



Research article

Determination of selected parameters regarding reproductive biology of sand bubbler crab (*Dotilla intermedia* De Man, 1888) in Laem Son National Park, Prapas Beach, Thailand

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Abstract

The reproductive biology of the sand bubbler crab (*Dotilla intermedia* De Man, 1888) is important, and its reproductive pattern is of great importance for development of conservation plans and the management of natural stocks. Specimens of sand bubbler crab were collected from Prapas Beach in the Laem Son National Park, Ranong province, Thailand during July 2018 to June 2019 to determine the reproductive period and size at first maturity and fecundity. In total, 960 specimens (613 males and 347 females) were collected. The male specimens had a carapace width range of 1.30–4.50 mm (mean \pm SD, 3.26 ± 0.04 mm) and a body weight range of 0.0122–0.1340 g (0.0663 ± 0.0022 g), while the females had a carapace width range of 1.00–4.20 mm (2.74 ± 0.09 mm) and a body weight range of 0.0011–0.1300 g (0.0494 ± 0.0038 g). The sex ratio was 1:1 (male: female) in most months of the year based on a χ^2 test ($p > 0.05$). The carapace width at 50% maturity was 2.05 and 2.03 mm for males and females, respectively. Three gonad developmental stages could be identified in males and five stages in females. Both male and female stages of maturity could occur throughout the year.

Introduction

Southeast Asia is one of the world's biodiversity hotspots (Hughes, 2017). Located at its center, Thailand has an abundance of aquatic animals including at least 570 species of freshwater fish, 1,160 estuarine and seawater species, 30 deep-sea species and 1,538 species of marine shellfish, including crabs (Nabhitabhata et al., 2000). The sand bubbler crab (*Dotilla intermedia* De Man, 1888), which is important to the ecological system of the seashore, lives in sandy beaches and feeds on organic matter or detritus

by filtering the sand through its mouthparts, leaving behind balls of sand that disintegrate with the incoming high tide.

Reproduction of *D. intermedia* is an extremely important biological process to ensure the continuity of the species, and knowledge of the reproductive pattern is of great importance as this facilitates the establishment of conservation mechanisms and the management of natural stocks (Cobo and Fransozo, 2000). As in many species of brachyuran crabs, determining the reproductive period of *D. intermedia* is mainly based on the months when ovigerous females are abundant and when males are found to have gonads (Giese, 1959; Pillay and Ono, 1978; Choy, 1988; Sumpton, 1990). The determinants used for characterizing the population structure are sex ratio, size at

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first maturity and the fecundity, which also indicate the reproductive effort (Gregati and Negreiros-Fransozo, 2007). Biased primary sex ratios could have detrimental effects on the growth and persistence of local populations (Patino-Martinez et al., 2012). Size at first maturity is often used to determine changes in the form and size of the abdomen or carapace width in crabs; thus, knowledge of these distinguishing characters and size relationships in sexually mature individuals is of particular importance in the study of important marine species.

Crabs of the genus *Dotilla* are ecologically important members of the tropical sandy shore intertidal communities and are found on tropical shores and mudflats from East Africa and the Red Sea all the way eastward to Japan (Alcock, 1900), living at high densities on beaches with numbers that reach over 500 individuals/m² (Hails and Yaziz, 1982). *Dotilla* spp. construct simple burrows where they remain while the beach is submerged by seawater during high tide events. Importantly, the burrows provide a refuge from predators and environmental exposure such as heat irradiation and desiccation (Warner, 1977). Although several dotillid species, such as *Dotilla myctiroides* (Tweedie, 1950; Takeda et al., 1996; Bradshaw and Scoffin, 1999) and *D. fenestrata* (MacNae and Kalk, 1962; Hartnoll, 1973) have been extensively examined, there have been only a few studies on *D. intermedia*. Specifically, *D. intermedia* was recorded on sandy beaches in the Laem Son National Park, Thailand (Allen et al., 2011). Usually living in excavated burrows and emerging only during low tides (Wada, 1981), Dotillid crabs utilize their microhabitats, with the burrow areas mainly for mating and breeding, and the saturated water mainly for feeding and growth. Chen et al. (2019) reported the behavior of sand bubbler crab (*D. wichmanni*) in responding to environmental interference, where not only did the crabs show resilience to disturbance in its foraging behavior, but also increased a propensity for risk in that it was slower in initiating burrow retreat with each repeated disruption.

While collecting information about some biological aspects such as reproductive period is important, estimating the size at which the species reaches sexual maturity is also necessary to understand its biology and consequential conservation measures. To estimate this value, the total percentage of adults per size class should be used, but some studies have considered individuals with rudimentary gonads as immature (Araújo et al., 2012) even if such a gonadal stage could also be indicative of spent gonads (Keunecke et al., 2009). If at such a stage, the individuals are classed as immature, the size at which the species reaches maturity could be overestimated, undermining the protection measures for stocking. Likewise, using the size of the smallest ovigerous female as a parameter of maturity may also be contentious, since this technique could underestimate the size at maturity of males due to the differential growths between the males and females (Costa and Negreiros-Fransozo, 1998). Accurate knowledge of the reproductive biology of these beach-dependent crabs is important, not only for the conservation of the species, but also, indirectly, for the environment because the crabs help in structuring the local beach communities.

Information on the reproductive periodicity and reproductive period of *D. intermedia* on the Andaman coast is limited (Allen et al., 2010; Wisespongpan et al., 2017). Therefore, the current study aimed to determine the reproductive period, size at maturity, fecundity and sex ratios of *D. intermedia* as a basis for managing crab resources at Prapas Beach in the Laem Son National Park, Ranong province, Thailand.

Materials and Methods

Specimens collection

Specimens of *D. intermedia* were collected from July 2018 to June 2019 from Prapas Beach in the Laem Son National Park, Ranong province, Thailand. The beach area was divided into quadrats measuring 1 m × 1 m, from where the specimens were randomly collected. In total, 80 specimens were collected by hand each month by excavating the burrows and capturing the resident crabs from eight sampling stations (Table 1, Fig. 1).

Table 1 Locations of sampling stations

Station	Latitude	Longitude
1	9°39'44"N	98°39'19"E
2	9°38'97"N	98°39'12"E
3	9°22'83"N	98°23'64"E
4	9°28'86"N	98°23'54"E
5	9°22'47"N	98°23'46"E
6	9°22'31"N	98°23'44"E
7	9°21'16"N	98°23'45"E
8	9°21'58"N	98°23'44"E

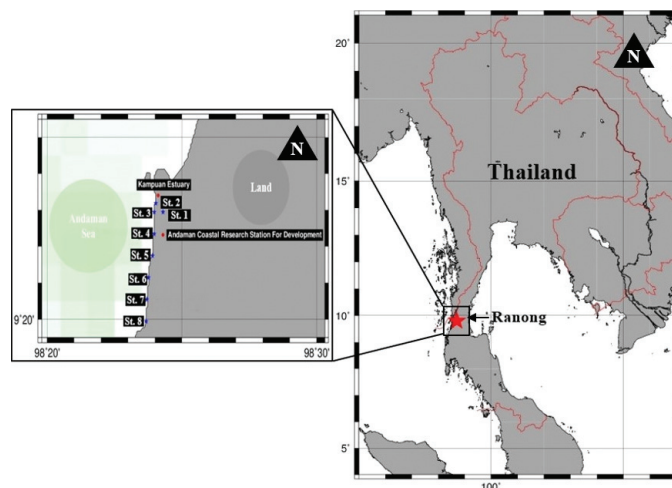


Fig. 1 Location of Laem Son National Park, Ranong province, Thailand, with insert showing Prapas Beach and locations of sampling sites (St.1–St.8)

Laboratory procedures and statistical analysis

The specimens of *D. intermedia* were transferred to the Laboratory of the Andaman Coastal Research Station for Development in Ranong province. After the sex was identified, the specimens were weighed to the nearest 0.0001 g using an electronic balance, and the carapace width (CW) was measured in millimeters. Male and female crabs were dissected to study the morphology of the reproductive tract to determine the stages of maturation, such as eggs in the gonads which were counted to determine the fecundity of the crab (Fig. 2).

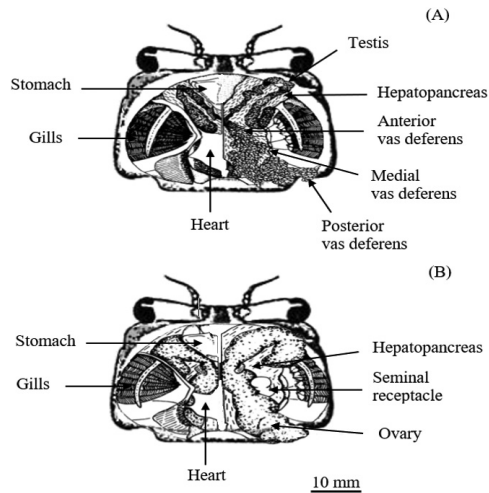


Fig. 2 Schematic diagrams of dorsal view of internal anatomy of *D. intermedia*: (A) male; (B) female

The male reproductive system was classified macroscopically based on the color and the size of the testis, and the female reproductive system was classified based on the color and the size of the ovary following Costa and Negreiros-Fransozo (1998).

The gonads and ovaries were weighed to the nearest 0.0001 g using an electronic balance. The number of eggs in each female crab was counted using a counting tray under a stereomicroscope.

Fecundity was estimated using a gravimetric method where a small sample of egg mass was weighed and then enumerated. Fecundity was calculated from the total weight of the egg mass (Kumar et al., 2003).

The sex ratio was determined for each month, and the total ratio for the whole year was calculated. Then, the sex ratio was tested against the expected 1:1 ratio using the heterogeneity χ^2 test (Zar, 1984) with significance tested at $p < 0.05$.

The size of *D. intermedia* at 50% maturity was estimated for males and females using curvilinear regression analysis, and calculated using equation 1 (Somerton, 1980):

$$P_w = \frac{1}{(1 + e^{(a+bw)})} \quad (1)$$

where P_w is the proportion of the number of all mature males and females to all males and females in the same length class, W is the carapace width in millimeters and a and b are correlation constants.

Results and Discussion

In total, 960 specimens of *D. intermedia* were collected during July 2018 to June 2019 from Prapas Beach in the Laem Son National Park, Ranong province, Thailand. The carapace width range of the 613 males was 1.30–4.50 (mean \pm SD = 3.26 ± 0.04 mm) and their body weight range was 0.0122–0.1340 g (0.0663 ± 0.0022), while the 347 females had a carapace width range of 1.00–4.20 mm (2.74 ± 0.09) and a body weight range of 0.0011–0.1300 g (0.0494 ± 0.0038).

Based on the gonad developmental stage of the sampled crabs, all males and females were mature all year round. The males had distinguishable peaks of maturity in February, May, June, November and December, while for the females it was in February, April, May, June, and August (Fig. 3).

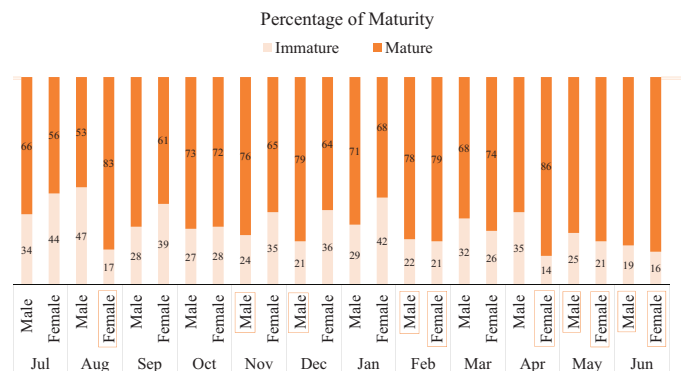


Fig. 3 Percentage of mature male and female *Dotilla intermedia*, where the dark color showed the mature stage of male and female sampled from July 2018 to June 2019

Studies on maturity periods in crustaceans can enhance understanding of the adaptive strategies and reproductive potential of the species and their relationship with the environment and other species. In the case of brachyurans, the breeding patterns are a result of a trade-off between growth and reproductive processes (Flores and Paula, 2010). According to Sastry (1983), determining the breeding period is a result of the complex interaction between endogenous and exogenous factors, allowing both inter- and intra-specific variations in the duration of the reproductive cycle. Peaks of higher breeding intensity may be associated with variations in the temperature, salinity, food availability, rainfall, photoperiod and solar radiation (Fransozo et al., 1999; Moura et al., 2000; Litulo, 2004). Generally, it has been observed that near the tropics, reproduction occurs year-round but seasonal patterns are also common, often dependent on variations in temperature and rainfall (Flores and Paula 2010). In addition, a prolonged reproduction period may indicate that individuals produce several broods during the breeding season or breed asynchronously. Such a breeding pattern can be applied to *D. intermedia*, since egg-bearing females were found throughout the year. Seasonal variability in the occurrence of ovigerous females as well as larval stages may

be related to the availability of food sources in the plankton (Sastry, 1983) and also as a strategy to avoid intraspecific competition for food (Morgan and Christy, 1995).

Sex ratio

The sex ratio of *D. intermedia* was skewed toward maleness in 9 of the 12 months (Table 2). However, the pooled data showed that the sex ratio was not different from 1:1 ($\chi^2_H < \chi^2_{0.05, nt-1}$, $p > 0.05$, degree of freedom = 11).

The sex ratio for optimal reproductive success should be 1:1 indicating an equal chance of a male and female meeting and having equal opportunities for mating (Hines et al., 2003). Studies on the sex ratio can be used to infer limitations in a population, with low ratios being cited as evidence for such limitations (Rondeau and Sainte-Marie, 2001; Hines et al., 2003; Sato and Goshima, 2006; Ogburn et al., 2014).

According to Emmerson (1994), the sex ratios of *Macrophthalmus grandidieri* and *Sesarma meinerti*, indicated there were significantly more males than females. Breeding periodicity may be controlled by a combination of factors, including latitude, temperature, food availability (both adult and larval) and intertidal zonation. Larval-interspecific competition in coexisting guilds (*Sesarma* and *Uca*) could be minimized by staggering the egg-bearing peaks, with breeding being delayed and more defined higher in the intertidal zone.

Gonadal development

Male

Males of *D. intermedia* were observed to have gonads that could be categorized into three developmental stages: stage I-immature, stage II-maturing and stage III-mature stage, where each stage was distinguished according to the size, color and internal morphological characteristics of the gonads (Fig. 4).

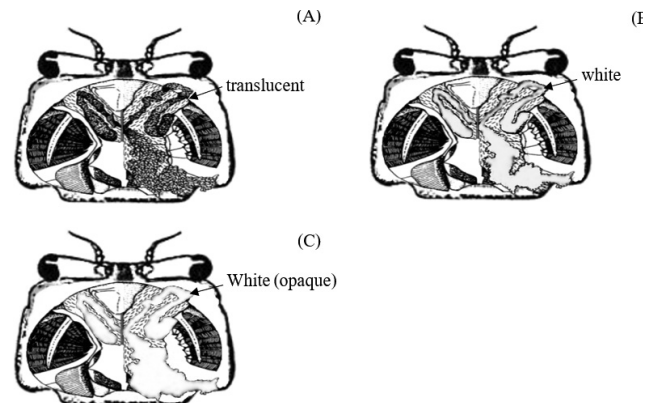


Fig. 4 Internal morphological view of gonads at various gonadal maturation stages of male *Dotilla intermedia*: (A) intermediate followed by stage I immature (translucent); (B) stage II maturing (white); (C) stage III mature (white in color but still opaque)

Immature (stage I) in male *D. intermedia* was defined as having a CW smaller than 2.00 ± 0.16 mm. In this stage, the gonad is small, translucent and on either side of the stomach; the testis and vas deferens are not clearly differentiated.

Maturing (stage II) was defined as the testis and vas deferens in a large tube and white in color are well developed and clearly differentiated; the CW is 2.50 ± 0.22 mm.

Mature (stage III) is usually found in male *D. intermedia* and was defined as CW greater than 2.50 ± 0.22 mm. In this stage, the testis shows further enlargement, while the vas deferens is swollen occupying the full body cavity. The anterior vas deferens is enlarged and milky to white in color but still opaque. The median vas deferens and posterior vas deferens and the ejaculatory duct are milky to white in color.

Table 2 Sex ratio of male and female *Dotilla intermedia* from July 2018 to June 2019

Month	Male	Female	Total	Ratio	χ^2	df
July	49	31	80	1:0.63	4.05*	1
August	46	34	80	1:0.73	1.80	1
September	53	27	80	1:0.59	8.45*	1
October	55	25	80	1:0.45	11.25*	1
November	46	34	80	1:0.73	1.80	1
December	48	32	80	1:0.66	3.20	1
January	53	27	80	1:0.50	8.45*	1
February	57	23	80	1:0.40	14.45*	1
March	54	26	80	1:0.48	9.80*	1
April	51	29	80	1:0.56	6.05*	1
May	49	31	80	1:0.63	4.05*	1
June	52	28	80	1:0.53	7.20*	1
TCs					80.55	12
Cst	613	347	960	1:0.56	73.70	1
χ^2_H					6.85	11

*significantly different from 1:1 at 95% confidence level; TCs = Total of χ^2 ; Cst = χ^2 of totals.

However, the sex cell development as observed in other crabs by Diesel (1991), such as *Cancer irroratus* for example, indicated five stages. Similarly, Krol et al. (1992) reported that *Callinectes amnicola* had five developmental stages, while in *Maja branchyadactyla* and *Portunus pelagicus*, there were four and three developmental stages, respectively (Haefner, 1976; Lestang et al., 2003; Lawal-Are, 2010).

Female

For the female *D. intermedia*, the ovary could be categorized into five developmental stages: stage I-immature, stage II-early maturing, stage III-late maturing, stage IV-ripe and stage V-spent, where the stages were distinguished according to the size, color and internal morphology of the ovaries (Fig. 5).

Immature (stage I) was defined as the ovary being small, translucent and occupying a small area of the body cavity; the CW is below 2.03 ± 0.24 mm.

Early maturing (stage II) was defined as ovary being larger than that in the immature stage, light orange in color and not extending into the hepatopancreas; the CW is 2.40 ± 0.20 mm.

Late maturing (stage III) was defined as the ovary being large, yellow to orange in color and extending into the hepatopancreas and in all spaces of the body cavity; the CW is larger than 2.40 ± 0.20 mm.

Ripe (stage IV) was defined as the ovary being large, yellow to deep orange in color, with the hepatopancreas completely hidden and the ovary fills up all space in the body cavity.

Spent (stage V) was defined as the ovary being small, thin-walled and translucent, where greatly reduced ovaries and not-spawned ovaries are visible throughout the fibrous connective tissues.

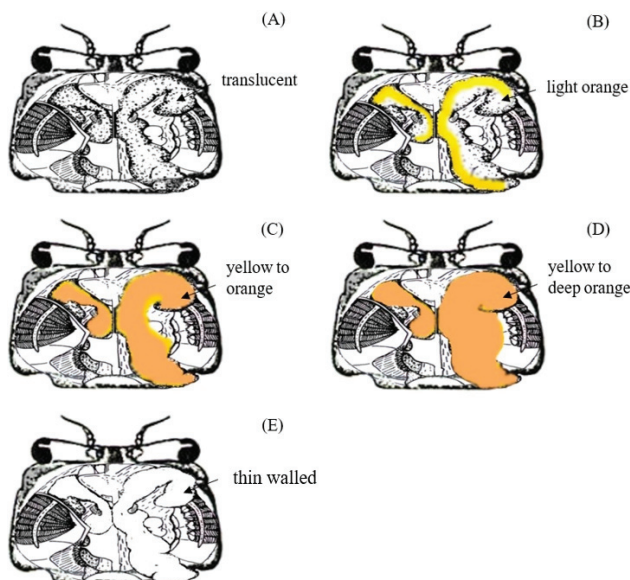


Fig. 5 Internal morphological view of ovaries at various ovarian maturation stages of female *Dotilla intermedia*: (A) stage I immature (translucent); (B) stage II early maturing (light orange); (C) stage III late maturing (yellow to orange); (D) stage IV ripe (yellow to deep orange); (E) stage V spent (ovary is small, thin-walled)

The morphological analysis of the ovaries of *D. intermedia* in the current study demonstrated that a gradual process of development of the ovaries confirmed their maturation into five developmental stages which was also observed by Sukumaran et al. (1986), where the stages of ovarian development were determined based on the morphological and histological characteristics of the ovary.

Size (carapace width) at first maturity

Male

The size at first maturity was estimated from the 613 male specimens, which were separated into those with either immature or mature gonadal stages. The minimum size at first maturity was 1.9 mm, the size at 50% maturity was 2.05 mm and in the 100% mature males, the size was 2.50 mm. The relationship between the proportion of mature males and the total number of males by carapace width expressed as a power regression and investigated using least square analysis was estimated as $p_w = \frac{1}{1+e^{(9.8680-4.8044w)}}$ (Fig. 6).

Female

In females, the size at first maturity was estimated from 347 specimens, which were separated into those with either immature or mature gonadal stages. The minimum size at first maturity was 1.9 mm, the size at 50% maturity was 2.03 mm and for 100% mature females, the size was 2.60 mm. The relationship between the proportion of mature females and the total number of females by carapace width expressed as a power regression and investigated using least square analysis was estimated as $p_w = \frac{1}{1+e^{(14.4415-7.1293w)}}$ (Fig. 7).

For many species of brachyurans, the size and weight of specimens indicating their sexual maturity can be evaluated by considering different criteria, including growth allometry, gonad developmental stages, presence of sperm, vestige eggs on the ovigerous areas and the presence of eggs (Flores and Paula, 2010). The consecutive changes observed during the gonadal development are important to estimate the physiological sexual maturity of the specimens (Muino, 2002).

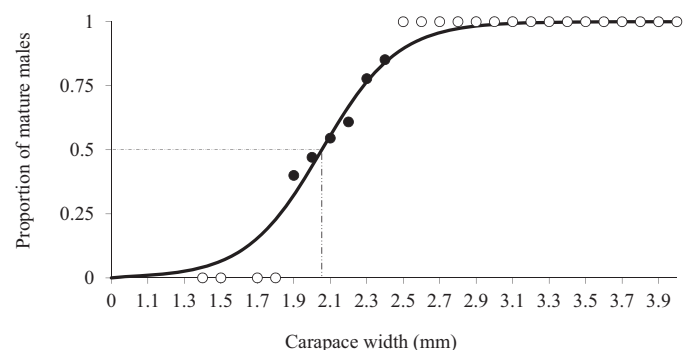


Fig. 6 Size at first maturity of male *Dotilla intermedia*, where open circles represent proportion of mature males for each size and filled circles represent data used in the regression analysis

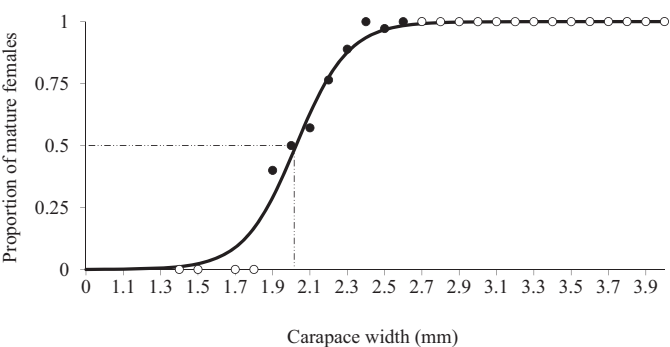


Fig. 7 Size at first maturity of female *Dotilla intermedia*, where open circles represent proportion of mature females for each size and filled circles represent data used in the regression analysis

Fecundity

The fecundity and carapace width of female *Dotilla intermedia* measured in each month are shown in Table 3.

In general, the fecundity of brachyuran crabs and the weight of females, as the main determinants of fecundity (Erdman and Blake, 1988), were substantially related to the carapace widths of female crabs. Litulo (2005) reported that larger females have the potential to produce more eggs than the smaller ones. For many species of brachyurans, the size and weight of crabs that are sexually matured can be evaluated considering different criteria, including growth allometry, gonad developmental stages, presence of sperm, vestige eggs on the ovigerous areas and the presence of eggs, as reported by Shields (1991).

In conclusion, the sex ratio of the sampled *D. intermedia* was skewed toward maleness in 9 of 12 months although the pooled data showed a sex ratio of almost 1:1. The carapace width at 50% maturity was 2.05 mm and 2.03 mm for males and females, respectively. The developmental stage of the gonads indicated three stages in males and five stages in females. Males and females were mature throughout the year. The fecundity of females was not high because *D. intermedia* is a small crab with only a small abdomen to carry eggs.

Table 3 Carapace width and fecundity of female *Dotilla intermedia* measured monthly from July 2018 to June 2019

Month	Carapace width (mm) (mean ± SD)	Fecundity (Fe) (mean ± SD)
Jul	2.77 ± 0.19	145.89 ± 72.84
Aug	2.76 ± 0.24	221.61 ± 122.24
Sep	2.74 ± 0.16	191.42 ± 84.40
Oct	2.82 ± 0.20	138.31 ± 66.40
Nov	2.77 ± 0.16	160.08 ± 95.91
Dec	2.85 ± 0.25	127.00 ± 57.93
Jan	2.74 ± 0.17	179.96 ± 79.37
Feb	2.77 ± 0.19	164.61 ± 86.98
Mar	2.78 ± 0.22	145.67 ± 72.50
Apr	2.88 ± 0.22	242.29 ± 122.15
May	2.85 ± 0.25	193.66 ± 94.60
Jun	2.70 ± 0.08	225.39 ± 125.59

Conflict of Interest

The authors declare that there are no conflicts of interest.

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References

Alcock, A. 1900. Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa, or Grapsoidea. J. Asiat. Soc. Bengal. 69: 279–456.

Allen, C.J., Clark, P.F., Paterson, G.L.J., Hawkins, L.E., Aryuthaka, C. 2011. New record of *Dotilla intermedia* (Brachyura: Ocypodidae) from Thailand. Mar. Biodivers. Rec. 4: e11. doi: 10.1017/S1755267211000091

Allen, C.J., Paterson, G.L.J., Hawkins, L.E., Hauton, C., Clark, P.F., Aryuthaka, C. 2010. Zonation on sandy tropical beaches: A case study using *Dotilla intermedia* (Brachyura: Ocypodidae). Mar. Ecol. Prog. Ser. 408: 97–107. doi: 10.3354/meps08565

Araújo, M.S., Negromonte, A.O., Barreto, A.V., Castiglioni, D.S. 2012. Sexual maturity of the swimming crab *Callinectes danae* (Crustacea: Portunidae) at the Santa Cruz Channel, a tropical coastal environment. J. Mar. Biol. Assoc. UK. 92: 287–293. doi.org/10.1017/S0025315411001135

Bradshaw, C., Scoffin, T.P. 1999. Factors limiting the distribution and activity patterns of the soldier crab *Dotilla myctiroides* in Phuket, South Thailand. Mar. Biol. 135: 83–87. doi.org/10.1007/s002270050604

Chen, P.J., Su, T.L., Lim, S.S.L. 2019. To hide or to feed: an evaluation of personality traits in the sand bubbler crab, *Dotilla wichmanni*, when responding to environmental interference. Behav. Processes. 164: 123–132. doi: 10.1016/j.beproc.2019.05.002

Choy, S.C. 1988. Reproductive biology of *Liocarcinus puber* and *Liocarcinus holsatus* (Decapoda, Brachyura, Portunidae) from the Gower Peninsula, South Wales. Mar. Ecol. 9: 227–241. doi: 10.1111/j.1439-0485.1988.tb00330.x

Cobo, V.J., Fransozo, A. 2000. Fecundity and reproduction period of the red mangrove crab *Goniopsis cruentata* (Brachyura, Grapsidae) São Paulo State, Brazil. In: Klein, J.C.V., Schram, F.R. (Eds.). Crustacean Issues, Biodiversity Crisis and Crustacea. Rotterdam, the Netherlands, pp. 527–533.

Costa, T.M., Negreiros-Fransozo, M.L. 1998. The reproductive cycle of *Callinectes danae* Smith, 1869 (Decapoda, Portunidae) in the Ubatuba region, Brazil. Crustaceana 71: 615–627. doi: 10.1163/156854098X00617

Diesel, R. 1991. Sperm competition and the evolution of mating behaviour in *Brachyura*, with special reference to spider crabs (Decapoda, Majidae). In: Bauer, R.T., Martin, J.W. (Eds.). Crustacean Sexual Biology, Columbia University Press. New York, NY, USA, pp. 145–163.

Emmerson, W.D. 1994. Seasonal breeding cycles and sex ratios of eight species of crabs from Mgazana, a mangrove estuary in Transkei, Southern Africa. J. Crust. Biol. 14: 568–578. doi.org/10.1163/193724094X00137

- Erdman, R.B., Blake, N.J. 1988. Reproductive ecology of female golden crabs, *Geryon fenneri* Manning and Holthuis, from Southeastern Florida. J. Crustac. Biol. 8: 392–400. doi.org/10.2307/1548278
- Flores, A.A.V., Paula, J. 2010. Sexual maturity, larval release and reproductive output of two brachyuran crabs from a rocky intertidal area in central Portugal. Invert. Reprod. Dev. 42: 21–34. doi.org/10.1080/07924259.2002.9652506
- Fransozo, A., Bertini, G., Correa, M.O.D. 1999. Population biology and habitat utilization of the stone crab *Menippe nodifrons* in the Ubatuba region, Sao Paulo, Brazil. In: Biodiversity Crisis and Crustacea v. 12. A.A. Balkema Publishers. Leiden, the Netherlands, pp. 275 – 281.
- Giese, A.C. 1959. Comparative physiology: Annual reproductive cycles of marine invertebrates. Ann. Rev. Physiol. 2: 547–576. doi.org/10.1146/annurev.ph.21.030159.002555
- Gregati, R.A., Negreiros-Fransozo, M.L. 2007. Relative growth and morphological sexual maturity of *Chasmagnathus granulatus* (Crustacea, Varunidae) from a mangrove area in southeastern Brazilian coast. Iheringia. Série Zoologia. 97: 268–272. doi.org/10.1590/S0073-47212007000300009
- Haefner, P.A. 1976. Distribution, reproduction and molting of the rock crab, *Cancer irrigatus* say 1917 in the mid-Atlantic Bight. J. Nat. Hist. 10: 377–397. doi.org/10.1080/00222937600770291
- Hails, A.J., Yaziz, S. 1982. Abundance, breeding, and growth of the ocapodid crab *Dotilla myctiroides* (Milne-Edwards) on a West Malaysian beach. Estuar. Coast. Shelf. Sci. 15: 229–239. doi.org/10.1016/0272-7714(82)90030-0
- Hartnoll, R.G. 1973. Factors affecting the distribution and behaviour of the crab *Dotilla fenestrata* on East African shores. Estuar. Coast. Mar. Sci. 1: 137–152. doi.org/10.1016/0302-3524(73)90066-2
- Hines, A.H., Jivoff, P.R., Bushmann, P.J., van Montfrans, J., Reed, S.A., Wolcott, D.L., Wolcott, T.G. 2003. Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. Bull. Mar. Sci. 72: 287–310.
- Hughes, A.C. 2017. Understanding the drivers of Southeast Asian biodiversity loss. Ecosphere 8: e01624. https://doi.org/10.1002/ecs2.1624.
- Keunecke, K.A., Silva, D.R., Vianna, M., Verani, J.R., D’Incao, F. 2009. Ovarian development stages of *Callinectes danae* and *Callinectes ornatus* (Brachyura, Portunidae). Crustaceana 82: 753–761.
- Krol, R.M., Hawkins, W.E., Overstreet, R.M. 1992. Reproductive components. In: Harrison, F.W., Humes, A.G. (Eds.). Microscopic Anatomy of Invertebrates, Vol. 10: Decapod Crustacea. Wiley-Liss. New York, NY, USA, pp. 295–343.
- Kumar, M.S., Xiao, Y., Venema, S., Hooper, G. 2003. Reproductive cycle of the blue swimmer crab, *Portunus pelagicus*, off Southern Australia. J. Mar. Biol. Assoc. UK. 83: 983–994. doi: 10.1017/S0025315403008191h
- Lawal-Are, A.O. 2010. Reproductive biology of the blue crab, *Callinectes amnicola* (De Rocheburne) in the Lagos Lagoon, Nigeria. Turk. J. Aquat. Sci. 10: 1–7. doi: 10.4194/trjfas.2010.0101
- Lestang, S.D., Hall, N.G., Potter, I.C. 2003. Reproductive biology of the blue swimmer crab (*Portunus pelagicus*, Decapods: Portunidae) in five bodies of water on the west coast of Australia. Fish. Bull. 101: 745–757.
- Litulo, C. 2004. Reproductive aspects of a tropical population of the fiddler crab *Uca annulipes* (H. Milne Edwards, 1837) (Brachyura: Ocypodidae) at Costa do Sol mangrove, Maputo Bay, Southern Mozambique. Hydrobiologia 525: 167–173.
- Litulo, C. 2005. Population biology of the fiddler crab *Uca annulipes* (Brachyura: Ocypodidae) in a tropical East African mangrove (Mozambique). Estuar. Coast. Shelf. Sci. 62: 283–290. doi: 10.1016/j.ecss.2004.09.009
- MacNae, W., Kalk, M. 1962. The fauna and flora of sand flats of Inhaca Island, Mozambique. J. Anim. Ecol. 31: 93–128. doi.org/10.2307/2334
- Morgan, S.G., Christy, J.H. 1995. Adaptive significance of timing of larval release by crabs. Am. Nat. 145: 437–479. doi: 10.1086/285749
- Moura, N.F.O., Coelho-Filho, P.A., Coelho, P.A. 2000. Population structure of *Goniopsis cruentata* (Latreille, 1803) in the Paripe estuary, Brazil. Nauplius 8: 73–78.
- Muino, R. 2002. Fecundity of *Liocarcinus depurator* (Brachyura; Portunidae) in the Ria de Arousa (Galicia, North-west Spain). J. Mar. Biol. Assoc. UK. 82: 109–116. doi: 10.1017/S0025315402005222
- Nabhitabhata, J., Chan-ard, T., Chuaynkern, Y. 2000. Checklist of Amphibians and Reptiles in Thailand. Office of Environmental Policy and Planning. Bangkok, Thailand.
- Ogburn, M.B., Roberts, P.M., Richie, K.D., Johnson, E.G., Hines, A.H. 2014. Temporal and spatial variation in sperm stores in mature female blue crabs *Callinectes sapidus* and potential effects on brood production in Chesapeake Bay. Mar. Ecol. Prog. Ser. 507: 249–262. doi: 10.3354/meps10869
- Patino-Martinez, J., Marco, A., Quinones, L. 2012. A potential tool to mitigate the impacts of climate change to the Caribbean leatherback sea turtle. Glob. Change Biol. 18: 401–411. doi.org/10.1111/j.1365-2486.2011.02532.x
- Pillay, K.K., Ono, Y. 1978. The breeding cycles of two species of grapsid crabs (Crustacea, Decapoda) from the north coast of Kyushu, Japan. Mar. Biol. 45: 237–248. doi:10.1007/BF00390606
- Rondeau, A., Sainte-Marie, B. 2001. Variable mate-guarding time and sperm allocation by male snow crabs (*Chionoectes opilio*) in response to sexual competition and their impact on mating success of females. Biol. Bull. 201: 204–217. doi: 10.2307/1543335
- Sastry, A.N. 1983. Ecological aspects of reproduction. In: Vernberg, F.J., Vernberg, W.B. (Eds.). The Biology of Crustacea, Vol. 8 Environmental Adaptation. Academic Press. New York, NY, USA, pp. 179–270.
- Sato, T., Goshima, S. 2006. Impacts of male-only fishing and sperm limitation in manipulated populations of unfished crab, *Hapalogaster dentata*. Mar. Ecol. Prog. Ser. 313: 193–204.
- Shields, J.D. 1991. The reproductive ecology and fecundity of cancer crabs. In: Wenner, A., Kuris, A. (Eds.). Crustacean Egg Production. A.A. Balkema. Rotterdam, the Netherlands, pp. 193–213.
- Somerton, D.A. 1980. A computer technique for estimating the size of sexual maturity in crabs. Can. J. Fish. Aquat. Sci. 37: 1488–1494. doi: 10.1139/f80-192
- Sukumaran, K.K., Teland, K.R., Thippeswamy, D. 1986. On the fishery and biology of the crab *Portunus sanguinolentus* (Herbst) along the south Kanara coast. Indian. J. Fish. 33: 188–200.
- Sumpton, W. 1990. Biology of the rock crab *Charybdis natator* (Herbst) (Brachyura: Portunidae). Bull. Mar. Sci. 46: 425–431.
- Takeda, S., Matsumasa, M., Yong, H.S., Murai, M. 1996. ‘Igloo’ construction by the ocapodid crab, *Dotilla myctiroides* (Milne-Edwards) (Crustacea; Brachyura): The role of an air chamber when burrowing in a saturated sandy substratum. J. Exp. Mar. Biol. Ecol. 198: 237–247. doi.org/10.1016/0022-0981(96)00007-X
- Tweedie, M.W.F. 1950. Notes on Grapsoid crabs from the Raffles Museum. Bull. Raffles Mus. 23: 310–324.
- Wada, K. 1981. Growth, breeding, and recruitment in *Scopimera globosa* and *Ilyoplax pusillus* (Crustacea: Ocypodidae) in the estuary of Waka River, middle Japan. Seto. Mar. Biol. Lab. 26: 243–259. doi: 10.5134/176012
- Warner, G.F. 1977. The Biology of Crabs. Paul Elek Pte. Ltd. London, UK.

- Wisespongpan, P., Jaingam, W., Kongkaew, W., Ratmuangkhwang, S. 2017. Species richness, density and distribution of soldier crabs in sandy beach around Andaman Coastal Research Station for Development, Ranong Province. In: Proceedings of 47th Kasetsart University Annual Conference. Bangkok, Thailand, pp. 770–778. [in Thai].
- Zar, J.H. 1984. Biostatistical Analysis, 2nd ed. Prentice Hall. Englewood Cliffs, NJ, USA.