density increases, handling time also increases. At the beginning of the curve, rate of prey capture increases nearly linearly with prey density and there is almost no handling time. As prey density increases, the predator spends less time searching for prey and more time handling the prey. Therefore, the rate of prey capture decrease, until it finally plateaus (Jeschke *et al.*, 2002).

Type III, functional response curve is a sigmoid curve. The rate of prey capture increases at first with prey density at a positively accelerated rate, but then at high densities changes to the negatively accelerated form, similar to that of the Type II curve. At high prey densities (the top of the curve), each new prey item is caught almost immediately. The predator is able to be choosy and doesn’t eat every prey items it finds. So, assuming that there are two prey types with different profitabilities that are both at high abundance, the predator will choose the prey item with the higher E/h. However, at low prey densities (the bottom of the curve) the rate of prey capture increases faster than linearly. This means that as the predator feeds and the prey type with the higher E/h becomes less abundant, the predator will switch its preference to the prey type with the lower E/h, because the prey type is relatively more abundant. This phenomenon is known as prey switching (Staddon, 1983).

(3) nutrition value: large prey items usually yield more nutrition than small prey items. However, the energy for capture and handling time may also increase with increasing prey size. Prey items may also be selected according to their value to the fish. If two different prey types are available, the forager would choose the nutritionally favorable prey. The optimal diet model can predict how predators choose between two prey types: Large $prey_1$ with energy value E_1 and handling time h_1, and small $prey_2$ with energy value E_2 and handling time h_2. In order to maximize its overall rate of energy gain, a predator must consider the profitability of the two prey types. If it is assumed that large $prey_1$ is more profitable than small $prey_2$, then $E_1/h_1 > E_2/h_2$. Thus, if the predator encounters $prey_1$, it should always choose to eat it, because of its higher profitability. It should never bother to go searching for $prey_2$. However, if the animal encounters $prey_2$, it should reject it to look for a more profitable $prey_1$, *unless* the time it would take to find $prey_1$ is too long and costly for it to be worth it. Thus, the animal should only eat $prey_2$ if $E_2/h_2 > E_1/(h_1+S_1)$, where S_1 is the search time for $prey_1$. Since it is always favorable to choose to eat $prey_1$, the choice to eat $prey_1$ is not dependent on the abundance of $prey_2$. But since the length of S_1 (i.e. difficult to find prey1) is logically dependent on the density of $prey_1$, the choice to eat $prey_2$ *is* dependent on the abundance of $prey_1$ (Krebs & Davies, 1989).

Most fish are flexible in their choice of foods, corresponding to the change in the availability and profitability of prey. Such flexibility confers important advantage in terms of both survival and mobility in estuaries. In term of prey selection, 3 categories in fish feeding type were proposed by Gerking (1994) and Elliott *et al.* (2002).

(1) Generalist: they are feeding on the available food source, usually abundant prey, not considering for food size or nutrition value. This group is not follows optimal foraging theory.

(2) Specialists: They selected the prey items accordingly to the optimal foraging theory with emphasis on nutrition value and energy. The specialist usually feed restrictly on certain prey items and prefer the stable environment.

(3) Opportunists: this group shows flexibility in feeding than the generalist. They usually feed on other prey items outside its usual diet. They are not restricted to certain feeding pattern.

2. Ontogenetic Niche Shift

The diets of most fish change with growth in order to achieve the maximum net gain from food according to optimal foraging theory. The ultimate objective of dietary change is to maximize energy intake, enhance growth rate and minimize the risk of predation in competing for food with larger predators (Brown, 1985). The diet shift is a change from one food source to a new and possibly unaccustomed one. Morphology development, environmental, predation and competition are important factors determine the shifts in diet of fish. Ontogenetic niche shift is a change in diet during development that provides the maximum possible profit for an individual (Werner & Gilliam, 1984). The feeding ecology of fish developmental stages are as follows:

(1) Larvae stage: most of marine fish larvae are planktonic larvae. In the beginning, the yolk sac provide the food source for larvae. After yolk sac was absorbed, the larvae turn to exogenous feeding. The food consumption in this stage does not follows the optimal foraging theory. Fish larvae feed by random feeding because they cannot control the ability to catch prey items. Therefore, 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).

(2) Juvenile stage: the food consumption in this stage follows the optimal foraging theory due to their controlled ability to catch and choose the suitable preys for maximum energy. The actual timing of shift in diet in the juvenile stage usually relates to the changes in morphology of jaws and teeth. The dietary shift also occur during juveniles becoming adults. However, size related morphological changes such as jaw length, mouth gape, gill rackers and position of mouth, are important in relation to the determinant of prey size (Eggold & Motta, 1992; McCormick, 1998; Platell *et al.*, 1998).

(3) Adult stage: food consumption in this stage also follows optimal foraging theory. The diet shifts in adults demonstrate the adaptations that maximize energy intakes. Changes in size of feeding structures also associated with the changes in foraging behavior and habitat use, thus altering the range of exploitable prey items (Brown, 1985).

The ontogenetic changes in prey items have been found in terapotid species. Davis *et al.* (2011) study ontogenetic dietary shifts and feeding classification in terapontid fish found that, *Terapon jarbua* in small size class (<60 mm) fed mainly on insect worm and shift to fed mainly on fish scale in larger size class (>60 mm).

Horinouchi *et al.* (2012) reported that, terapontid fish such as, *Pelates quadrilineatus* collected in seagrass habitats in Trang Province showed ontogenetic changes in food patterns. Smaller individuals generally preyed on small planktonic items (e.g., copepods larvae) or small benthic/epiphytic crustaceans (e.g., harpacticoid copepodss), with subsequent changes to other prey items (e.g., shrimps, crabs, detritus and filamentous algae) with growth.

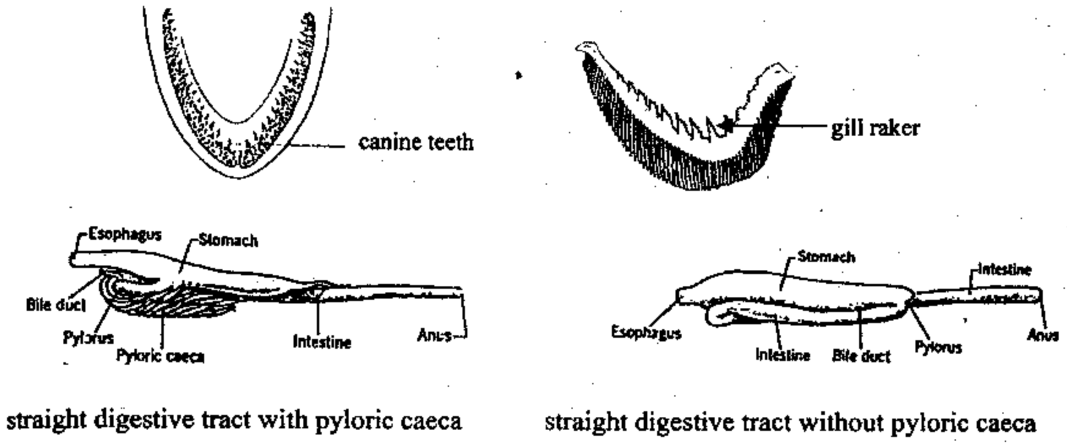
3. Food Partitioning

Food partitioning is the partitioning of food by two or more species or age 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 was due to: (1) actual agonistic competition for food; (2) resource utilization, where one species is better adapted to utilize a food source than other species; (3) territoriality, aggressive action used to space individuals or species; (4) predation risk, forcing to leave its normal habitat and take refuge in an unaccustomed area; and (5) other behavior factors including body size, movement, coloration and sound that lead to interspecific avoidance. Food partitioning may be result in different feeding type or different food source in the same habitat. On the other hand, differences in feeding structure morphology and time of feeding may also be the outcome of partitioning. The result of food partitioning may be alternative process in reducing competition for fish sharing the same feeding ground (Blaber, 1997). Whenever food partitioning is detected, food overlap is found. Degree of food overlap varied according to the abundance of resources and the range of resource utilization. Food overlap often occurs, in the non-competition area which foods are superabundance while discrete food almost found in lower food abundance. The number of fish species able to overlap on a resource use generally depends on the following factors (1) resource available (2) the range utilize by each species, and (3) the tolerable of overlap in resource use among species (Elliott *et al.*, 2002).

Davis *et al.* (2012a) reported on the food partitioning in terapontid fish, *Amniataba percoides*, *Hephaestus fuliginosus*, *Scortum parviceps* and *Leiopotherapon unicolor* in Australian estuary. There were food partitioning between fish in each size class with fish size less 40 mm which were planktonivore that feed mainly on zooplankton. Fish size of 40-80 mm were herbivore feed mainly on seaweed, while fish size of 80-160 mm were omnivore. Large fish size larger 160 mm were piscivore and detritivore. Mouth gape and body size were the important factors determining the shift in diets in fish (Wootton, 1990). Hajisamae *et al.* (2006) found *Sillago sihama* and *Sillago ingenuua* in Pattani Bay the food partitioning between fish in each size class in the juvenile stages of both species feed mainly on calanoid copepods in the water column. The adult stage of *Sillago sihama* feed mainly on polychaetes and *Sillago ingenuua* feed mainly on shrimps. The food overlap in juveniles *Sillgo* indicated that there was abundance of calanoid copepods as food source.

4. Feeding Patterns in Terapontid Fishes

Terapon jarbua and *P. quadrilineatus* are both carnivorous fish. The feeding structure consisted of large mouth gape and strong jaw. Dentition was with sharp and canine teeth. Small gill rakers were presented. The Y-shape stomach was large with several pyloric caeca. The intestinal length to body length was less than 1.12 (Lagler (Lagler *et al.*, 1962; Norman & Greenwood, 1975) (Figure 4.3).



straight digestive tract with pyloric caeca

straight digestive tract without pyloric caeca

Figure 4.3 Feeding structure morphology in carnivorous fish. Figures were after Lagler *et al.* (1962) and Norman and Greenwood (1975).

4.1 Feeding Patterns of *Terapon jarbua*

Many literature reviews revealed, *T. jarbua* feed on various prey items in different developmental stage. They can feed on various food items both in the water column and from benthic source. Dietary change between developmental stage was observed. The larval stage feeds mainly on insect larvae and small zooplankton such as diptera larvae, ephemeroptera, calanoid copepods, cyclopoid copepods and fish larvae (Davis *et al.*, 2011; Kanou *et al.*, 2004). During juvenile stage, *T. jarbua* shift to feed mainly on larger zooplankton (i.e. *Acetes* sp., Planktonic crustaceans), fish (i.e. *Mugil* spp., *Chanos chanos*, *Trichiurus* spp.), zoobenthos (i.e. amphipod, crabs, bivalves, shrimps/prawns, polychaetes) and organic matter (Whitfield, 1985 (Hajisamae *et al.*, 2003; Kulbicki *et al.*, 2005; Monkolprasit & Pramong, 1994; L. Rao & Prasad, 2002; Whitfield, 1985). Major prey items of *T. jarbua* adult stage were similar to those of the juvenile stage with fish scale additionally (Davis *et al.*, 2011; Nakane *et al.*, 2011). Diet composition of *T. jarbua* in each stage were as follows in Table 4.1.

Table 4.1 Diet composition of *Terapon jarbua* in different stages.

Food Item	Larvae	Juvenile	Adult	References
Insect				
Insects			✓	Whitfield (1985)
Diptera larvae	✓		✓	Davis *et al*. (2011)
Ephemeroptera	✓		✓	Davis *et al*. (2011)
Zooplankton				
Plankton	✓	✓	✓	Whitfield (1985)
Calanoid	✓			Kanou *et al*. (2004)
Cyclopoid	✓			Kanou *et al*. (2004)
Copepods			✓	Hajisamae *et al*. (2003)
Acetes sp.		✓	✓	Rao and Prasad (2002)
Mysids			✓	Nakane *et al*. (2011)
Megalopa			✓	Hajisamae *et al*. (2003)
Fish				
Fishes larvae	✓		✓	Davis *et al*. (2011)
Juvenile fish			✓	Nakane *et al*. (2011)
Bony fish		✓	✓	Whitfield (1985)
Mugil spp.		✓	✓	Rao and Prasad (2002)
Chanos chanos		✓	✓	Rao and Prasad (2002)
Trichiurus spp.		✓	✓	Rao and Prasad (2002)
Fish scales			✓	Davis *et al*. (2011)
Zoobenthos				
Amphipod		✓	✓	Hajisamae *et al*. (2003)
Benthic		✓	✓	Kulbicki *et al*. (2005)
Macrocrustacea			✓	Davis *et al*. (2011)
Crabs		✓	✓	Kulbicki *et al.* (2005)
Bivalvesves		✓	✓	Whitfield (1985)
Shrimps/prawns		✓	✓	Kulbicki *et al*. (2005)
Metapenaeus		✓	✓	Rao and Prasad (2002)
Penaeus indicus		✓	✓	Rao and Prasad (2002)
Penaeus monodon		✓	✓	Rao and Prasad (2002)
Squilla sp.		✓	✓	Rao and Prasad (2002)
Polychaetes		✓	✓	Whitfield (1985); Kanou *et al*. (2004)
Organic matter				
Digested organic		✓	✓	Monkolprasit (1994)

4.2 Feeding Patterns of *Pelates quadrilineatus*

Ontogenetic niche shift in *P. quadrilineatus* with dietary change throughout the developmental stage was found as reported in *T. jarbua*. Juvenile stage of *P. quadrilineatus* feeds mainly zooplankton (i.e. copepods larvae, calanoid copepods), zoobenthos (i.e. harpacticoid copepods, gammarid amphipods, bivalves) and organic matter (Hajisamae & Ibrahim, 2008; Horinouchi *et al.*, 2012; Lugendo *et al.*, 2006). The adult fish feeds mainly on shrimps (Hajisamae & Ibrahim, 2008; Horinouchi *et al.*, 2012). Diet composition of *P. quadrilineatus* in each stage were as in Table 4.2.

Table 4.2 Diet composition of *Pelates quadrilineatus* in different stages.

Food Item	Larvae	Juvenile	Adult	Reference
Insect				
Insect			✓	Lugendo *et al.* (2006)
Zooplankton				
Copepods		✓		Lugendo *et al.* (2006)
Copepods larvae		✓		Horinouchi *et al.* (2012)
Calanoid copepodss		✓		Hajisamae and Ibrahim (2008)
Small shrimps			✓	Hajisamae and Ibrahim (2008)
Mantis shrimp			✓	Hajisamae and Ibrahim (2008)
Fish				
Small fishes			✓	Hajisamae and Ibrahim (2008)
Zoobenthos				
Harpacticoid copepodss		✓	✓	Horinouchi *et al.* (2012)
Gammarid amphipod		✓	✓	Hajisamae and Ibrahim (2008)
Bivalves		✓	✓	Hajisamae and Ibrahim (2008)
Shrimps			✓	Horinouchi *et al.* (2012)
Organic matter				
Detritus		✓		Lugendo *et al.* (2006)
Sediment		✓		Lugendo *et al.* (2006)

C. Materials and Methods

1. Description of Study Area and Sampling Period

The study area is part of Sikao Bay, which located in coastal area of Trang Province on the southwest coast of Thailand. The study area consists of 8 sampling stations as shown in Figure 4.4 and Table 4.3. The two terapontid fishes, *T. jarbua* and *P. quadrilineatus* were found distributed among these sampling stations. The samples were collected monthly during January to December 2013. Availabled food sources in the coastal area of Trang Province, mainly zooplankton and macrobenthos, were sampled accordingly in each study site.

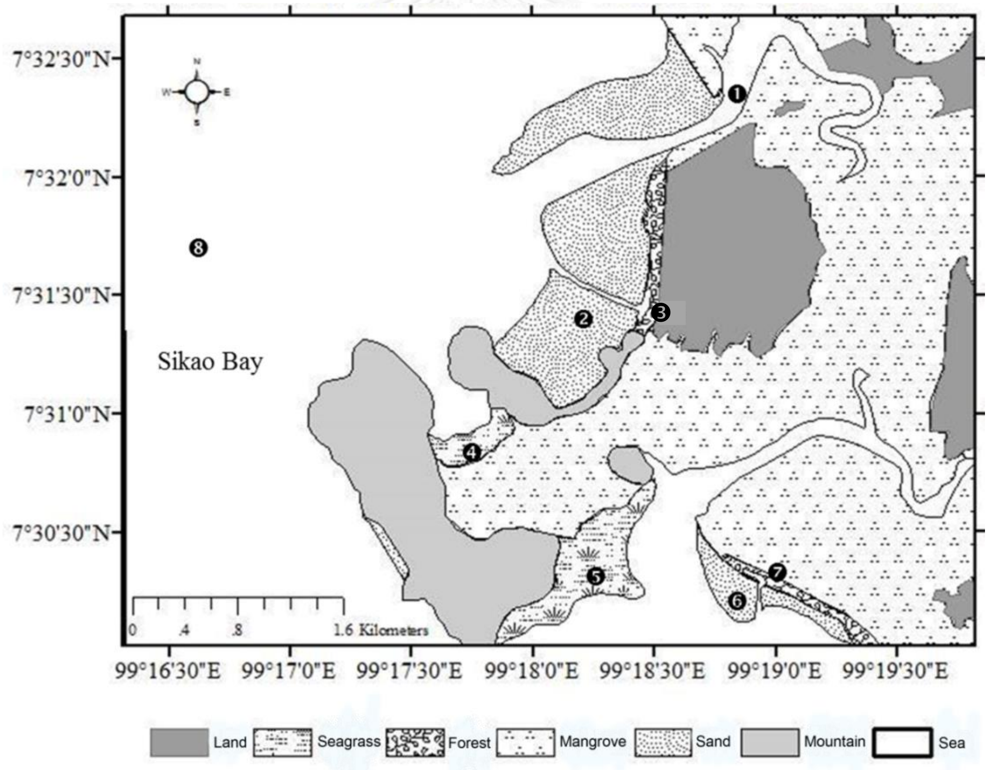


Figure 4.4 Study area located in the coastal area of Trang Province on the southwest coast of Thailand (❶: Sikao Creek, ❷: Rajamangala Beach, ❸: Rajamangala Coastal Swamp, ❹: Boonkong Bay, ❺: Makham Bay, ❻: Pakmeng Beach, ❼: Pakmeng Coastal Swamp and ❽: Offshore area).

Table 4.3 A description of characteristics of each study sites from the coastal area of 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 Coastal Swamp	0.35-0.75	Sand	Small forest coastal swamp of *Casuarina equisetifalia*, *Rhizophora apiculata* and *Pandanus tectorius*. The coastal 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	Makham 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 Coastal Swamp	0.34-0.80	Sand	Small forest coastal 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

2. Fishery Survey

Preflexion, flexion and Postflexion larvae stages of fish were collected by surface tows using plankton net (0.5 m mouth diameter; 330 µm mesh size). The plankton net was tow by low-speed boat (3 min) at each station except for station 3 and station 5 where the towing of plankton net was not possibled. The plankton collection at these two stations were carried out by filtering 100 L of seawater through the plankton net. Three replicates were carried out in each station. Samples were preserved in 4% neutral formalin.

Transforming larvae and juvenile fish were collected by small seine net with two 5 m long x 0.5 m high wings and a 2.5 m long cod end of 2.5 mm stretched mesh, 3 replicates in each station. For each tow, the net was initially laid out at the randomly established starting point in order for the net mouth opening to be 5 m and slowly pulled by two persons for the distance of 20 m. Samples were preserved in 10% neutral formalin.

Adult fish were collected from the fisherman gill net (30m long, mesh size of 30 mm) at the fishery landings. All samples were kept on ice and preserved in the refrigerator at 4°C in the laboratory.

3. Avilabled Food Sources in the coastal area of Trang Province

3.1 Species composition and abundance of zooplankton

Zooplankton samples were collected by using plankton net 330 µm equipped with the flowmeter. Triplicated horizontal tows were conducted with low speed boat at each station except for station 3 and station 5 where the towing of plankton net was not possibled. The plankton collection at these two stations were carried out by filtering 100 L of seawater through plankton net. Zooplankton samples were then preserved in 4% neutral formalin for further sorting and identifications.

3.2 Species composition and abundance of benthos

Macrobenthic fauna at each station were collected by core sample of 15 cm diameter at depth of 30 cm, 3 replicates in each station. Sediment samples were sieved through 0.5 mm mesh sieve. The sieving residuals were washed in sea water and fixed in 10% neutral formalin for further sorting and identifications.

4. Stomach Content Analysis

All samples of 1183 *T. jarbua* (preflexion larvae n=6; flexion larvae n=7; postflexion larvae n=8; transforming larvae n=619; juvenile n=385; adult n=158) and 694 *P. quadrilineatus* (preflexion larvae n=4; flexion larvae n=6; postflexion larvae n=7; transforming larvae n=208; juvenile n=319; adult n=150) were used for the identification of the major prey item by stomach content analysis. SL was measured for each specimen prior to the 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 1mm x 1mm 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).

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

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.

Mann-Whitney U test was used to test for significant differences between the dietary composition and the developmental stages of the species, using IBM SPSS Statistics 21. A significance level of $p < 0.05$ was used for the statistical analyses.

5. Morphological Study on Feeding Structure

Ninety specimens *T. jarbua* (transforming larvae n=30; juvenile n=30; adult n=30) and 90 specimens *P. quadrilineatus* (transforming larvae n=30; juvenile n=30; adult n=30) were randomly taken from the catch and used for collecting counts and measurements for the description of feeding structure morphology. Fish measurement such as total length, SL, body depth, mouth gape, mouth diameter, intestinal length were carried out by using vernier caliper as in Table 4.4. All measurements were measured down to ± 0.01 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.

Table 4.4 Measurements and counts of feeding structure morphology in *Terapon jarbua* and *Pelates quadrilineatus*.

Character	**Description**
Total length	From tip of snout to posterior margin of the body
Standard length	From tip of snout to posterior tip of the caudal peduncle
Body depth	From dorsal to the anus
Body weight	Weight as wet weight in gram
Mouth position	Description of the mouth position
Mouth gape	From tip of the upper jaw to tip of the lower jaw
Mouth diameter	From posterior tip of left jaw to posterior tip of right jaw
Teeth on upper jaw	Description of the type and number of teeth on upper jaw
Teeth on lower jaw	Description of the type and number of teeth on lower jaw
Number of gill rakers	Count the number of gill rakers
Shape of stomach	Description on the shape of stomach
Number of pyloric caeca	Count the number of pyloric caeca
Intestine length (mm)	From end of stomach to the anus
Intestine length / Standard length	Ratio of intestine length and standard length

6. Allometric Relationships of Morphological Character and Size

Raw measurements of the 13 morphometric characters (except TL and SL) were regressed against the SL on a logarithmic scale (log10). This produced simple linear regressions described by the equation $\mathrm{Log}(y) = \log(a) + (b \times \log(x))$ A scaling relationship was considered allometric if the 95% confidence interval for its slope failed to overlap the slope predicted for isometry (a slope = 1.0). If slope did not significantly differ from 1, variables showed isometric growth. Significant values of $b > 1$ indicated positive allometric growth, whereas values of $b < 1$ indicated negative allometry (Fuiman, 1983). All regression procedures were conducted using IBM SPSS statistics 21.

7. Analysis of Diet breadth and Diet Overlap

7.1 Diet breadth (Bi)

Diet breadth is calculated using Levin’s standardized index (Krebs & Davies, 1989). The formula for this index is;

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

where B_i represents Levin's standard index for predator i; P_{ij} represents proportion of diet of predator i that is made up of prey j; n represents number of prey categories. The index ranges from 0 to 1; low values (<0.6) indicate a diet dominated by few prey items or specialist consumer and higher values (>0.6) indicate generalist consumer.

7.2 Diet overlap

In order to sort the fishes into groups that took similar food, dietary overlaps were calculated and a cluster analysis applied. Calculation of the dietary overlap between all group pairs was based on mean percentage volumetric composition of each prey category. The comparative level of dietary overlap evident between species, developmental stage and seasonal change were compared similarly by means of an unequal variance t-test of average Bray-Curtis diet similarity from all percentage volume. The intensity of overlap was assessed at 60% similarity which shows high intensity of diet overlap (Ross, 1986).

D. Results and Discussions

1. Availabled Food Sources in the Coastal Area of Trang Province

As revealed from the previous studies that both *T. jarbua* and *P. quadrilineatus* were carnivores, fed on various prey items both in the water column and the benthic substrate. They also demonstrated the ontogenetic dietary shifts. Zooplankton in the water column and the macrobenthos in the bottom substrate played the important roles as the main prey items (Davis *et al.*, 2011; Davis *et al.*, 2012a; Hajisamae *et al.*, 2003; Hajisamae & Ibrahim, 2008; Horinouchi *et al.*, 2012; Kanou *et al.*, 2004; Kulbicki *et al.*, 2005; Lugendo *et al.*, 2006; Monkolprasit & Pramong, 1994; Nakane *et al.*, 2011; L. Rao & Prasad, 2002; Whitfield, 1985). The potential food sources in coastal area, Trang Province were investigated. Food availability in habitat helps determine indicated the diet composition in the fishes. Fish may have to choose among different habitats that provide different prey density and abundance to reduce food competition (Crowder & Cooper, 1982).

1.1 Zooplankton community in the coastal area of Trang Province

Zooplankton community in the coastal area of Trang Province in size >330 µm comprised of 12 groups namely hydromedusae, polychete larvae, cladocera, ostracods, calanoid copepodss, cyclopoid copepods, harpacticoid copepods, mysids, amphipods, *Lucifer* sp., crustacean nauplii, veligers, arrow worms and fish larvae. The density of zooplankton during the dry season varied from 1.12×10^3 to 3.23×10^4 individuals/100 m^3. High density of zooplankton observed during wet season varied from 1.85×10^3 to 4.91×10^4 individuals/100 m^3. The density of zooplankton in the coastal area of Trang Province was in the moderate to low productivity according to the marine productivity standard of Department of Marine and Coastal Resource of Thailand (2008). The density of zooplankton in this area varied from 10^3 to 10^4 individuals/100 m^3. The highest density of zooplankton was found at Pakmeng Beach in both dry and wet seasons. The lowest density of zooplankton was found in the Sikao Creek both dry and wet seasons. The zooplankton community in the coastal area of Trang Province was dominated by calanoid copepods which contributed more than 28.45% of the total zooplankton density. The second most abundance zooplankton was *Lucifer* sp. contributed about 24.59% of the total zooplankton density (Figure 4.5). Other dominant zooplankton observed in respective order were crustacean nauplii, cyclopoid copepods and mysid. Harpacticoid copepods was also found in small percentage. The zooplankton diversity and density found in the coastal area in Sikao Bay were lower than previous studies by Chuaypanang (1998) and Punnarak (2004). Chuaypanang (1998) reported the total of 42 groups from 15 phyla of zooplankton in the coastal area and mangrove forests in Sikao Bay. The density was in the range of 1.02×10^6 -3.95×10^6 individuals/100 m^3. Punnarak (2004) also reported the higher density of zooplankton in the range of 1.93×10^5-3.68×10^7 individuals/100 m^3 in the coastal area of Pakmeng Beach. However, the dominant zooplankter were similar to Chuaypanang (1998) which dominant zooplankter was mainly calanoid copepods, crustacean nauplii and sergestid shrimps.

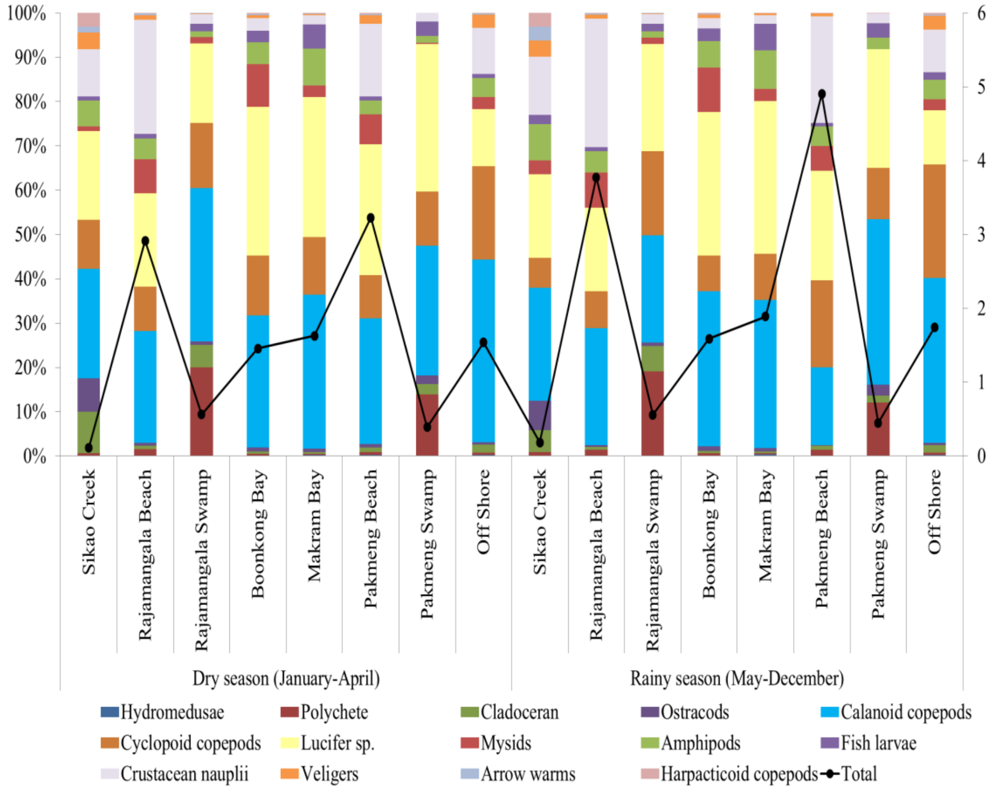


Figure 4.5 Density of zooplankton >330 µm in the coastal area of Trang Province.

1.2 Macrobenthos community in the coastal area of Trang Province

Macrobenthos community in the coastal area of Trang Province comprised of 10 groups namely polychaetes, nematodes, gastropods, bivalves, amphipods, isopods, copepods mainly harpacticoid copepods, ostracods, grapsid crabs and echinoderms. The density of macrobenthos during the dry season varied from 282 to 3193 individuals/100 m^2. The density of macrobenthos observed during wet season varied from 166 to 1868 individuals/ 100 m^2. The highest density of macrobenthos during the dry season was found in Makham Bay while the lowest density of macrobenthos was found offshore area. During the wet season, the highest density of macrobenthos was found at Rajamangala Coastal Swamp while the lowest density of macrobenthos was found in Sikao Creek. The macrobenthos community in the coastal area of Trang Province was dominated by polychaetes, contributed more than 61.15% of the total macrobenthos density. The second most abundance macrobenthos was nematodes, contributed more than 16.89% of the total macrobenthos density (Figure 4.6). Other dominant benthos found in respective order were ostracods, harpacticoid copepods, bivalves, gastropods and amphipods. Large benthos such as crabs, hermit crabs and shrimps were found in small numbers. According to the standard on marine productivity in Thai coastal waters (Department of marine and coastal resource of Thailand 2008) the macrobenthic community in this area was low in abundance and diversity. The ratio between the major benthic groups of polychaetes, crustaceans and molluscs indicated the deteriorating habitats with the highest ratio in polychaetes.

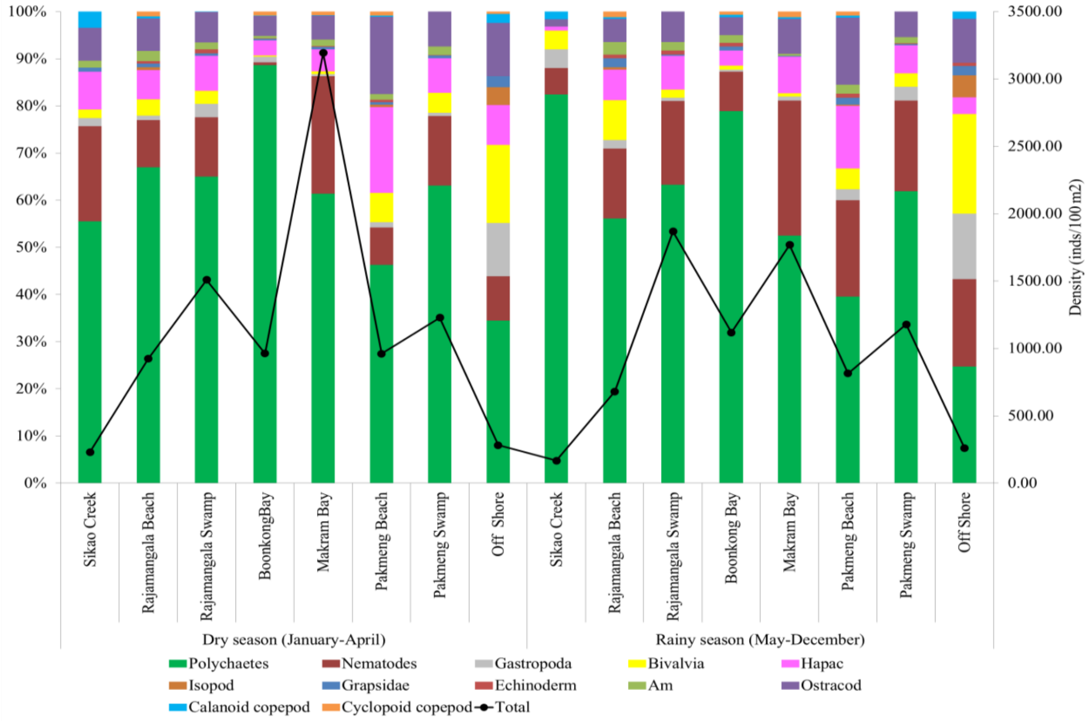


Figure 4.6 Density of macrobenthos in the coastal area of Trang Province.

2. Ontogenetic Dietary Shift and Feeding Habits in *Terapon jarbua*

The feeding habit of *T. jarbua* was carnivores with the prey items ranged from zooplankton, small and large benthos, fish and fish scales to insect worms. Diet compositions of *T. jarbua* in different development stages as revealed from the stomach content analysis were shown in Table 4.5. Most of the stomachs used in the stomach content analysis in the *T. jarbua* specimen were full (98.9%) with only few (1.1%) were empty.

Ontogenetic dietary shift was evidenced in *T. jarbua*. Main prey items in the stomach of *T. jarbua* in different stages changed as in Figure 4.7. Minimal seasonal changes in the diet composition of each stage except in the juveniles that fed more on fish scale in the dry season. Zooplankton played the major role in the diet of planktonic larval stage. Calanoid copepods was the dominant prey item. 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 mainly on the bottom sediment. Juveniles of *T. jarbua* shifted to fed on small benthic animals mainly harpacticoid copepods, amphipods and ostracods. Large benthos such as grapsidae crab, hermit crabs, shrimps and isopods also presented in the diet composition of juveniles. Large zooplankters such as crab zoea, *Lucifer* sp. and arrow worms were found in small percentages in the stomach 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 along with sipunculids and polychaetes.

Table 4.5 Dietary compositions expressed as percentage of index relative important (%IRI) from stomach content analysis in *Terapon jarbua* of different developmental stages and seasons from the coastal area of Trang Province.

Developmental Stage	**Larvae**								**Juvenile**		**Adult**	
	Preflexion		**Flexion**		**Postflexion**		**Transforming**					
Season	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
n	3	3	3	4	3	5	112	507	146	239	44	114
Prey items												
Zooplankton												
Calanoid copepods	100.00	100.00	100.00	100.00	100.00	100.00	86.38	89.10	-	-	-	-
Cladocerans	-	-	-	-	-	-	-	-	-	-	0.01	0.01
Crab zoea	-	-	-	-	-	-	0.47	1.01	1.70	1.53	-	-
Lucifer spp.	-	-	-	-	-	-	4.60	3.02	4.28	0.21	-	-
Arrow worm	-	-	-	-	-	-	-	-	0.10	0.20	-	-
Small benthos												
Harpacticoid copepods	-	-	-	-	-	-	1.38	0.48	51.02	69.28	-	-
Amphipods	-	-	-	-	-	-	6.96	5.80	4.45	8.41	-	-
Ostracods	-	-	-	-	-	-	-	-	1.83	2.05	-	-
Large benthos												
Polychaetes	-	-	-	-	-	-	-	-	-	-	0.69	0.63
Crustaceans												
Crabs	-	-	-	-	-	-	0.01	-	4.63	10.39	6.59	4.50
Hermit crabs	-	-	-	-	-	-	-	-	0.29	3.88	1.27	5.52
Shrimps	-	-	-	-	-	-	0.05	0.09	0.22	0.17	3.05	3.41
Isopods	-	-	-	-	-	-	-	-	0.10	-	-	-
Molluscs												
Gastropods	-	-	-	-	-	-	-	-	-	-	0.20	-
Sipunculids	-	-	-	-	-	-	-	-	-	-	0.17	0.02
Sea cucumbers	-	-	-	-	-	-	-	-	-	-	-	0.35
Fishes												
Fishes	-	-	-	-	-	-	-	-	7.45	0.79	40.08	46.46
Fish scales	-	-	-	-	-	-	-	-	22.81	1.23	47.86	39.08
Squids	-	-	-	-	-	-	-	-	-	-	-	-
Insect												
Insect worms	-	-	-	-	-	-	0.17	0.51	1.13	1.84	-	-

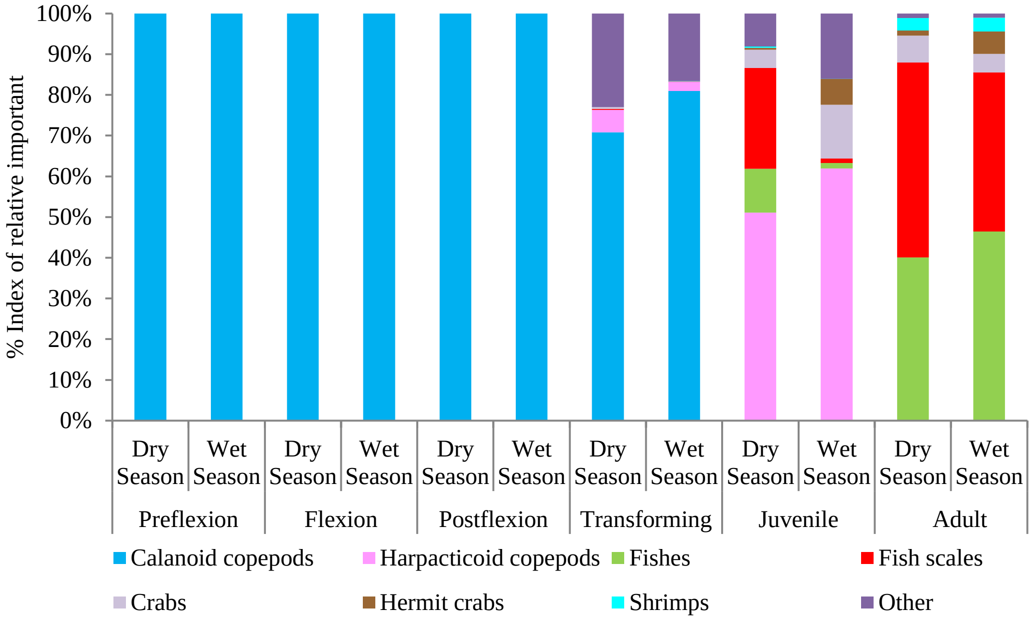


Figure 4.7 Ontogenetic dietary shift of *Terapon jarbua* (n =1183) from the coastal area of Trang Province.

There was a correlation between the ontogeny changes in morphological characters in relation feeding and the carnivorous nature in *T. jarbua*. The planktonic larvae fed mainly on the small size calanoid copepods while transforming larvae fed on the larger size calanoid copepods and other large zooplankters. During this phase, the transforming larvae also fed on small benthos, harpacticoid copepods and amphipods. Juveniles of *T. jarbua* shifted to fed on benthic animals, fishes, fish scales and insect worms. Feeding of piscivores and lepidophagy were the diets of adults *T. jarbua*. The morphology of the feeding structure in *T. jarbua* corresponded to the feeding structure in carnivorous fish as described by Lagler *et al.* (1962) and Norman and Greenwood (1975). Significant allometric relationships were evidenced in the growth of *T. jarbua* morphological characters in Table 4.6 as reported in all terapontid species (Davis *et al.*, 2012a, 2012b; Davis *et al.*, 2013). Positive allometric growth was observed during ontogeny except for the predorsal length and eye diameter.

Significant negative allometric scaling in eye diameter was identified in most fishes. Eye diameter became disproportionately smaller in most species as they increased in size (Davis *et al.*, 2012b). The interactions between body size and allometric growth of particular morphological characters such as mouth width, mouth gape and intestinal length played the important role in determining the dietary habits in terapontids (Davis *et al.*, 2012a, 2012b; Davis *et al.*, 2010; Davis *et al.*, 2013).

Table 4.6 Allometric relationships among standard length and morphological characters of *Terapon jarbua* from the coastal area of Trang Province (+ = positive allometric growth, - = negative allometric growth, blank cells = no measurment).

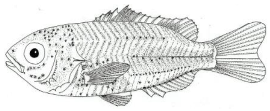
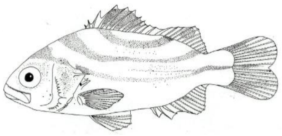
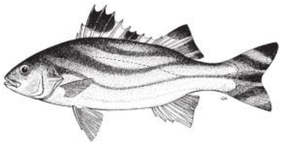
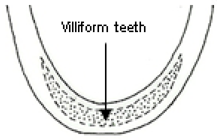
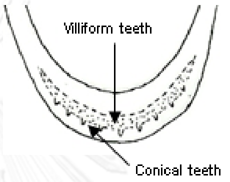
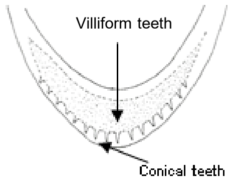
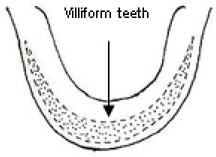
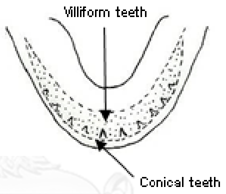
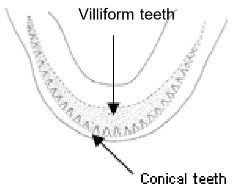
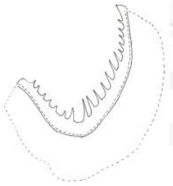
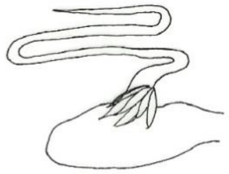
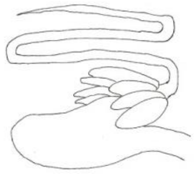
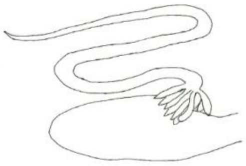
Morphological variable	***Terapon jarbua***			
	Planktonic larvae	**Transforming larvae**	**Juvenile**	**Adult**
n	21	30	30	30
Body depth	+ (r = 0.998)	+ (r = 0.976)	+ (r = 0.725)	+ (r = 0.875)
Head length	+ (r = 0.725)	+ (r = 0.824)	+ (r = 0.699)	+ (r = 0.924)
Mouth gape	+ (r = 0.998)	+ (r = 0.635)	+ (r = 0.999)	+ (r = 0.998)
Mouth diameter	+ (r = 0.995)	+ (r = 0.999)	+ (r = 0.899)	+ (r = 0.950)
Predorsal length		- (r = 0.835)	- (r = 0.728)	- (r = 0.992)
Base of dorsal fin		+ (r = 0.983)	+ (r = 0.855)	+ (r = 0.965)
Snout length	+ (r = 0.825)	+ (r = 0.997)	+ (r = 0.999)	+ (r = 0.980)
Eye diameter	+ (r = 0.899)	- (r = 0.919)	- (r = 0.989)	- (r = 0.828)
Jaw length	+ (r = 0.999)	+ (r = 0.999)	+ (r = 0.999)	+ (r = 0.889)
Longest dorsal fin spine		+ (r = 0.875)	+ (r = 0.850)	+ (r = 0.759)
Longest dorsal fin ray		+ (r = 0.915)	+ (r = 0.895)	+ (r = 0.828)
Longest anal fin spine		+ (r = 0.995)	+ (r = 0.897)	+ (r = 0.890)
Longest anal fin ray		+ (r = 0.950)	+ (r = 0.915)	+ (r = 0.998)
Intestinal length		+ (r = 0.875)	+ (r = 0.998)	+ (r = 0.990)

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 Table 4.7 and 4.8. These ontogenetic changes were important in the partition of the diet and habitat of this species. *Terapon jarbua* has a subterminal mouth showing the benthic feeding habitat. The width of mouth gapes and mouth diameter varied from 0.13-22.12 and 0.10-18.57 mm. The planktonic larvae in preflexion, flexion and postfiexion stages were found distributed in the offshore area. High density of the planktonic larvae were found during April-June and September-October. This coincided with the high density of zooplankton in the offshore area. Calanoid copepods was the major prey category. During the dry season, Calanoid copepods made up to 41% of the total zooplankton density. Calanoid copepods made up to 37% of the total zooplankton density in the wet season. At these stages, the larval fish depended on random feeding. Their swimming ability was poor. Prey size selection was considerably less than their mouth gape (Gerking, 1994). The abundance of calanoid copepods highly affected their survival. The feeding in preflexion, flexion and postflexion larvae followed the optimal foraging theory base on the food density. The rate of prey capture gradually increased with the food density as Type II functional response curve (Staddon, 1983). This indicated that there is an increase of the prey taken with the increasing prey density but with a logarithmic deceleration to a plateau. Feeding by random encounter as in the larval feeding can take progressively smaller increment of prey with increasing prey density.

Table 4.7 Measurement on feeding structure morphology of *Terapon jarbua* from the coastal area of Trang Province.

Feeding structure	***Terapon jarbua***					
	Preflexion Larvae	**Flexion Larvae**	**Postflexion Larvae**	**Transforming Larvae**	**Juveniles**	**Adults**
n	6	7	8	30	30	30
Total length (mm)	2.59±0.97	4.14±0.37	5.67±0.50	16.24±3.22	40.99±19.02	199.15±43.76
Standard length (mm)	2.34±1.20	3.64±0.22	4.86±0.83	13.46±2.88	34.29±15.39	166.75±38.15
Body depth (mm)	0.35±0.02	0.76±0.12	1.15±0.55	4.66±2.35	12.72±6.19	59.57±14.50
Body weight (g)	< 0.01	<0.01	<0.01	0.16±0.11	3.24±4.59	145.64±70.18
Mouth gape (mm)	0.13±0.02	0.44±0.27	0.78±0.10	1.76±1.08	5.57±3.33	22.12±4.81
Mouth diameter (mm)	0.10±0.05	0.39±0.11	0.75±0.08	1.33±0.87	4.24±2.12	18.57±4.59
Number of gill rakers	-	-	-	20±0.12	21±0.55	23±0.10
Number of pyloric caeca	-	-	-	7±0.58	10±0.12	10±0.85
Intestine length (mm)	-	-	-	10.51±2.12	30.58±18.97	167.95±49.03
Intestine length / Standard length	-	-	-	0.78	0.89	1.00
% of food in stomach	100	100	100	74.74±28.85	71.09±32.46	75.96±27.72

Table 4.8 Comparative study on feeding structure morphology of *Terapon jarbua* from the coastal area of Trang Province.

Characteristic	**Transforming Larvae**	**Juveniles**	**Adults**
Body form			 Vari (2001)
Mouth position			
Teeth on upper jaw			
Teeth on lower jaw			
Gill rakers			
Shape of stomach			
Intestine			

The nutrition value in the prey items selected by *T. jarbua* larvae also evidenced. The importance of zooplankton as s nutritional resource for larval and postlarval fishes had been recognized. Zooplankton often have a higher energy content than benthic invertebrate groups. They also have the ability to store large amount of lipids, the important energy reserve for fishes (Lee *et al.*, 2006).

Size selection is important in larval feeding because the maximum and median length of consumed prey were considerably less than fish mouth gape (Gerking, 1994). Larval and postlarval fishes are restricted by mouth dimension to the size of invertebrate prey that can be consumed. Larval fishes fed mainly on microzooplankton whereas postlarval fishes utilize both microzooplankton and macrozooplankton (Whitfield, 1985). A factor of prime important in the process of prey search and capture is the morphology of the larva. Larval structure and developmental stage determine its ability to detect, approach and attack prey, while constaints such as the size of the mouth set the maximum size of prey that they can ingest. During growth, mouth size will increase and larval swimming and manoeuvring abilities will improve, increasing the efficiency of foraging. Prey/gape ratio of 25-50% seems to be most appropriate for larval fish (Østergaard *et al.*, 2005). As evidenced from this study, calanoid copepods was the major prey items for the planktonic larvae of *T. jarbua* ranging from preflexion, flexion, postflexion and transforming larvae. The preflexion, flexion, postflexion larvae fed on the small size calanoid copepods while the transforming larvae fed on the larger size calanoid copepods and other large zooplankton such as crab zoea and *Lucifer* spp. Prey size to mouth size ratio in the planktonic larvae and transforming larvae of *Terapon jarbua* was range 0.25 to 0.80 (Table 4.9). The ratio of prey diameter to mouth diameter that maximized the net energy return to predator lies between 0.4-0.7 (Wainwright & Richard, 1995).

Table 4.9 Prey size to mouth size ratio in the planktonic larvae and transforming larvae of *Terapon jarbua* from the coastal area of Trang Province.

Stage	**Mouth size (mm)**	**Prey size (mm) (Calanoid copepods)**	**Prey size : Mouth size**
Planktonic larvae			
Mouth gape	0.52±0.22	0.25	0.48:1
Mouth diameter	0.48±0.19	0.25	0.52:1
Transforming larvae			
Mouth gape	1.76±1.08	0.80	0.45:1
Mouth diameter	1.33±0.87	0.80	0.60:1

Transforming larvae and juveniles of *T. jarbua* were found distributed in the coastal swamp habitat under the tidal influences of Rajamangala and Pakmeng coastal swamp. During metamorphosis, size-specific shifts in food types often associated with the shift in habitat. Transforming larvae and juveniles choose the mangrove coastal swamps as nursery area to avoid the predator and search for food. Apart from large size calanoid copepods as the major prey items, the transforming larvae also fed on large zooplankton such as crab zoea and *Lucifer* spp. in the water column. They also fed on the bottom substrate in the mangrove habitat. Small benthos, harpacticoid copepods and amphipods made up the small partitions in the diets of the transforming larvae. Teeth are mainly villiform type with small teeth forming in bands on the upper and lower jaw in the transforming larvae. The development of teeth on the jaws indicate that they are capable of catching preys. Short gill raker varied from 20-23 gill raker appeared in the transforming larvae juveniles and adults. As the fish consume zooplankton and small benthos, they seem to pick their preys up rather than filter them. A reduction number of gill rakers is related to a more benthic feeder (Kramer & Bryant, 1995). The stomach is 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 diversed 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 diversed food items (Rust, 2002). Juveniles of *T. jarbua* shifted to fed on benthic animals, fish, fish scales and insect worms. Harpacticoid copepods was the major prey item. Large benthos such as crabs, hermit crabs, shrimps, fishes and fish scales were the important prey items in the stomach content of the juveniles. Juveniles of *T. jarbua* also fed on crab zoea, *Lucifer* spp. and arrow worm in the water column. During this stage, the morphological changes such as increase of body depth, fin length, larger eyes and dentition permit the juveniles to have well controlled swimming and good visual in the turbid habitat in order to catch their preys and the same time avoiding the predators. Juveniles and adults of *T. jarbua* have band of villiform teeth with 1 row of conical teeth on the upper and lower law. Adults of *T. jarbua* have sharper and greater numbers of conical teeth than juveniles. Dentition typically provides a reasonable approximation of diet with conical hold teeth corresponding to canivory (Davis *et al.*, 2012b). *Terapon jarbua* has 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 relative orientation of the mouth indicates the depth at which feeding typically occurs or of predator position in relation to prey (Davis *et al.*, 2012b). The subterminal mouth, corresponded to the downward movement from the water column to the benthic environment during metamorphosis, allowing the juveniles to prey on more diversed prey species. Thus this study confirmed that the mangrove coastal swamps in the coastal area of Trang Province played the important roles as the nursery and feeding grounds for the transforming larvae and juveniles of *T. jarbua*.

Adults of *T. jarbua* were found distributed in the offshore area. Feeding habits of piscivores and lepidophagy were prominent in the adult stage. Diversed prey items in the diet composition of the adults ranging from large benthos mainly grapsidae crabs, hermit crabs, shrimps, polychaetes, sipunculids and sea cucumbers to the cladocerans in the water column. The size of important prey items consumed was determined by mouth gape and jaw of fish. An increase in predator size will widen the range of prey. The amount of energy and handling time also increase with prey size (Gill, 2003). Larger fish have more chance to find profitability prey and find suitable feeding habitat than small fish because the morphology related to feeding were well developed. Larger mouth size allow the fish to fed on larger prey size (Wainwright (Mittelbach & Persson, 1998; Wainwright & Richard, 1995). According to the dietary habits category assigned by Davis *et al.* (2012b), adult of *T. jarbua* would fall into the category of microphagous carnivores (diets dominated by large animal prey, fish, macrobenthos, terrestrial invertebrates) and lepidophagous (diets dominated by fish scales and fish). In this study, piscivores and lepidophagy should be kept separately. A fish can be considered truly lepidophagous when scales are found in the stomach without bones of flesh present (Peterson & McIntyre, 1998). Lepidophagy (scale-eating) is regarded as a derived, highly specialized dietary habit. Behavioral and morphological feeding adaptation such as specialized dentition, jaw structure, snout teeth and attack methods are found in the lepidophagous fish (Blaber, 2000; Peterson & McIntyre, 1998). The result showed that *T. jarbua* increasingly fed on fish scales from juvenile to adult. Blaber (2000) reported *T. jarbua* was able to digest the scales, which have a relatively high calorific value. Lepidophagous species often complement their diets with food types other than scales. In Figure 4.8, the large size fish (>180 mm) consumed higer 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. High percentage of macrobenthos was found in the mature fish. 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 are more flexible in their resource use (Mittelbach & Persson, 1998).

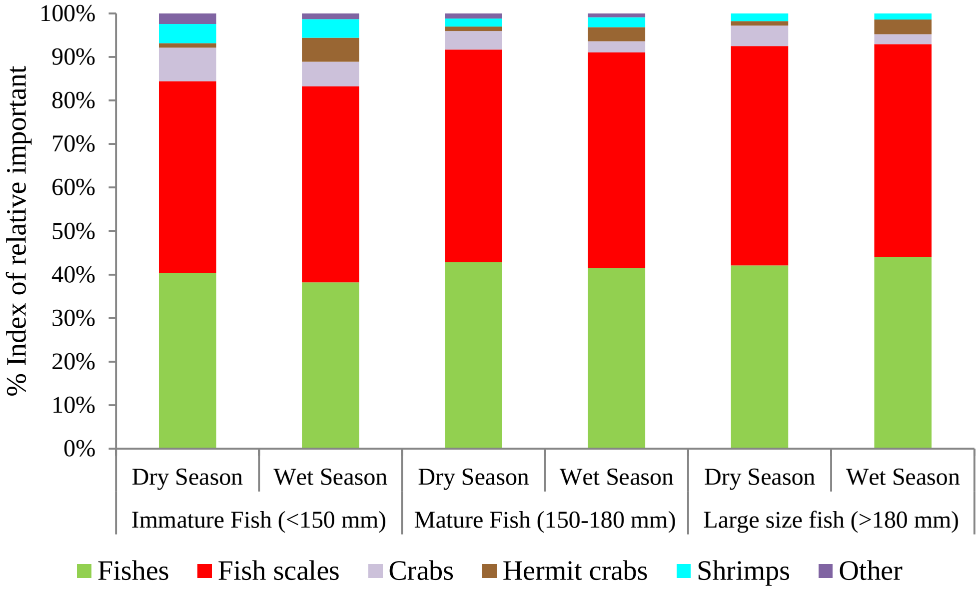


Figure 4.8 Diet composition in adult *Terapon jarbua* (n =158) from the coastal area of Trang Province.

The diet breadths of *T. jarbua* increased with growth allowing more chance to fed on diversed preys and to find suitable feeding habitat. However, the diet breadths of *T. jarbua* showed the high level of dietary specialization in all developmental stages (Diet breadth <0.6). This indicated that *T. jarbua* was a specialist consumer with diet dominated by few prey items (Table 4.10). The selection of prey items, based on nutrition values and energy gained which followed the optimal foraging theory (Elliott *et al.*, 2002; Gerking, 1994). The planktonic larvae stage fed mainly on calanoid copepods which was abundant in the feeding ground. High density prey as calanoid copepods was chosen in order to reduces the handling time, searching time and energy spent for capturing their preys. Zooplankton provided the nutritive food source for fish larvae and juveniles (Whitfield, 1985). Size selection was also important in larval feeding. The constraints of mouth size set the maximum size of prey that the planktonic larvae can ingested. The preflexion, flexion and postflexion larvae fed on the small size calanoid copepods while the transforming larvae fed on the larger size calanoid copepods. The ratio of prey diameter to mouth diameter in both larval stages indicated the maximum net energy return. During metamorphosis, transforming larvae and juveniles of *T. jarbua* demonstrated the ontogenetic niche shift to seek the mangrove coastal swamps as the nursery and feeding ground. The transforming larvae fed mainly on zooplankton, large size calanoid copepods, crab zoea and *Lucifer* sp. in the water column. Juveniles shifted to fed mainly on benthos, fish, fish scales and insect worms. Adult stage fed mainly on fish and fish scale. They chose to fed on large and movable preys. Although more energy and time are required to captured these preys but they get high nutritive preys providing maximum net gain energy for growth.

Table 4.10 Diet breadths in *Terapon jarbua* (n=1183) of different developmental stages and seasons from the coastal area of Trang Province.

Season	**Stage**	**% of food in stomach**	**No of prey categories**	**Diet breadth**
Dry	Preflexion	83.33	1	0.00
	Flexion	93.33	1	0.00
	Postflexion	100.00	1	0.00
	Transforming	71.96	9	0.04
	Juvenile	69.18	13	0.18
	Adult	75.35	11	0.17
Wet	Preflexion	83.33	1	0.00
	Flexion	95.00	1	0.00
	Postflexion	100.00	1	0.00
	Transforming	73.55	8	0.03
	Juvenile	76.36	12	0.08
	Adult	76.19	11	0.19

3. Ontogenetic Dietary Shift and Feeding Habits in *Pelates quadrilineatus*

The feeding habit of *P. quadrilineatus* was also carnivores as in *T. jarbua.* The prey items ranged from zooplankton, small and large benthos and fish scales. High percentage of stomach fullness (94.9%) was observed from the 669 stomach of *P. quadrilineatus* used in the stomach content analysis. Only 5.1% of the stomach were found empty. Ontogenetic dietary shift was evidenced in *P. quadrilineatus* as in Table 4.11 and Figure 4.9. Calanoid copepods was the dominant prey item in 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. The transforming larvae fed both in the water column and in the bottom substrate. As the calanoid copepods was in abundance during the wet season, the larvae choose to fed more on the abundant food source.

Table 4.11 Dietary compositions expressed as percentage of index relative important (%IRI) from stomach content analysis in *Pelates quadrilineatus* of different developmental stages and seasons from the coastal area of Trang Province.

Developmental Stage	**Larvae**											
	Preflexion		**Flexion**		**Postflexion**		**Transforming**		**Juvenile**		**Adult**	
Season	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
n	2	2	3	3	3	4	112	96	248	71	54	96
Prey items												
Zooplankton												
Calanoid copepods	100.00	100.00	100.00	100.00	100.00	100.00	48.04	87.42	0.68	-	-	-
Cladocerans	-	-	-	-	-	-	-	-	-	-	0.48	0.41
Lucifer spp.	-	-	-	-	-	-	-	-	6.31	7.41	-	-
Small benthos												
Harpacticoid copepods	-	-	-	-	-	-	51.96	12.58	93.01	92.52	-	-
Amphipods	-	-	-	-	-	-	-	-	-	-	18.32	13.78
Ostracods	-	-	-	-	-	-	-	-	-	-	0.23	0.06
Large benthos												
Polychaetes	-	-	-	-	-	-	-	-	-	-	14.12	21.67
Crustaceans												
Crabs	-	-	-	-	-	-	-	-	-	-	-	0.64
Hermit crabs	-	-	-	-	-	-	-	-	-	-	15.67	14.43
Shrimps	-	-	-	-	-	-	-	-	-	-	1.40	10.03
Isopod	-	-	-	-	-	-	-	-	-	-	0.12	0.09
Molluscs												
Gastropods	-	-	-	-	-	-	-	-	-	-	12.88	6.61
Bivalves	-	-	-	-	-	-	-	-	-	-	24.42	22.11
Fishes												
Fish scale	-	-	-	-	-	-	-	-	-	0.01	12.38	10.17

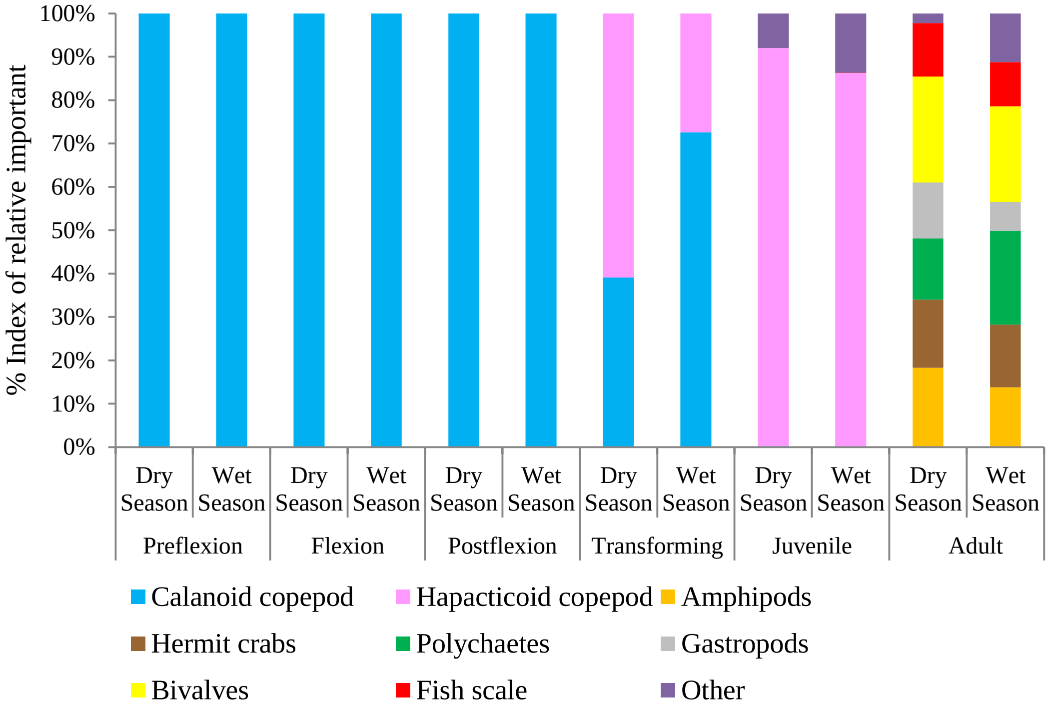


Figure 4.9 Ontogenetic dietary shift in *Pelates quadrilineatus* (n =694) from the coastal area of Trang Province.

In juvenile *P. quadrilineatus*, harpacticoid copepods, the small benthos, was the major prey item. Zooplankton, *Lucifer* spp. and calanoid copepods made up the smaller percentage in diet composition of juvenile. Adults *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* increased with growth. Lepidophagy behavior found in *P. quadrilineatus* with size over 20 mm in standard length.

The morphology of the feeding structure in *P. quadrilineatus* corresponded to those in the carnivorous fish (Lagler *et al.*, 1962; Norman & Greenwood, 1975). Significant allometric relationships were also evidences in the ontogeny of *P. quadrilineatus* as in *T. jarbua* and other terapontid fishes as in Table 4.12 (Davis *et al.*, 2012a, 2012b; Davis *et al.*, 2013).

Table 4.12 Allometric relationships among standard length and morphological characters of *Pelates quadrilineatus* from the coastal area of Trang Province (+ = positive allometric growth, - = negative allometric growth, blank cells = no measurement).

Morphological variable	***Pelates quadrilineatus***			
	Planktonic larvae	**Transforming larvae**	**Juvenile**	**Adult**
n	17	30	30	30
Body depth	+ (r = 0.780)	+ (r = 0.999)	+ (r = 0.850)	+ (r = 0.899)
Head length	+ (r = 0.859)	+ (r = 0.835)	+ (r = 0.872)	+ (r = 0.925)
Mouth gape	+ (r = 0.724)	+ (r = 0.742)	+ (r = 0.819)	+ (r = 0.899)
Mouth diameter	+ (r = 0.999)	+ (r = 0.995)	+ (r = 0.950)	+ (r = 0.820)
Predorsal length		- (r = 0.948)	- (r = 0.999)	- (r = 0.999)
Base of dorsal fin		+ (r = 0.858)	+ (r = 0.958)	+ (r = 0.988)
Snout length	+ (r = 0.825)	+ (r = 0.778)	+ (r = 0.923)	+ (r = 0.995)
Eye diameter	+ (r = 0.925)	- (r = 0.855)	- (r = 0.915)	- (r = 0.954)
Jaw length	+ (r = 0.998)	+ (r = 0.995)	+ (r = 0.999)	+ (r = 0.913)
Longest dorsal fin spine		+ (r = 0.925)	+ (r = 0.725)	+ (r = 0.826)
Longest dorsal fin ray		+ (r = 0.915)	+ (r = 0.819)	+ (r = 0.919)
Longest anal fin spine		+ (r = 0.990)	+ (r = 0.853)	+ (r = 0.899)
Longest anal fin ray		+ (r = 0.999)	+ (r = 0.997)	+ (r = 0.724)
Intestinal length		+ (r = 0.872)	+ (r = 0.996)	+ (r = 0.999)

The ontogenetic change in the mouth gape and diameter, dentition, gill rakers, stomach and pyloric caeca and intestinal length were observed (Table 4.13, Table 4.14). Subterminal mouth presented in *P. quadrilineatus.* The width of mouth gapes and mouth diameter varied from 0.33-15.83 and 0.31-9.90 mm. The preflexion, flexion and postflexion larvae were found distributed in the offshore area. Calanoid copepods was the major prey item. The transforming larvae also fed on calanoid copepods in the same proportion as harpacticoid copepods. The mouth size limited the prey size of calanoid copepods. The preflexion, flexion and postflexion larvae fed on the small size calanoid copepods while the transforming larvae fed on the larger size calanoid copepods. The prey size to mouth size ratio in the planktonic larvae of *P. quadrilineatus* (Table 4.15) were in the range of 0.45-0.67. This indicated that the maximum net energy return to the planktonic larvae of *P. quadrilineatus*. High density of preflexion, flexion and postflexion larvae in the offshore area corresponding to the spawning period and the zooplankton abundance during November to December.

Table 4.13 Measurements on feeding structure morphology of *Pelates quadrilineatus* from the coastal area of Trang Province.

Feeding structure	***Pelates quadrilineatus***					
	Preflexion Larvae	**Flexion Larvae**	**Postflexion Larvae**	**Transforming Larvae**	**Juveniles**	**Adults**
n	4	6	7	30	30	30
Total length (mm)	2.56±0.54	4.02±0.57	4.78±0.25	18.29±4.05	36.93±9.08	148.75±9.17
Standard length (mm)	2.31±0.95	3.66±0.22	4.56±0.79	15.34±3.33	31.16±7.52	126.82±8.26
Body depth (mm)	0.34±0.05	0.70±0.10	1.12±0.05	4.31±2.37	9.46±2.34	40.83±4.31
Body weight (g)	< 0.01	<0.01	<0.01	0.13±0.10	0.77±0.53	45.96±9.71
Mouth gape (mm)	0.13±0.00	0.44±0.05	0.75±0.04	1.77±0.50	3.95±1.27	15.83±2.81
Mouth diameter (mm)	0.11±0.05	0.42±00	0.75±0.01	1.20±0.35	2.72±2.00	9.90±2.16
Number of gill rakers	-	-	-	39±1.12	42±0.50	45±1.25
Number of pyloric caeca	-	-	-	13±0.00	14±0.55	15±0.50
Intestine length (mm)	-	-	-	10.40±6.35	22.90±8.74	118.03±27.94
Intestine length / Standard length	-	-	-	0.68	0.73	0.93
% of food in stomach	100	100	100	60.80±34.62	68.99±32.77	65.33±34.21

Table 4.14 Comparative study on feeding structure morphology of *Pelates quadrilineatus* from the coastal area of Trang Province.

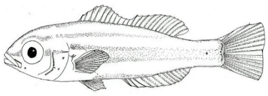
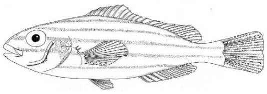
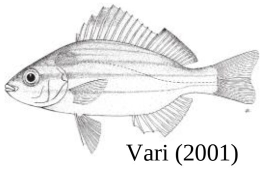
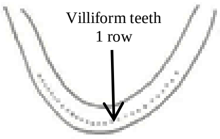
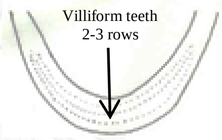
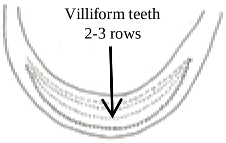
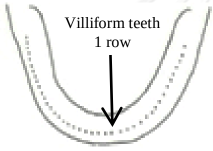
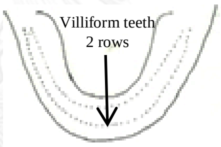
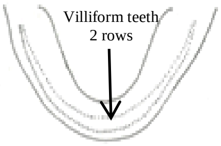
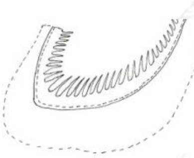
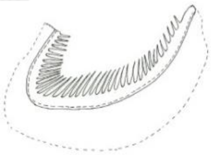
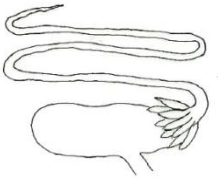
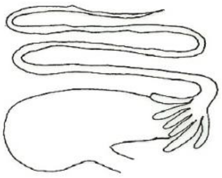
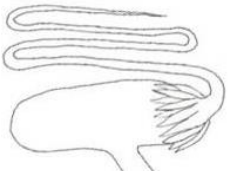
Characteristic	Transforming Larvae	Juveniles	Adults
Body form			 Vari (2001)
Mouth position			
Teeth on upper jaw	 	 	
Teeth on lower jaw	 	 	
Gill rakers			
Shape of stomach			
Intestine			

Table 4.15 Prey size to mouth size ratio in the planktonic larvae and transforming larvae of *Pelates quadrilineatus* from the coastal area of Trang Province.

Stage	**Mouth size (mm)**	**Prey size (mm)** **(Calanoid copepods)**	**Prey size : Mouth size**
Planktonic larvae			
Mouth gape	0.51±0.34	0.25	0.49:1
Mouth diameter	0.49±0.31	0.25	0.51:1
Transforming larvae			
Mouth gape	1.77±1.08	0.80	0.45:1
Mouth diameter	1.20±0.87	0.80	0.67:1

Ontogenetic niche shift in diet and habitat also occurred in the metamorphosis of *P. quadrilineatus* as in *T. jarbua.* Transforming larvae and juveniles of *P. quadrilineatus* were found distributed in the seagrass beds of Boongkong Bay and Makham Bay and also at Pakmeng Beach. Makham Bay showed the high density of transforming larvae and juveniles during the dry season. The morphological changes allow them to fed in the water column and on the bottom substrate. Teeth are mainly villiform type. Small teeth forming in rows on the upper and lower jaw in all stages. The number of rows of villiform teeth increased as the fish grow. The gill rakers were long with 39-45 gill rakers. The stomach of Y-shape with the number of pyloric caeca varied from 13-15 pieces. Juveniles of *P. quadrilineatus* fed on harpacticoid copepods in the bottom substrate and small percentage of *Lucifer* spp. and calanoid copepods. Adults of *P. quadrilineatus* moved offshore area for breeding and spawning ground. Adults of *P. quadrilineatus* fed mainly on large benthic animals and fish scales. The ratio of intestinal length/standard length showed that this species was classified as specialist carnivorous fish corresponded to Davis *et al.* (2013). They reported that the ratio of intestine length/standard length of the carnivorous fish range from 0.9 to 1.02. Amphipods, bivalves, hermit crabs and polychaetes were the main prey items in all size of adult of *P. quadrilineatus* (Figure 4.10). The proportion of fish scales in the diet increased with size. Their villiform teeth were used in crushing the hard shells and exoskeletons of the invertebrate preys.

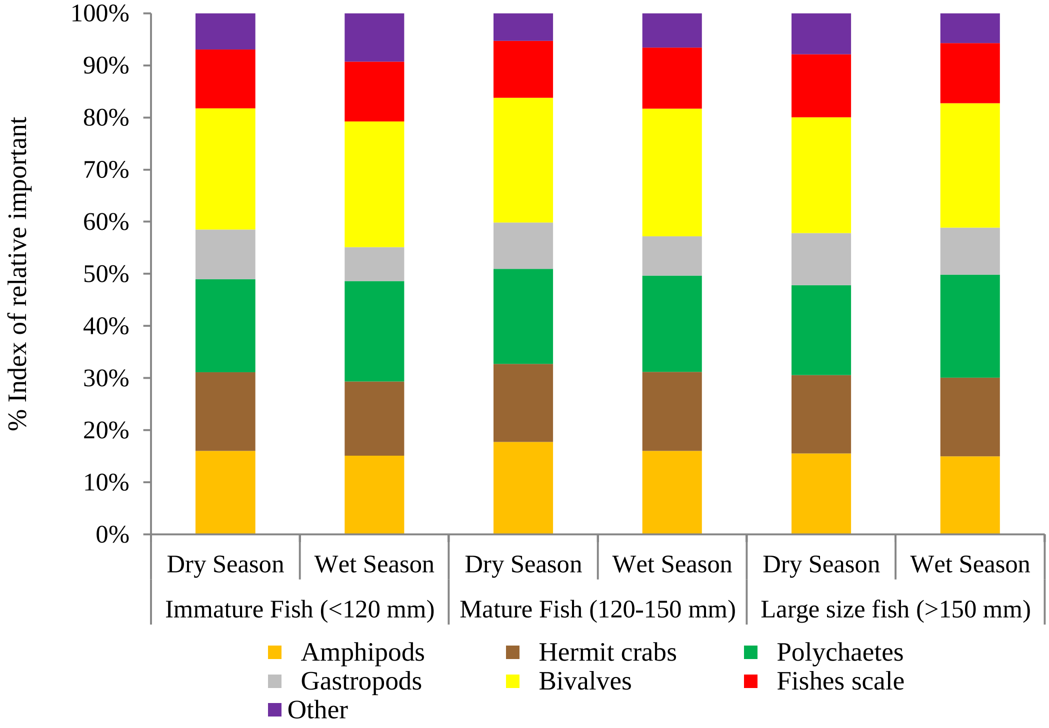


Figure 4.10 Diet composition in adult of *Pelates quadrilineatus* (n = 150) from the coastal area of Trang Province.

Diet breaths of *P. quadrilineatus* increased as the fish grow. The diet breadth indicated that this species was specialist consumers with diet dominated by few prey items as found in *T. jarbua* (Table 4.16).

Table 4.16 Diet breadths in *Pelates quadrilineatus* (n = 694) of different developmental stages and seasons from the coastal area of Trang Province

Season	**Stage**	**% of food in stomach**	**No of prey categories**	**Diet breadth**
Dry	Preflexion	75.00	1	0.00
	Flexion	83.33	1	0.00
	Postflexion	83.33	1	0.00
	Transforming	61.79	2	0.00
	Juvenile	66.98	3	0.07
	Adult	49.26	10	0.54
Wet	Preflexion	75.00	1	0.00
	Flexion	83.33	1	0.00
	Postflexion	87.50	1	0.00
	Transforming	58.75	2	0.00
	Juvenile	56.71	6	0.03
	Adult	74.36	11	0.52

The prey items chosen by *P. quadrilineatus* were based on the nutritional value and energy gained following the optimal foraging theory (Elliott *et al.*, 2002; Gerking, 1994). This factors limited main prey items in each stage. Larval stage fed mainly on calanoid copepods base on their size and abundance. Juvenile *P. quadrilineatus* fed on harpacticoid copepods on the bottom substrate and also on *Lucifer* spp. in the water column. Adult stage fed mainly on bivalves, polychaetes and hermit crabs. They choose to fed on large preys but sedentary and slow-moving preys. These benthos in particular bivalves and polychaetes were in high density in their habitat. Lepidophagy increased with growth to complement the energy gained required.

4. Food Partitioning in The Two Terapontid Fishes, *Terapon jarbua* and *Pelates quadrilineatus*

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 segregation fish species in community. Food partitioning is the partitioning of food by two or more species or age 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. Food partitioning may be result in different feeding habitats or different food sources in the same habitat. On the other hand, differences in feeding structure morphology and time of feeding may also be the outcome of partitioning. The result of food partitioning may be alternative process in reducing competition for fish sharing the same feeding ground (Blaber, 1997). Ontogenetic niche shift is one of the important process in niche partitioning with the shift of resource during development. The ontogenetic niche shift were often detected as clear shifts in diet or habitat use with increasing body size. The ultimate objective of dietary change with growth is to maximize energy intake, enhance growth rate and minimize the risk of predation in competing for food with larger predators (Brown, 1985). The study revealed that the two terapontid fish, *T. jarbua* and *P. quadrilineatus* shared the same feeding habit of predominantly specialist carnivorous fish throughout the different stages in the life cycle. Ontogenetic dietary shifts are the prominent features in these two terapontid fishes as previously reported by several studies. The cluster analysis, based on the dietary overlap among species, developmental stage and season confirmed the ontogenetic dietary shifts. Four trophic guilds were categorized at the level of 60% similarity as in Figure 4.11.

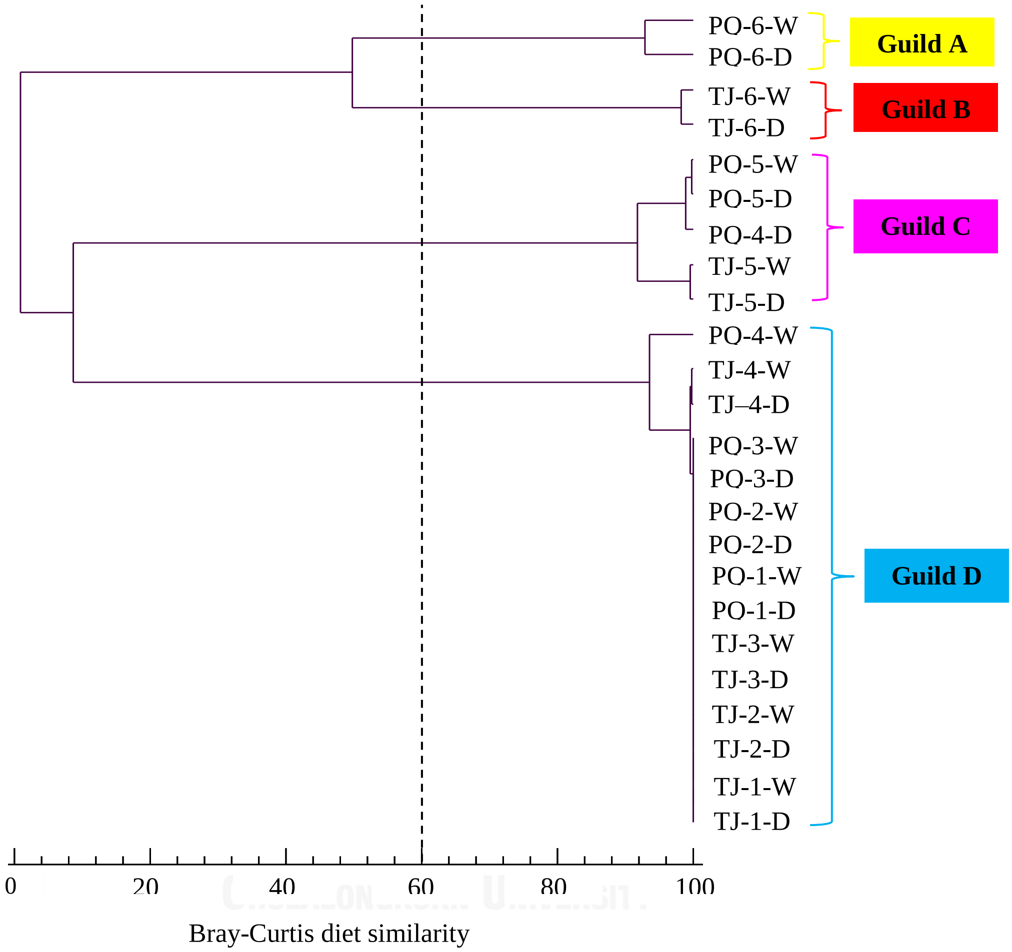


Figure 4.11 Dendrogram constructed based on dietary overlap data and mean percentage volume of food items (%V) for each fish group.Trophic guilds are identified as: A, large benthic feeder; B, fish and fish scale feeder; C, harpacticoid copepods feeder; D, calanoid copepods feeder. Species names are coded according to genus and species initials: TJ, *T. jarbua* and PQ, *P. quadrilineatus*. Developmental stage codes follow species name: 1, Preflexion larvae; 2, flexion larvae; 3, postflexion larvae; 4, transforming larvae; 5, juvenile; 6, adult. Season codes follow developmental stage: D, dry season; W, wet season.

Guild A, large benthic feeders consisted of the adult *P. quadrilineatus*, both in the wet season and dry season. Amphipods, bivalves, hermit crabs and polychaetes were the main prey items in all size of adult *P. quadrilineatus* ranging from immature fish (<120 mm), mature fish (120-150 mm) and large size fish (>150 mm); **Guild B, fish and fish scale feeders** comprised the adult *T. jarbua* in both the wet and dry season. The percentage of fish prey mainly juvenile fishes and fish scales increased with growth; **Guild C, harpacticoid copepods feeders** comprised of the juveniles *T. jarbua* both the wet and dry season, the transforming larvae of *P. quadrilineatus* in the dry season, and the juvenile *P. quadrilineatus* both in the wet and dry season. Juvenile *T. jarbua* fed mainly on harpacticoid copepods in the bottom substrate. Large benthos such as crabs, hermit crabs, shrimps, fishes and fish scales were the important prey item in the stomach content of the juveniles. Transforming larvae of *P. quadrilineatus* fed on both harpacticoid copepods and calanoid copepods in the same proportion during the dry season. Juvenile *P. quadrilineatus* fed mainly on harpacticoid copepods. Zooplankton, *Lucifer* sp. and calanoid copepods made up in small percentage in the diet of juveniles; **Guild D, calanoid copepods feeder** representing most of the larvae of both species, *T. jarbua* and *P. quadrilineatus*, ranging from preflexion, flexion, postflexion and transforming larvae except for the transforming larvae of *P. quadrilineatus* in the dry season.

Whenever food partitioning is detected, food overlap is found. Degree of food overlap varied according to the abundance of resources and the range of resource utilization. Food overlap often occurs in the habitat where foods are in high abundant. Discrete food/prey items usually found in the lower food abundance. Changes in size of feeding structure through the ontogeny also associated with the change in foraging behavior and habitat use thus altering the range of exploitable prey items (Brown, 1985).

The relationship of the feeding structure morphology and feeding habitat supported that *T. jarbua* and *P. quadrilineatus* display an ontogenetic dietary shift and food partitioning. Planktonic larvae of *T. jarbua* and *P. quadrilineatus* utilized the same area of offshore area as the feeding ground. Larval stage in *T. jarbua* fed mainly on small zooplank and insect larvae suchas calanoid copepods, cycopoid copepods, fish larvae and diptera larvae (Davis *et al.*, 2011; Kanou *et al.*, 2004). At these stage fish begin feeding on calanoid copepods in the water column. The feeding ability of fish in this 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 *et al.*, 2005). Size selection is important in larval feeding. The size of the two terapontid fishes in the planktonic stage were in the same range. The mouth gape in *T. jarbua* ranged from 0.13-0.78 mm while the mouth gape in *P. quadrilineatus* ranged from 0.13-0.75 mm. The size of calanoid copepods chosen by the planktonic larvae was within the range of prey size to mouth part of 0.48-0.52 indicating the maximum energy gained. Their teeth are mainly villiform type and very small. They are able to fed on small planktons (Lagler *et al.*, 1962; Norman & Greenwood, 1975). In addition, their swimming ability was classified as poor. The development of their mouth and other structure such as, jaw, body, eye, and fin was found to be incomplete. The planktonic larval phase of the two terapontid fishes were competing for the same major food items, calanoid copepods. The availability of food items has a greater effect on their feeding ability than feeding structure in this growth stage. Therefore, planktonic larvae choose to fed mainly on calanoid copepods which was the dominant zooplankton in the coastal area of Trang Province. The selection of prey items, based on nutrition values and energy gained followed the optimal foraging theory (Elliott *et al.*, 2002; Gerking, 1994). High density prey as calanoid copepods was chosen in order to reduce the handling time, searching time and energy spent for capturing their preys. Zooplankton provided the nutritive food source for the planktonic larvae. In addition, this study found that the larvae of both species demonstrated the temporal resource partitioning to live offshore area. Due to the differences in the spawning period, *T. jarbua* spawned twice a year during April to June and September to October, while *P. quadrilineatus* spawned once a year with short definite period from November to December. The different in spawning period of adult fish help to reduce competition between their offspring.

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 and nursery ground. High density of transforming larvae and juveniles of *T. jarbua* were found in the natural coastal mangrove coastal swamps. Juvenile *T. jarbua* shifted to fed mainly larger zooplankton, *Acetes* spp. and zoobenthos such as amphipods, polychates, crabs, bivalves and shrimps/prawns. Juvenile fish and organic matter also made up small portions in the stomach content of juveniles (Hajisamae *et al.*, 2003; Hajisamae *et al.*, 2006; Kulbicki *et al.*, 2005; Monkolprasit & Pramong, 1994; L. Rao & Prasad, 2002; Whitfield, 1985). Transforming larvae and juveniles of *P. quadrilineatus* were distributed in the natural seagrass beds. Juvenile stage of *P. quadrilineatus* fed mainly on zooplankton, copepod larvae and calanoid copepods, and zoobenthos, harpacticoid copepods, gammarid amphipods and bivalves. Organic matter also found in the stomach content of the juveniles (Hajisamae & Ibrahim, 2008; Horinouchi *et al.*, 2012; Lugendo *et al.*, 2006). Living in different habitat types in both species during metamorphosis help to reduce the interspecific competition between them. The feeding ecology of both species in these stage reveals that transforming larvae of both species still fed mainly on calanoid copepods. Transforming larvae in both *T. jarbua* and *P. quadrilineatus* fed in the water column and near bottom. The transforming larvae fed on the larger size calanoid copepods. However, the importance of calanoid copepods was decreasing. Transforming larvae of *T. jarbua* fed more on larger prey namely amphipods, *Lucifer* spp., harpacticoid copepods and crab zoea. The transforming larvae of *P. quadrilineatus* fed mainly on calanoid copepods and harpacticoid copepods.

Juveniles of *T. jarbua* shift to fed mainly on small benthic animals (harpacticoid copepods), large benthic animals (crabs) and fish scales. Juveniles of *P. quadrilineatus* shift to fed mainly on small benthic animals (harpacticoid copepods) and large zooplankter (*Lucifer* spp.). Juveniles 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* partitioned their food sources between the transforming larvae and juvenile stage. Jaw and mouth size increased in juveniles. This helped to facilitate the increase in the prey size (Olsen *et al.*, 1999). Juvenile of *T. jarbua* have conical teeth on the upper and lower jaw allow them to bite on their preys.

In the adult stage of both species, they use the offshore areas as feeding, breeding and spawning grounds. Food consumption in adult stages follows the same pattern of optimal foraging theory. The dietary shift allowed maximize energy intake.

Changes in size of feeding structures have been associated with changes in foraging behavior, thus altering the range of exploitable prey items (Brown, 1985). Adult of *T. jarbua* and *P. quadrilineatus* can easily capture the moving preys such as fish or fed on benthic prey. Adult of *T. jarbua* fed mainly on fish and fish scales while adult stage of *P. quadrilineatus* fed mainly on large benthic animal, amphipods, bivalves, hermit crabs and polychaetes. The proportion of fish scales in the diet increased with growth in both species. This provided nutrition value for fish. Food partitioning strategy as different feeding habits in the adult of *T. jarbua* and *P. quadrilineatus* helped to reduced interspecific competition.

Widespread existence of ontogenetic shifts in diet and habitats and the consequences of such shifts served as the important process in the resource utilization and partition in the coexisting species. Differences in body size is another means by which species avoid direct overlap in resource use and size-selective predation. The competing species using the same habitat must differ in size by a factor of 2 in weight in order for them to coexist (Werner & Gilliam, 1984). In this study, the body weight of *T. jarbua* and *P. quadrilineatus* as in Table 4.17 ranged from 1.2-4.2 which allow them to coexist and partition their resources.

Table 4.17 Ratio of body weight of *Terapon jarbua* to body weight of *Pelates quadrilineatus*.

Species	**Body weight (g)**		
	Transforming Larvae	**Juveniles**	**Adults**
Terapon jarbua	0.16±0.11	3.24±4.59	145.64±70.18
Pelates quadrilineatus	0.13±0.10	0.77±0.53	45.96±9.71
Terapon jarbua : *Pelates quadrilineatus*	1.2 : 1	4.2 : 1	2.9 : 1

E. Conclusion

This study has demonstrated the ontogenetic dietary shifts in two terapontid fish. The main prey items of *T. jarbua* larvae, juvenile and adult changed from small planktonic animals, benthic animals to fish and fish scale, respectively. The main prey items of *P. quadrilineatus* larvae, juvenile and adult shifted from small planktonic animals, small benthic animals to large benthic animals, respectively. Changes in the diet were related to the development of feeding structure and feeding habits based on the optimal foraging theory. In larval stage, they chose to fed on small and abundant prey items suitable for their mouth gapes in order to reduce energy and handling time. As fishes grow, they chose to fed on larger prey items. Larger preys provided more nutrition and maximum net gain energy for growth than small preys despite the increased handling time. The development of feeding structure (i.e. mouth, teeth, jaw, gill raker and intestine) is the important factor allowing the ontogenetic dietary shift from small to larger sized preys. In addition, ontogenetic dietary shifts found in the two terapontid fishes, *T. jarbua* and *P. quadrilineatus* help them to coexist and reduce competition by partitioning food sources between developmental stages and species.

CHAPTER 5

SYNTHESIS AND RECOMMENDATION

A. Research Synthesis

Terapon jarbua and *Pelates quadrilineatus* are widely distributed along the coastal areas of the tropical, especially in the Indo-West Pacific region (Blaber, 2000; Leis & Rennis, 1983). These two fish species were also found to coexist in the coastal area of Trang Province on the southwest coast of Thailand. Coastal area of Trang Province is importance for both species not only as habitat but also as spawning ground, nursing ground and feeding ground (Paterson & Whitfield, 2000). Positions of coexcisting species in a community were usually described along differences resource dimension of an ecological space (Piet, 1998). Resource partitioning was an important mechanism for competing species to coexist. Habitats and food types are the two major resource partitioning usually observed. The clarification of resource utilization patterns has been a topic of considerable interest in the coexisting species. Ontogenetic niche shifts is one of the important processes in resource partitioning. The shift of resources during development corresponed to changes in morphology (Hjelm *et al.*, 2003; Persson *et al.*, 1998). The ontogenetic niche shifts were often detected as clear shifts in diet or habitat use with increasing body size (Wainwright, 1988). Ontogenetic niche shift in fishes was due to the functional morphological limitation on prey choice and habitat use (Osenberg *et al.*, 1992; Wainwright, 1988).

The study on the development pattern and definding length at juvenile of *T. jarbua* and *P. quadrilineatus* is essential in understanding their ontogenetic niche shift. Morphological development in fish involves the process of growth and adaptation. The changes of morphology can also lead to structural defects affecting the development and feeding in fishes (Koumoundouros *et al.*, 1999). Associating with these changes, there is a sudden shift in diet or habitat (Osenberg *et al.*, 1992). The changes in morphometric characters, meristic characters and pigmentation in the two terapontid fishes can divided into 6 development stages as follows: (1) preflexion larvae, (2) flexion larvae, (3) postflexion larvae, (4) transforming larvae, (5) juvenile and (6) adult. The length at juvenile of *T. jarbua* and *P. quadrilineatus* were 23.16 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 on the adaptation for coexistent species. *Terapon jarbua* and *P. quadrilineatus* showed the relationship between morphological changes in body depth, mouth, jaw, eyes and fin 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 eyes and pigment pattern were important to the feeding performance and predator avoidance. Changes of these characters allow them to coexist in the same area.

Distribution patterns of fishes in different stages as well as the gonadal maturation can be use to identify the habitat utilization as spawning and nursing area of these two coexisting species. The spawning area is defined by the area with high abundant of mature adults and fish larvae while the nursery area is where high abundance of juvenile fish is found (Ellis *et al.*, 2012). Coastal area of Trang Province provided the important habitat use as spawning ground and nursery ground. *Terapon jarbua* and *P. quadrilineatus* showed the clear habitat utilization between developmental stages. Preflexion larvae, flexion larvae and postflexion larvae of both species live offshore area. The transforming larvae and juveniles move to shallow nearshore habitats. However, they have demonstrated habitat partitioning during metamorphosis. They choose different habitat type for nursery area. *Terapon jarbua* were found in the coastal swamps while *P. quadrilineatus* were found in seagrass beds. The complexity of microhabitat structure in coastal swamps and seagrass beds provided the refuges from predators. Mature adult of both species live offshore area as spawning and breeding ground. Adult of *T. jarbua* and *P. quadrilineatus* were broadcast spawners with pelagic eggs in the offshore area. Although both species shared the same breeding and spawning ground, but they showed the temporal resource partitioning due to the differences in their size at first sexual maturity, fecundity and egg size and spawning season. Different spawning period is one of the important strategy for coexisting species to reduce food and habitat competition between their offspring. The gonad investigation indicated that *T. jarbua* had two peak of spawning period were April to June and September to October. *Pelates quadrilineatus* spawned once a year with short definite period from November to December. The transforming larvae and juveniles of *T. jarbua* and *P. quadrilineatus* showed the resource partitioning in term of spatial and temporal habitat utilization.

The study on the feeding structure morphology and stomach content analysis in these two terapontid fishes can be use to identify the main diets and feeding area in each stage. Dietary shift in fish help gain maximum energy for growth and also to reduce food competition. Many fishes show distinct ontogenetic changes in feeding habits and prey selection (Davis *et al.*, 2011; Davis *et al.*, 2012a; Horinouchi *et al.*, 2012; Jobling, 1995; Kanou *et al.*, 2004; McCormick, 1998; Wainwright, 1988). Difference 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, 1997). *Terapon jarbua* and *P. quadrilineatus* in coastal area of Trang Province are specialist carnivorous fish. These fish utilized the coastal area as feeding ground. Ontogenetic dietary shift were prominent in both species. Larval stage in *T. jarbua* consumed predominantly zooplankton, such as calanoid copepods. The importance of calanoid copepod decreased significantly in the diet of juveniles. Juvenile stage of *T. jarbua* shift to feed on small benthic animal such as harpacticoid copepods. Adult stage of *T. jarbua* feed mainly on fish and fish scales. The major prey items in the larval stage of *P. quadrilineatus* were calanoid copepods and harpacticoid copepods. Harpacticoid copepods became more important in the diet of juvenile stage of *P. quadrilineatus*. Adult stage of *P. quadrilineatus* feed mainly on large benthic animals, amphipods, bivalves, hermit crabs and polychaetes. The ontogenetic differences in feeding habits have resulted from acquiring high energy diets to accompany growth as well as the development of feeding structure such as mouth gape, mouth diameter, jaw length, stomach, number of pyloric caeca and intestinal length. This allows the change in diet from small planktonic animal to increasing levels of larger sized preys. Food partitioning in the two terapontid fishes *T. jarbua* and *P. quadrilineatus* was evidenced. Food partitioning was shown by differences in feeding habits and development of feeding structure in each developmental stage. This was the strategy to reduce competition among coexisting species.

Terapon jarbua and *P. quadrilineatus* demonstrated the resource utilization in the coastal area of Trang Province by partitioning the three dimensions of resources namely trophic, spatial and temporal to coexist as in Figure 5.1.

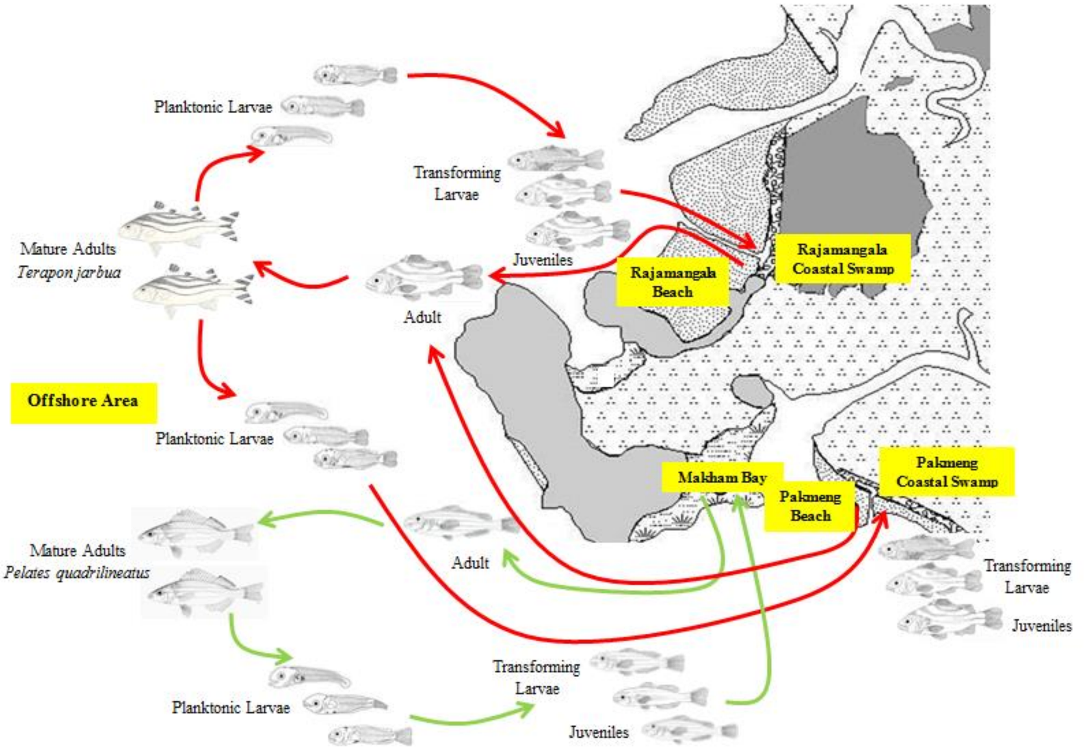


Figure 5.1 Habitat utilization of *Terapon jarbua* and *Pelates quadrilineatus* from the coastal area of Trang Province.

It can be concluded that *T. jarbua* and *P. quadrilineatus* were both marine migrant species that utilized and partitioned resource in the coastal area of Trang Province for spawning ground, nursing ground and feeding ground. Planktonic larvae stage (preflexion, flexion and postflexion) and mature adults of the two terapontid fishes were found distributed in offshore area. This indicated that the offshore area is the spawning and feeding ground of adult fish and feeding ground for the planktonic larvae. *Terapon jarbua* had two peaks of spawning periods during April to June and September to October. *Pelates quadrilineatus* had only a short discrete period for spawning from November to December. The different in spawning period lead to temporal resource partitioning in planktonic larvae stage of both species. The planktonic larvae of both species feed mainly on the calanoid copepods which was the dominant zooplankton. Feeding in larval stage depended on the abundance of food and prey size. Zooplankton provide the nutrition food source. Adults of *T. jarbua* and *P. quadrilineatus* showed the different dietary habits indicating trophic partitioning. Adult stage of *T. jarbua* feed mainly on fish and fish scales while adult stage of *P. quadrilineatus* feed mainly on large benthic animals, amphipods, bivalves, hermit crabs and polychaetes.

Transforming larvae and juveniles of two terapontid fishes migrated to the estuarine area to seek for specific habitats. Both species displayed habitat shift and showed preference for different habitat type for nursery and feeding ground. Transforming larvae and juveniles of *T. jarbua* were found distributed in the coastal swamp habitat of Rajamangala and Pakmeng coastal swamp. Transforming larvae and juveniles of *P. quadrilineatus* were distributed in the seagrass beds of Boonkong bay and Makham bay. The different in nursery and feeding ground lead to spatial resource partitioning in transforming larvae and juveniles stage between both species. Moreover, the transforming larvae and juveniles in both species also showed the different in trophic dimension in resource utilization. Transforming larval stage of *T. jarbua* and *P. quadrilineatus* consumed predominantly on calanoid copepods. Larger preys such as harpacticoid copepods, amphipods and *Lucifer* spp. were also found in the diets of transforming larvae *T. jarbua*. The transforming larvae of *P. quadrilineatus* were found to feed on harpacticoid copepods in the same proportion as the calanoid copepods. Juveniles of *T. jarbua* shifted to feed mainly in the bottom substrate on benthos. Harpacticoid copepods, crabs and fish scales were the major prey items in the juveniles of *T. jarbua*. Juveniles of *P. quadrilineatus* shifted to feed mainly on harpacticoid copepods and large zooplankton, *Lucifer* spp.

B. Fishery management of *Terapon jarbua* and *Pelates quadrilineatus*

Adults, *T. jarbua* and *P. quadrilineatus* are sympatric offshore area but their transforming larvae and juveniles are estuarine dependent. The benefits of having the estuarine phase in the life cycle of the two terapontid fishes were the reduction in predation, more food and shelters. This study support the relationship of high densities of fish and the dependency of certain species on coastal habitats such as mangrove coastal swamps, seagrass beds and mudflats. The dependence of certain fish species on these coastal habitats were relate to (1) reduce predation linked with turbidity and depth; (2) increased food supply for post larvae and juveniles ; and (3) shelters for post-larvae and juveniles (Blaber, 2000; Hajisamae *et al.*, 2003; Hajisamae & Ibrahim, 2008; Hajisamae *et al.*, 2006; Horinouchi, 2007; Horinouchi *et al.*, 2012; Horinouchi *et al.*, 2009; Ikejima *et al.*, 2003; Laegdsgaard & Johnson, 2001; Lugendo *et al.*, 2007; Robertson & Blaber, 1993; Tongnunui *et al.*, 2002). Sikao bay may not be the feeding ground for adults terapontid fishes due to the degree of mangrove and seagrass beds inundation and the size of the coastal habitats. However the mangrove coastal swamps and the seagrass beds in Sikao Bay played the important role of nursery and feeding ground for the post larvae and juveniles of *T. jarbua* and *P. quadrilineatus.* The degree to which size and productivity of coastal and offshore area fisheries in the tropics is dependent on the extent of healthy nursery and feeding area in the coastal areas (Blaber, 2000). From the fishery survey revealed the drastic decline of *T. jarbua* and *P. quadrilineatus* in the coastal area of Trang

Province in term of size and abundance. Two major issues on the declining populations of the two terapontid fishes should be addressed. Overfishing, resulting from more fishers, more efficient fishing gears as well as the ineffective management control, is the major underlining factors. Habitat loss or degradation in the coastal area leads to loss of nursery habitat and increased industrial and sewage pollution from anthropogenic input.

In order to sustain the populations of the two terapontid fishes, *T. jarbua* and *P. quadrilineatus*, the target species and habitats require several measures for primary protection (Alverson, 1994) (Figure 5.2). Effective management controls to lessen the problem of overfishing require accurate scientific data on stock status, biology and socio-economics of the fishery. This is the major problems in fishery management world wide (Blaber, 2000). In term of protection of target species, it is necessary to ban or put size restriction fishing on particular stages of a species life-cycle that are especially vulnerable to capture, or are critical to overall production. The mature adult of *T. jarbua* and *P. quadrilineatus* should be protected as the potential parental stock. The protection of mature adult can be carried out by the imposition of size restriction and fishing season/period. This study indicated the size at first sexual maturity of female and male of *T. jarbua* was 156.92 mm and 153.77 mm, respectively while the size at first sexual maturity of female and male *P. quadrilineatus* was 120.31 mm and 124.02 mm, respectively. Therefore, to increasing their population and increasing their opportunity for reproduction have to limit size of both species for capture. The appropriate size for captured *T. jarbua* should be larger than 160 mm. Those that are smaller than 160 mm should be release, to allow them to reproduce. As for

P. quadrilineatus, the immature size fish of less than 130 mm. should be released. Size at capture that should be allow for *P. quadrilineatus* should be over 130 mm.

Terapon jarbua had two peaks of spawning period were April to June and September to October. *P. quadrilineatus* had the spawning period from November to December. The imposition of fishing season should consider both the scientific data to support the fishery stock and the socio-economic data to support the income and welfare of the fisherman. Therefore the time restriction for fishing of the two terapontid fishes during the spawning period should be the southwest monsoon or the wet season. Fishing efforts in the coastal area of Trang Province usually ceased during the monsoon season. Imposing the fishing season during this time would have minimal impacts on the fishermen income and welfare.

There is the need for the declaration of the nursing grounds as the protection or conservation zone. There might be a need to protect areas where juveniles are particularly abundant. If fishing is allowed on these nursing grounds, it might be affected by fishing on juveniles and lead to undesirably high levels of mortality on juveniles. *Terapon jarbua* and *P. quadrilineatus* from this study choose different habitat types for nursery area. *Terapon jarbua* were found in the coastal mangrove coastal swamp while *P. quadrilineatus* were found in seagrass beds. Differences in habitat types lead to difference strategies for the protection of nursery areas. Coastal mangrove coastal swamps, served as the nursery area of *T. jarbua*, is the small and noncommercial fishery area. A permanent area closure as conservation zone may be easy and appropriate. On the other hand, seagrass beds which served as nursery areas of *P. quadrilineatus*, is one of the large and commercial fishery area. The biodiversity and abundance of commercial fishery resources in seagrass beds lead to excessive fishing. As choosing only one important seagrass beds as the conservation zone may be possible. Makham bay is the seagrass bed area that is recommended for conservation measures. Restricted fishing access in particular season can be carried out. Alternatively, the closure of the nursing area during the highest abundance of juvenile *P. quadrilineatus* may be sufficient. This study revealed juveniles of *P. quadrilineatus* was the highest abundance on January. In addition, the rehabilitation of the coastal mangrove coastal swamps and seagrass beds also is important to sustain the juvenile fish population. In this study found the difference in abundance of juveniles *P. quadrilineatus* between seagrass beds in Makham bay and Boonkong bay. *Halophila ovalis* (71.47%) were dominant species in seagrass bed of Boonkong Bay. On other hand, *Cymodocea serrulata* (87.0%) were dominant species in seagrass bed of Makham Bay (Kongwatmai, 2015). The tall leaf and complex morphology of *C. serrulata* is suitable for avoidance of predators and use for shelters than *H. ovalis*. Therefore, seagrass (*C. serrulata*) plantation also support *P. quadrilineatus* in term of food and shelter. Mangrove reforestation in the Sikao Bay should be carried out to enhance the plant diversity and growth. Diversed suitable mangrove plants should be introduced in the area other than *R. apiculata*. The planting technique should be carried out in the mosaic patterns, filling the open spaces in the degraded forest. The releasing of *T. jarbua* and *P. quadrilineatus* juveniles into their nursery ground to enhance fishery production should be incorporated into the habitat rehabilitation program. Figure 5.2 outlined the fishery management of *T. jarbua* and *P. quadrilineatus* from the coastal area of Trang Province.

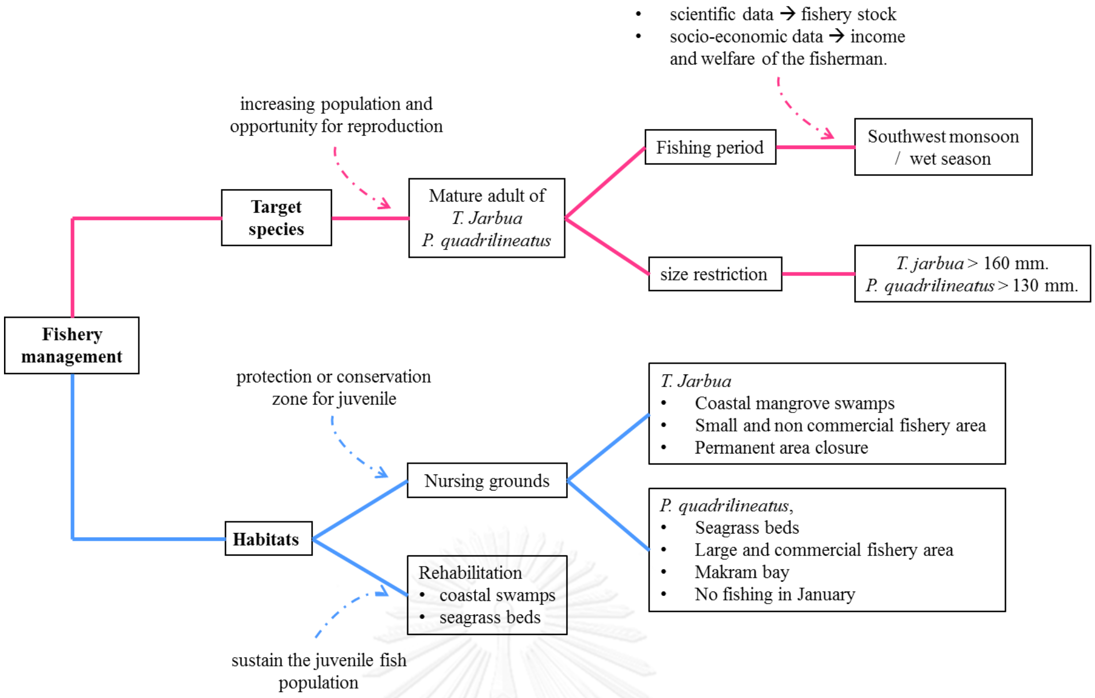


Figure 5.2 Fishery management of *Terapon jarbua* and *Pelates quadrilineatus* from the coastal area of Trang Province.

C. Promoting *Terapon jarbua* and *Pelates quadrilineatus* as Aquaculture Species

Terapon jarbua and *P. quadrilineatus* has long been recognized as one of the economically important fish in Thailand in particular in the coastal provinces. The sale price of both species for household consumption is about 50-70 baht/kg. In addition, *T. jarbua* is one of the ornamental fish. *Terapon jarbua* of the size 3-4 inch cost 150-180 baht/individual. Ornamental fish is one of the important items among the various types of commercially important fishes marketed nationally and internationally and are popularly known as aquarium fishes (Rao *et al.*, 2013). Vidthayanon and Premcharoen (2002) also identify *T. jarbua* as popular aquarium fish in Thailand because of their unique characteristics such as body color. However, the culture of both terapontid fishes is limited. Terapontid fish has demonstrated several outstanding attributes for culture especially *T. jarbua*. They are highly tolerant of the environmental changes in particular salinity and turbidity. They are wide salinity tolerance, between 0-72 ppt (Whitfield, 1990) and are high turbidity tolerance, between <10-80 NTU (Cyrus & Blaber, 1987). The ability to adjust in a different environment is a major factor contributing to *T. jarbua* able to survive in diversed ecosystem. *Terapon jarbua* should be promoted as aquaculture species as the supplementary income for the coastal communities. The success culture of this fish, not only provide the alternative supply for market but also provide information on the reproductive biology of this species, which is critical to understanding the response of natural stocks to anthropogenic effect. Several data on the reproductive and feeding ecology can be used in the *T. jarbua* culture. The breeding and spawning ground of *T. jarbua* is in deep water offshore area. Size at first sexual maturity of female and male of *T. jarbua* was 156.92 mm and 153.77 mm, respectively. *Terapon jarbua* had two peak of spawning period were April to June and September to October. During culture, the mature males and females in size larger 153 mm should be used in the artificial spawning to increase reproductive rate and their offspring. After hatching, the adequate and suitable food for larvae should be prepared. High abundance of calanoid copepods should be the suitable food source for larvae. Fish will feed mainly on calanoid copepods until they become juveniles (23.16 mm) when shift to feed mainly on harpacticoid copepods. During the juvenile stage, the juveniles can be released in coastal mangrove coastal swamps as the nursery ground in order to increase the juvenile stock in nature. The morphology during juvenile stages have been well developed. The ability to swim and search for food were in full capacity.

Lived fish and fish meat are recommend for food source in the culture of adult fish. They feed by pulling scales off other living fish and able to digest the scales, which have a relatively high calorific value should be provide growth rate for adult fish (Blaber, 2000).

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APPENDIX

VITA

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