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Male Reproductive Biology of Mud Crab *Scylla olivacea* in a Tropical Mangrove Swamps

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ABSTRACT

Mud crabs of the genus *Scylla* are commercially important and conspicuous crustaceans provide basic source of income for coastal fishing communities throughout the Indo-Pacific region. The reproductive traits and size at sexual maturity of the male mud crab *Scylla olivacea* were investigated in Pak Phanang mangrove swamps, Thailand. Samples were taken seven times from the local middlemen mud crab traders during June 2006 to January 2008. Gonad development was determined based on histological appearance that was classified into three stages: (1) Immature (Spermatogonia) (2) Maturing (Spermatocytes) and (3) Mature (Spermatids and Spermatozoa). Among the sample population, the highest 56% was under gonad development stage I, whereas mature stage III was only 18%. The size at first maturity was estimated by the external allometric growth and histological observation of gonad. The size at which 50% of individuals attain sexual maturity was estimated by the two mathematical models such as probit analysis and logistic curve. The mean size at first sexual maturity and 50% maturation of male *S. olivacea* were 87 and 103 mm Internal Carapace Width (ICW) which revealed that 80% of individuals were immature. The present result suggested that the minimum legal size of male mud crab capture should be >100 mm ICW.

Key words: Gonad development, maturity size, *Scylla olivacea,* mangroves

INTRODUCTION

The reproductive information on a commercially exploited species is crucial for understanding its population dynamics which is fundamental for developing an effective management models. The minimum legal size for catch is one of the popular management regimes in mud crab fisheries with the purpose of protecting the reproductive potential of resource stock (Goshima *et al*., 2000; Conan *et al*., 2001). The restriction of the harvest to males has been considered to have relatively little impact on the reproductive output of the stock. However, concern for the effects of reduction of males has prompted recently which triggered out the importance of research on male maturity (Van Engel, 1990; Knuckey, 1996; Castilho *et al*., 2008).

In male crustaceans, there are three common methods to determine maturity. First is the morphometric method; using change of allometric relationship between sizes of body parts (e.g., Somerton, 1980; Somerton and Macintosh, 1983; Haefner, 1990; Knuckey, 1996; Viau *et al*., 2006). Second is the histological (gonad) method; histological examination of the gonad to see if spermatozoa are present in the testes and/orvas deferentia (Hartnoll, 1969; Haefner, 1990;

Robertson and Kruger, 1994; Leal *et al*., 2008). The third is functional maturity; usually refereed as to ability of mate successfully (Conan and Comeau, 1986). In fact, the main criteria for determining functional maturity in crustaceans are the presence of scars on the sternum or forward walking legs which are produced by abrasion with the female during the precopulatory embrace (Prasad and Neelakantan, 1990; Robertson and Kruger, 1994; Knuckey, 1996). Another commonly considered criterion for the maturity estimation is the presence of spermatozoids or spermatophores in the testes or vas deferentia as well as copulation marks (Hartnoll, 1969; Krouse, 1973; Haefner, 1990; Viau *et al*., 2006).

However, the mating scar in male could not find less than 125 mm internal carapace width (ICW) (Knuckey, 1996) and completely absence in smaller individuals than 115 mm (Robertson and Kruger 1994). In the present study, it is noticed that no sample crab exceeds the size of 130 mm ICW and very few were >115 mm ICW. On the other hand, no prominent scars were found in the samples. Moreover, maturity in male crabs is not easily determined from external characteristics (Robertson and Kruger, 1994). Thus present study was concentrate on the histological observation of vas deferens/testes to establish the maturity status of wild male mud crab population.

The male reproductive biology and maturity size of mud crab (*Scylla* sp.) has been established in Australia (Knuckey, 1996) and in South Africa (Hill, 1975; Robertson and Kruger 1994). There were very few study have been taken in Asian countries like, Ong (1966) from Malaysia and Lavina (1980) from Philippines. However, there was no subsequent study. Moreover, all the previous studies focused on *S. serrata* and no study on other *Scylla* species particularly on *S. olivacea* which is the most commercial important species in Asian region. Thus paucity of information existed on the male reproductive biology of *S. olivacea* in Asian countries was the trigger to conduct the present study to provide detailed reproductive information of male mud crab.

MATERIALS AND METHODS

Study site: The Pak Phanang estuary is located in Nakhon Si Thamarat province, on the east coast of southern Thailand (8°9'-11' N and 100°9'-18' E). The eastern half of the estuary is fringed by a wide mangrove forest (approximately 9,000 hectares) which is associated with an extensive mud flat (1-3 km wide) that emerges at low tide (Fig. 1). There are three distinct seasons: Hot-dry season (February-May), rainy season (June-September) and the highest rainfall period of monsoon season (October-January) with water temperature ranging 25-36°C (Thampanya *et al*., 2002). Average annual rainfall ranges about 2000-3000 mm and salinity fluctuates between 1-25 ppt (Boromthanarath *et al*., 1991). Crab fishing is conducted throughout the year within mangrove channels as well as associated channels connected to the bay. In the present study, survey was focused on the communities within the mangrove (Fig. 1).

Sampling: Male *S. olivacea* were collected during June 2006 to January 2008 from the local mud crab middle trades which were contributed 49% of the total sample population. In the laboratory, 84 male crabs were examined which did not include any morphological anomalies. The following measurements of body size were taken with a digital caliper to the nearest 0.1 mm: Internal Crapace Wdth (ICW), Lower Paddle Width (LPW), Propodus Length (PL) and Chela Height (CH) of left cheliped.

Histological study: Tissue from the middle vas deferens/testes from each male was dissected and preserved in Davidson's fixation for further histological examination. The tissues were dehydrated

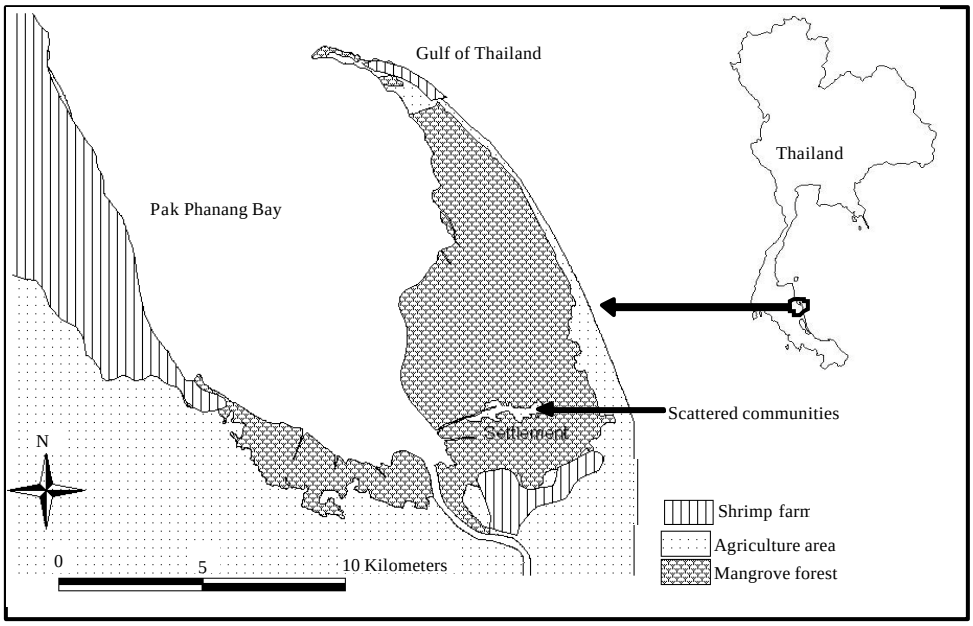

Fig. 1: Study area, Pak Phanang mangrove ecosystem and the sampling place (scattered communities) inside of the mangrove

in ascending ethanol concentrations from 70 to 100%, transferred to Lemosol (Wako Pure Chemical Industries, Osaka, Japan) and embedded in paraffin. The tissues were sectioned to 5 μm and stained with Mayer's Hematoxylin-Eosin (HE). The histological stage of development was determined by making reference to those of other crustaceans (Comeau and Conan, 1992; De Lestang *et al*., 2003; Mura *et al*., 2005; Viau *et al*., 2006). The development stages of the gonad were determined by the macroscopic appearance based on the formation of spermatocytes and presence of spermatozoa.

Estimation of size at maturity: The middle vas deferentia were used for the histological study and maturity estimation. Sexual maturity was classified with the visibility of vas deferentia and the presence of spermatophores within their lumina. The relative frequencies of each stage of sexual maturity in the samples were analyzed to describe the reproductive cycle of males.

The size at first maturity was estimated by using three methods that are described following:

- Allometric increments proportional to ICW; the allometric growth increments of CH, PL and LPW were plotted against the increments of ICW and existence of the flexion point was investigated and treated at the size of first maturation in male crab
- The minimum size at maturity recorded through histological studies of the male mud crabs (>70 mm ICW)
- Chela Height (CH)/internal carapace width (ICW) index is another method which calculated as the divides of CH by ICW. The samples were categorized to two groups by the critical point of CH/ICW and the histological developments of the gonad were compared between two groups. Regression analysis was performed to determine the relation of Chela Height (CH) with internal carapace width (ICW). A significant level of $p>0.05$ was considered

Two mathematical models (1 and 2) were used to estimate the size at which 50% of the individuals had reached sexual maturity that are described below.

- **Model 1:** Probit analysis (Robertson and Kruger 1994) was performed using abdomen-width data using probit analysis to determine the size at which 50% of females reach sexual maturity (ICW_{50}). The data from sample crabs were allocated to 10-mm ICW size classes. The proportion (p) of mature male in each size class was calculated according to Mikhaylyuk (1985) that was converted to logit (logit (p) = ln (p/1-p)). The logistic data were then converted to probit (P) = p + 5. Finally, the probit data were plotted against ICW and a regression line was fitted to the data points. The ICW value equivalent to probit 5 was extrapolated as the median size at sexual maturity
- **Model 2:** Ratio of matured individuals determined by the histological observation in each size class was fitted to the sigmoid curve (see the formula below)

Where, p_{ICW} is the proportion of mature to immature crabs in each ICW class (10 mm interval) and M_1 and M_2 are the equation coefficients. The best fit curve was estimated by the using of Kaleida graph software (Kaleida graph, version 3.6) (KoolKalya *et al*., 2006).

$$P_{ICW} = \frac{1}{1 + e^{(M1 - M2\,ICW)}}$$

RESULTS

Allometric growth: The male Chela Height (CH), Propodus Length (PL) and Lower Paddle Width (LPW) were scattered plotted against the Internal Carapace Width (ICW) and found that the relative growth of these secondary sexual allometric parts were increased sharply at the size of 87 mm ICW (Fig. 2). Figure 3 shows the relation between CH/ICW and ICW that represent a clear allometrical growth of CH/ICW with the increments of boy size.

Gonad development: A total of 84 male crabs ≥70 mm ICW) were assessed to observe the ovarian condition. The progress of ovarian maturation was classified into three stages based on external appearance of ovary and the development stage of the most advanced oocytes with the histological

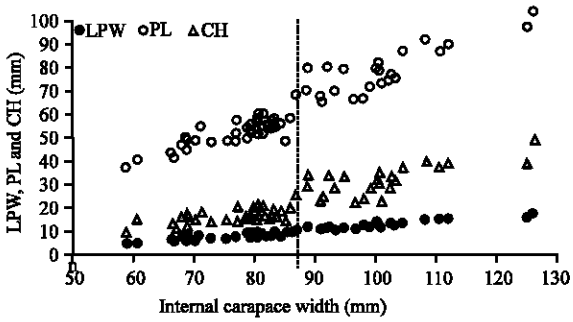

Fig. 2: Scatter plotted of chela height (mm), propodus length (PL) and lower paddle width (LPW) against internal carapace width (mm) of male *Scylla olivacea* collected from Pak Phanang mangrove swamps, Thailand. Vertical dash line represents the probable discontinuity increments (growth at maturity) with observed body parts at the ICW of 87.34 mm

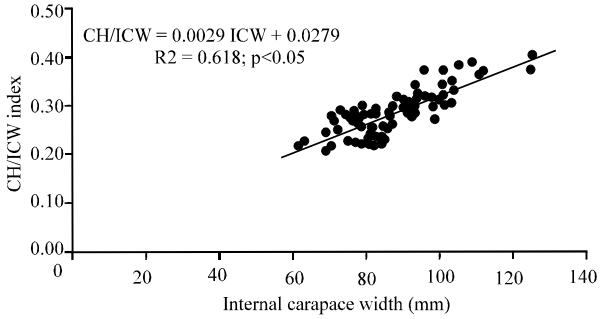

Fig. 3: The relationship of CH/ICW values regarding body size of male *Scylla olivacea* collected at Pak Phanang mangrove swamps during June 2006 to January 2008. The critical CH/ICW values estimated to be 0.31 at the body size of 90 mm ICW

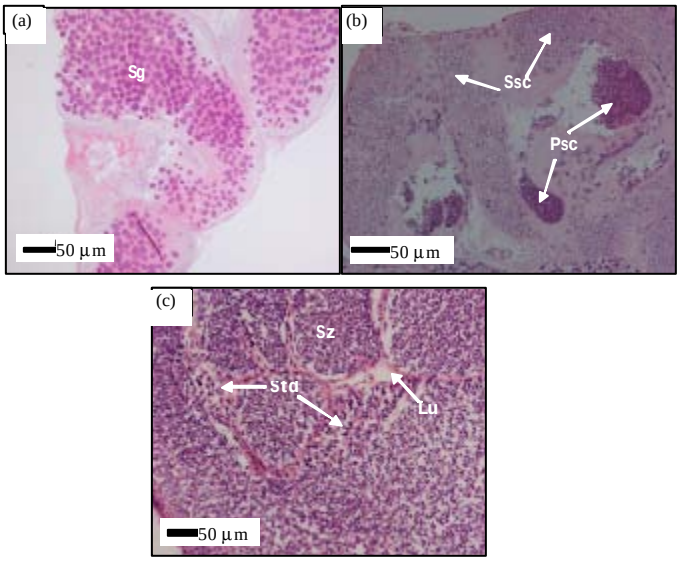

Fig. 4(a-c): Histological sections of Vas deference in *Scylla olivacea*. (a): Immature (Spermatogonia), (b): Maturing (Spermatocytes) and (c): Mature (Spermatids and Spermatozoa). Sg, spermatogonia; Psc, primary spermatocyte; Ssc, secondary spermatocyte; Sz, spermatozoa; Std, spermatid; Lu, lumen

observation (Table 1, Fig. 4). The histological examination showed that among the sample population, the highest 56% was under gonad development stage I whereas only 18% was belong to the mature stage III (Table 1). The smallest mature male and largest immature male were recorded 84 mm ICW and 102 mm ICW, respectively.

The immature stage (stage I) was represented by gonad with spermatogonia and primary spermatocytes (Fig. 4a). The maturing stage (stage II) was characterized with the containing of secondary spermatocytes as predominately, but with the presence of primary spermatocytes in few (Fig. 4b). The mature stage was defined as the dominancy of spermatozoa with the presence of spermatids (Fig. 4c).

The size distribution of stage I, II and III ranged from 60-97 mm, 80-101 mm and 84-123 mm ICW, respectively. No spent males were registered during the study period. In the present study, sexually mature male were defined with the gonad stage of III as the presence of spermatozoa.

Table 1: Stages of physiological sexual maturity of male *Scylla olivacea* and their composition in respective stage

Stage	Characteristics	Remarks	% of individuals
I	Testes not visible to the naked eye; vas deferens resemble translucent filaments; presence of spermatogonia	Immature	56
II	Small testes and thin vas deferentia; formation of primary and secondary spermatocytes	Maturing	26
III	Testes swollen, opaque and white; vas deferens swollen andpink; containing spermatophores	Mature	18

Table 2: Proportion of male chela height (CH) and internal carapace width (ICW) of *Scylla olivacea* with reflecting the different stages of gonadal development

	Percentage of gonad development		
	Immature		Mature
Range of CH/ICW	Stage I	Stage 2	Stage 3
0.21-0.25	77.8	22.0	20
0.26-0.30	68.4	21.1	10.5
0.31-0.35	0	18.2	82.8
0.36-0.40	0	12.5	87.5

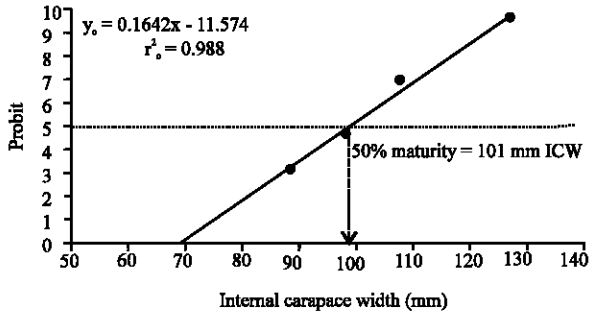

Fig. 5: Percentage maturity, after histological observation, plotted on a probit scale against internal carapace width to obtain the size at M_{50} (the point at which 50% of the male crabs are mature) of *Scylla olivacea* from Pak Phanang mangrove swamps, Thailand.

Relation between allometric growth and maturation: A significant relationship was observed between CH/ICW and carapace width ($R^2 = 0.618$, $p<0.05$) (Fig. 3). Table 2 shows the assemblage of the CH/ICW index relating to stages of the gonad development. The CH/ICW values ranging from 0.21 to 0.30 were completely belongs to stage I-II, indicating the immature male. On the contrary, majority of the individuals were stage III in 0.31-0.40 class in and no individual was in stage I within mentioned ranged. Thus, the critical values of CH/ICW for maturation were estimated to be 0.31 in *S. olivacea*.

Estimation of size at 50% maturity: Probit analysis of the abdomen-width data resulted in an M_{50} value of ICW 101 mm (Fig. 5). This value represents the body size at which 50% of the males are assumed to reach sexual maturity. In another model, the logistic curve fitting with the equation

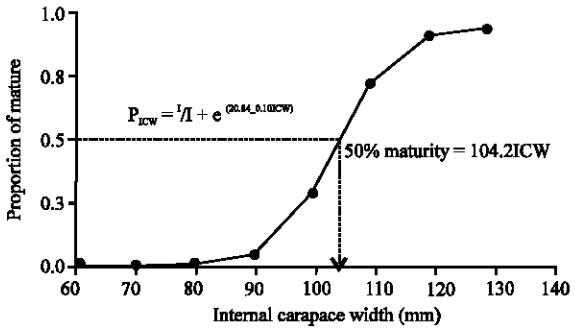

Fig. 6: Logistic fitted curve to the proportion of mature *Scylla olivacea* males in Pak Phanang mangrove swamps at each internal carapace width class (size class = 10 mm)

of Koolkalya *et al.* (2006) it is noticed that 50% of individuals attained sexual maturity at the size of about 104 mm (Fig. 6). So, the mean size of the above two mathematical analysis indicate that 50% individuals reached sexual maturity in 103 mm ICW in the Pak Phanang mangrove swamps.

DISCUSSION

Possibility of external morphological observation for maturity: In the present study there were no clear mating scars noticed and hence the estimate of functional maturity is vague. Knuckey (1996) found less than a third of all adult crabs are scarred and pointed out that there would be no evidence that every mated crabs developed scars and mating scars lost during molt. Thus the absence of scars does not necessarily mean that a crab has never mated. In the present study, the size-distribution ranged 60-130 mm ICW and 98% of individuals were less than 110 mm ICW. Whereas, 125 mm ICW was the minimum size recorded of scarred crabs in Australia (Knuckey, 1996). Though Perrine (1978) noted that the majority of males in Ponape only mate after they have attained a size of 138 mm ICW, smaller scarred crabs noticed in Asia (Ong, 1966). Thus, it is questionable to adopt the absence of the mating scars as the evidence of the virginity of males.

On the other hand, crabs can produce spermatozoa without mating (Conan and Comeau, 1986; Robertson and Kruger, 1994). Several authors have regarded the presence of spermatophores as indication of functional maturity (Hartnoll, 1969; Paul, 1992), although this relationship is debated in other species where morphological development seems to be an important determinant of functional maturity (Comeau and Conan, 1992; Sainte-Marie *et al.*, 1995; Knuckey, 1996). Thus, in the present study, maturity estimation of male mud crab was tried with the pattern of allometric relationship as well as presence of spermatozoa.

Although all allometric variables showed discontinuity in relative growth associated with sexual maturity, propodus length and chela height showed a clear sharply increment in its relative growth. Although, the ratio of chela height to ICW is commonly used to identify maturity stages in male brachyurans (Hartnoll, 1974; Somerton, 1980; Knuckey, 1996), other parameters like PL, CH can also be used to indicate the sexual maturity of *S. olivacea*. This sexual character in present study also showed different growth rates before and after sexual maturity, therefore indicating the end of the immature phase and the beginning of the adult phase such as in major crustaceans (Hartnoll, 1978).

Gonad development: Histological examination on male gonad development is scare in case of crustacean and particularly on *Scylla* spp. Robertson and Kruger (1994) described the presence of spermatophores in Anterior Vas Deferens (AVD) in *S. serrata* but did not describe details on the development stages. Sainte-Marie and Sainte-Marie (1999) describe the formation and development of spermatophores in snow crab (*Chionoecetes oplilio*). Spermatophore formation has also been studied for a number of crustaceans using light microscopy, including the crab species; *Scylla serrata* (Uma and Subramoniam, 1979), *Callinectus sapidus* (Cronin, 1947; Johnson, 1980), *C. opilio* (Beninger *et al*., 1988), *Portunus pelagicus* (El-Sherief, 1991) and *Lithodes maja* (Tudge *et al*., 1998).

In the present study, three gonad development stages observed by histological microscopic observations and appear to be equivalent to those (De Lestang *et al*., 2003) in portunid crab (Viau *et al*., 2006) in anomuran crab and the first three of the five stages defined by (Leal *et al*., 2008) in stone crab. The stage I and II defined as the males with undifferentiated vas deferens and males with differentiated vas deferens but no spermatophores. The final stage characterized as males with prominent and convoluted vas deferens containing spermatophores. There was no spent or postovulatory stage in both studied species. Therefore it was not clear whether male crabs are multiple breeders or not which found in other crustacean (Leal *et al*., 2008).

However, as female mud crab showed continuous multiple breeds and they stored sperm at the first time of mating and used that for subsequent breeding (Robertson and Kruger, 1994; Onyango, 2002; Moser *et al*., 2005) male probably also have multiple breed patterns. In the gonad development stages, the rarity of stage III could be due to a short duration of existence and probably turned back to stage I.

Legal size for management: In fishery management, minimum legal size limit is usually determined based on size at maturity, allowing individuals to mate at least once after reaching maturity before they are large enough to harvest in order to protect reproductive potential of the stocks (Donaldson and Donaldson, 1992; Stevens *et al*., 1993).

The 50% maturity size is the common minimum legal size used in many open water mud crab fisheries but exclusively for female crab (Brown, 1993; Machintosh *et al*., 1993; Robertson and Kruger 1994; Overton and Macintosh, 2002). In addition (Overton and Macintosh, 2002) emphasized on the account of male in maturity estimation. In the present study, though maturity started at the size of about 90 mm ICW, the two mathematical models showed 50% maturity was 103 mm ICW. Although each method has its limitations and the small sample size in the present study, their close agreements in both aspects of maturity make the results credible. Thus, to conserve mature stock in Pak Phanang mangrove swamps, an effective minimum legal size of capture for male *S. olivacea* would be >100 mm ICW. The same size limit also proposed for the female *S. olivacea* in the same area (Islam *et al*., 2010) which indicates maturity size does not vary widely with the sexes of *S. olivacea*. Although, maturity size did not show much difference in sexes in *S. olivacea*, there could be in case of other species as the paucity of information. Thus, It is necessary to investigate reproductive traits and maturity size in both sexes of other *Scylla* species in the study area, because Overton and Macintosh (2002) suggested that the legal size of capture for mud crab should be species-specific due to difference in their maturity size.

CONCLUSION

The present study described details about the gonad development stages of male mud crab, *Scylla olivacea*. The study revealed that 80% of the captured population was under immature stage

which indicates the great threat to the sustainability of the population. Thus, present result suggested that the minimum legal size of male mud crab capture should be >100 mm ICW. For indication of more specific legal size limitation, it is needed to further research on the other co-existence *Scylla* species of the locality.

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REFERENCES

Beninger, P.G., R.W. Elner, T.P. Foyle and P.H. Odense, 1988. Functional anatomy of the male reproductive system and the female spermatheca in the snow crab *Chionoecetes opilio* (*O. fabricius*) (Decapoda, Majidae) and a hypothesis of fertilization. J. Crustacean Biol., 8: 322-332.

Boromthanarath, S., S. Cobb and V. Lee, 1991. Coastal management in Pak phanang: A historical perspective of the resources and Issues. Hat Yai, Thailand: Coastal Resources Institute, Prince of Songkla University, p: 16-21.

Brown, I.W., 1993. Mangrove Crabs. In: Nearshore Marine Resources of the South Pacific, Wright, A. and L. Hill (Eds.). International Centre for Ocean Development, Canada, pp: 609-642.

Castilho, G.G., A. Ostrensky, M.R. Pie and W.A. Boeger, 2008. Morphology and histology of the male reproductive system of the mangrove land crab *Ucides cordatus* (L.) (Crustacea, Brachyura, Ocypodidae). Acta Zool., 161: 157-161.

Comeau, M. and G.Y. Conan, 1992. Morphometry and gonad maturity of male snow crab *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci., 49: 2460-2468.

Conan, G.Y. and M. Comeau, 1986. Functional maturity and terminal molt of male snow crab, *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci., 43: 1710-1719.

Conan, G.Y., M. Comeau and M. Moriyasu, 2001. Are morphometrical approaches appropriate to establish size at maturity for male american lobster *Homarus mericanus*. J. Crustacean Biol., 21: 937-947.

Cronin, L.E., 1947. Anatomy and histology of the male reproductive system of *Callinectes sapidus* (Rathbun). J. Morphol., 81: 209-239.

De Lestang, S., N.G. Hall and I.C. Potter, 2003. Reproductive biology of the blue swimmer crab (*Portunus pelagicus*, Decapoda: Portunidae) in five bodies of water on the west coast of Australia. Fish B-Natl. Oceanic Atmos. Administration, 101: 745-757.

Donaldson, W.E. and W.K. Donaldson, 1992. A review of the history and justification for size limits in Alaskan king, tanner and snow crab fisheries. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fisheries Research Bulletin No. 92-02, pp: 1-33

El-Sherief, S.S., 1991. Fine structure of the sperm and spermatophores of *Portunus pelagicus* (L.) (Decapoda, Brachyura). Crustaceana, 61: 171-179.

Goshima, S., M. Kanazawa, K. Yoshino and S. Wada, 2000. Maturity in male stone crab *Hapalogaster dentate* (Anomura, Lithodidae) and its application for fishery management. J. Crustacean Biol., 20: 641-646.

Haefner, P.A., 1990. Morphometry and size at maturity of *Callinectes ornatus* (Brachyura, Portunidae) in Bermuda. Bull. Mar. Sci., 46: 272-286.

Hartnoll, R.G., 1969. Mating in the brachyura. Crustaceana, 16: 161-181.

Hartnoll, R.G., 1974. Variation in growth pattern between some secondary characters in crabs (Decapoda Brachyura). Crustaceana, 27: 131-136.

Hartnoll, R.G., 1978. The determination of relative growth in crustacea. Crustaceana, 34: 281-293.

Hill, B.J., 1975. Abundance, breeding and growth of the crab *Scylla serrata* in two South African estuaries. Mar. Biol., 32: 119-126.

Islam, M.S., K. Kodama and H. Kurokura, 2010. Ovarian development and size at maturity of the mud crab *Scylla olivacea* in Pak Phanang mangrove swamps, Thailand, Mar. Biol. Res., 4: 503-510.

Johnson, P.T., 1980. Histology of the Blue Crab, *Callinectes Sapidus*. A Model for the Decapoda. Praeger Publishers, CBS Educational and Professional Publishing, New York, USA., Pages: 440.

Knuckey, I.A., 1996. Maturity in male mud crabs, *Scylla serrata* and the use of mating scares as a functional indicator. J. Crustacean Biol., 16: 487-495.

Koolkalya, S., T. Thapanand, S. Tunkijjanujij, V. Havanont and T. Jutagate, 2006. Aspects in spawning biology and migration of the mud crab *Scylla olivacea* in the Andaman Sea, Thailand. Fish. Manage. Ecol., 13: 391-397.

Krouse, J.S., 1973. Maturity, sex ratio and size composition of the natural population of American lobster, *Homarus americanus*, along the maine coast. Fish B-Natl. Oceanic Atmos. Administration, 71: 165-173.

Lavina, A.F., 1980. Notes on the Biology and Aquaculture of *Scylla serrata* (F.) de Haan. In: Aquabusiness Project Development and Management, Diliman, U.P. and T. Iloilo (Eds.). Vol. 2. Department of Aquaculture, South-East Asian Fisheries Development Center, Philippines, pp: 1-19.

Leal, G.A., J.B. Dima, F.G. Dellatorre and P.J. Baron, 2008. Schedule of reproductive events and maturity at size of the patagonian stone crab, *Platyxanthus patagonicus* (Brachyura, Platyxanthidae). J. Crustacean Biol., 28: 262-269.

Machintosh, D.J., C. Thongkum, K. Swamy, C. Cheewasedtham and N. Paphavisit, 1993. Brood stock management and the potential to improve the exploitation of mangrove crabs, *Scylla serrata* (Forskal), through pond fattening in Ranong, Thailand. Aquacul. Res., 24: 261-269.

Mikhaylyuk, A.N., 1985. Use of probit analysis for studying the dependence of maturation on body length of fishes. J. Ichthyol., 25: 61-65.

Moser, S., D. Macintosh, S. Laoprasert and N. Tongdee, 2005. Population ecology of the mud crab *Scylla olivacea*: A study in the Ranong mangrove ecosystem, Thailand, with emphasis on juvenile recruitment and mortality. Fish. Res., 71: 27-41.

Mura, M., F. Orru and A. Cau, 2005. Size at sexual maturity of the spidder crab *Anamathia rissoana* (Decapoda: Majoidea) from the Sardinian Sea. J. Crustacean Biol., 25: 110-115.

Ong, K.S., 1966. Observations on the post-larval life history of *Scylla serrata* Forskal, reared in the laboratory. Malays. Agri. J., 45: 429-443.

Onyango, S.D., 2002. The breeding cycle of *Scylla serrata* (Forskal, 1755) at Ramisi River estuary, Kenya. Wetl. Ecol. Manag., 109: 257-263.

Overton, J.L. and D.J. Macintosh, 2002. Estimated size at sexual maturity for female mud crabs (genus *Scylla*) from two sympatric species within the Ban Don Bay, Thailand. J. Crust. Biol., 22: 790-797.

Paul, A.J., 1992. A review of size at maturity in male Tanner (*Chionoecetes bairdi*) and king (*Paralithodes camtschaticus*) crabs and the methods used to determine maturity. Am. Zool., 32: 534-540.

Perrine, D., 1978. The mangrove crab (*Scylla serrata*) on Ponape. Marine Resources Division, Ponape, East Caroline Islands, Trust Territory of the Pacific Islands.

Prasad, P.N. and B. Neelakantan, 1990. Size at maturity in the male crab *Scylla serrata* as determined by chela allometry and gonad condition. Fish. Tech., 27: 25-29.

Robertson, W.D. and A. Kruger, 1994. Size maturity, mating and spawning in the Portunid crab *Scylla serrata* (Forskal) in Natal, South Africa. Estuar. Coast. Shelf. Sci., 29: 185-200.

Sainte-Marie, B., S. Raymond and J.C. Brethes, 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura: Majidae). Can. J. Fish. Aquatic Sci., 52: 903-924.

Sainte-Marie, G. and B. Sainte-Marie, 1999. Reproductive products in the adult snow crab (*Chionoecetes opilio*). I. Observations on spermatogenesis and spermathophore formation in the vas deferens. Can. J. Zool., 77: 440-450.

Somerton, D.A. and R.A. Macintosh, 1983. The size at sexual maturity of the blue king crab, *Paralithodes platypus*, in Alaska. Fish. Bull. (US), 81: 621-628.

Somerton, D.A., 1980. A computer technique for estimating the size of sexual maturity in crabs. Can. J. Fish. Aquatic Sci., 37: 1488-1494.

Stevens, B.G., W.E. Donaldson, J.A. Haaga and J.E. Munk, 1993. Morphometry and maturity of paired Tannercrabs, *Chionoecetes bairdi*, from shallow- and deepwater environments. Can. J. Fish. Aquat. Sci., 50: 1504-1516.

Thampanya, U., J.E. Vermaat and C.M. Duarte, 2002. Colonization success of common Thai mangrove species as a function of shelter from water movement. Mar. Ecol. Prog. Ser., 237: 111-120.

Tudge, C.C., B.G.M. Jamieson, L. Sandberg and C. Erseus, 1998. Ultrastructure of the mature spermatozoon of the king crab *Lithodes maja* (Lithodidae, Anomura, Decapoda): Further confirmation of a lithodid-pagurid relationship. Invertebrate Biol., 117: 57-66.

Uma, K. and T. Subramoniam, 1979. Histochemical characteristics of spermatophore layers of *Scylla serrata* (Forskal) (Decapoda: Portunidae). Int. J. Inver. Rep. Dev., 1: 31-40.

Van Engel, W.A., 1990. Development of the reproductively functional form in the male blue crab, *Callinectes sapidus*. Bull. Mar. Sci., 46: 13-22.

Viau, V.E., L.S.L. Greco, G. Bond-Buckup and E.M. Rodriguez, 2006. Size at the onset of sexual maturity in the anomuran crab, *Aegla uruguayana* (Aeglidae). Acta Zool., 87: 253-264.