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Reproductive dynamics of a swimming crab (*Monomia haanii*) in the world's crab basket

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ABSTRACT

Red swimming crab *Monomia haanii* is an important export fishery in southern China. *M. haanii* is mainly sold as lump crabmeat, generating an annual trade of tens of millions of US dollars over the last decade. For such a commercially important crab species, little attention has been paid to the sustainable use of the stocks and there remains much to learn about its biology and ecology. Monthly fishery-dependent samplings were conducted from August 2018 to April 2019 from bottom trawler catches obtained in the southern Taiwan Strait waters to characterize the biological attributes of *M. haanii* (N = 3222 individuals). Growth parameters, fecundity, sex ratios and maturity ogives were estimated, and spawning dynamics were characterized. The overall male: female ratio was 1: 1.07; however, significant variations monthly were detected ($p < 0.01$). Consistent with other portunids, sexual dimorphism with males typically reaching a larger average size was confirmed (carapace width, CW) ($p < 0.01$). Mature females (carrying eggs on abdominal pleopods) were found in all months sampled, with one clear peak spawning season in February–April and a possible second peak around August. Size at 50 % female maturity was 6.3 cm CW. Female absolute fecundity (Fa) was significantly related to CW via a power function relationship (N = 72, $p < 0.01$). The estimated average meat yield was 18.46 % (N = 93), irrespective of sex and size ($0.1 > p > 0.05$). These results provide the first in-depth characterization of *M. haanii* and may pave a way towards the first *M. haanii* stock assessment.

1. Introduction

The global marine crab capture landings have grown dramatically over the past 40 years. The total annual production surpassed one million metric tons (mmt) in 1996 and 1.6 mmt in 2014 (http://www.fao.org) (Fig. 1). Collectively, China has contributed more than 40 % of the total global marine crab capture production since 2004. The category "swimming crabs" is the most important taxonomic group in global marine crab capture fisheries, and generally refers to the species from the family Portunidae. Swimming crabs collectively contributed to at least 80 % of the total national marine crab catches from 2003–2018. High-resolution statistical data for capture production of portunids in China are available from 1987 to present from Chinese Fishery Statistical Yearbooks, mainly coming from Zhejiang, Fujian, Jiangsu, and Guangdong Provinces (MOA, 1987–2018; MARA, 2019). Despite the importance of swimming crabs to domestic fisheries, there are only limited biological studies available, mainly focusing on the blue swimming crab *Portunus pelagicus*, the three-spot swimming crab *P. sanguinolentus*, the gazami crab *P. trituberculatus* and the sand crab *Ovalipes punctatus* (Dai et al., 1977; Song et al., 1988; Jiang and Yu, 2012; Liu et al., 2014; Yang et al., 2014). Further work on population dynamics and stock assessments is needed for effective management of these natural resources.

The red swimming crab *Monomia haanii* (Stimpson, 1858) (synonyms of *Portunus haanii* and *P. gladiator*) is widely distributed in the Indo-Pacific Oceans, and commonly found in the southern East China Sea and South China Sea (Dai et al., 1986; Zhang, 1997; Windsor et al., 2019). It inhabits sandy and rocky bottoms within the 10–100 m depth

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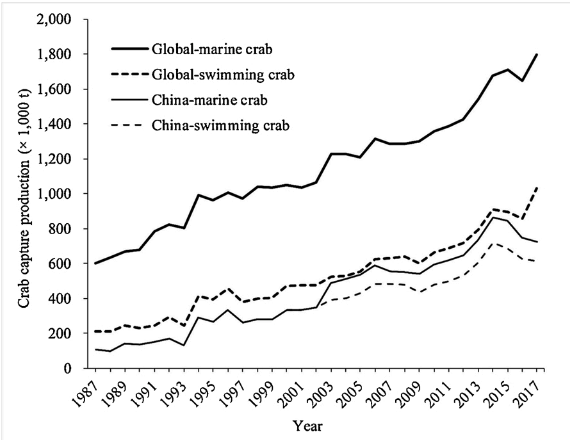

Fig. 1. Marine crab and swimming crab capture productions (× 1000 mt) globally and in China from 1987-2017. (Data source from FAO Global Production Statistics 1950-2018: http://www.fao.org/fishery/statistics/global-production/en; the production of global-swimming crab includes 13 categories of crab species or species groups: Blue crab, Blue swimming crab, Callinectes swimcrabs nei, *Charybdis* crabs nei, dana swimcrab, Gazami crab, Green mud crab, Henslow's swimming crab, Indo-Pacific swamp crab, Orange mud crab, *Portunus* swimcrabs nei, Swimming crabs, etc. nei and velvet swimcrab; the production of China-swimming crab includes *Portunus* crabs, the mud crab *Scylla paramamosain* and *Charybdis* crabs).

range (Dai et al., 1986; Zhang, 1997), and feeds on demersal invertebrates and fishes (Huang, 2004). Based on historical fishing catch reports, the southern Taiwan Strait, including the Taiwan Bank fishing ground and its adjacent waters, are the most important habitats for *M. haanii* (Zhang, 1997; Wang et al., 1998). Catches of *M. haanii* come mainly from bottom trawlers, baited crab traps, and gill nets. In the southern Taiwan Strait, the estimated annual capture production of *M. haanii* was 30,000–35,000 mt in the 1990s, ranking No. 1 in crab catches in the areas, and contributing 16–23 % of the total capture production in bottom trawl fisheries operated in these waters. The catches of *M. haanii* in China were mainly discarded before the 1990s due to its low value; however, this situation has changed (Zhang, 1997). With the growing demand in international trade, the processing industry for *M. haanii* meat products has developed since the 1990s, particularly in Fujian Province. More than 30 % of the total Chinese export volumes for processed crab products hail from Fujian, creating an international trade of millions of US dollars annually (Chinese Customs Datasets, 2008–2018). Of that, most are the lump crabmeat products from *M. haanii*. Dongshan County in Fujian is the most important area for *M. haanii* processing, contributing to approximate 80 % and 65 % of the provincial volume (20,646.28 t) and value (48.34 million US dollars) for *M. haanii* lump meat products, respectively (Liu and Lin, 2019; http://www.dongshandao.gov.cn).

As a commercially important crab species in China, the *M. haanii* fishery is indeed under intense fishing pressure. A detailed examination for its sustainable use is needed after over 20 years of heavy exploitation. This study examines the reproductive dynamics of *M. haanii* caught in its main habitat, i.e., the southern Taiwan Strait, China, based on monthly sampling from August 2018 to April 2019. Such data are essential for conducting fishery stock assessments. Creating an effective fisheries management strategy will be a big step towards a sustainable *M. haanii* fishery, jointly beneficial for fishers, processors, and managers (Boenish et al., 2020).

2. Material and methods

2.1. Monomia haanii collection

Monthly portside sampling of *M. haanii* was conducted from August 2018 to April 2019. Due to the national fishing moratorium regulation (i.e., no bottom trawler fishing from 1st May to 15th August) in China, it was not possible to sample crabs in May–July of 2018 and 2019. A total of 205–575 crabs were randomly collected each month from 5–10 trawler catches at landing ports in Dongshan County, Fujian Province (Fig. 2). About 1 kg "feed-grade fish" from the same trawlers were collected for obtaining smaller crabs that eventually went to aquaculture facilities as feed (Zhang et al., 2020). The trawlers operated in the Taiwan Bank fishing ground and its adjacent waters in the southern Taiwan Strait – the most important fishing area for *M. haanii* known in

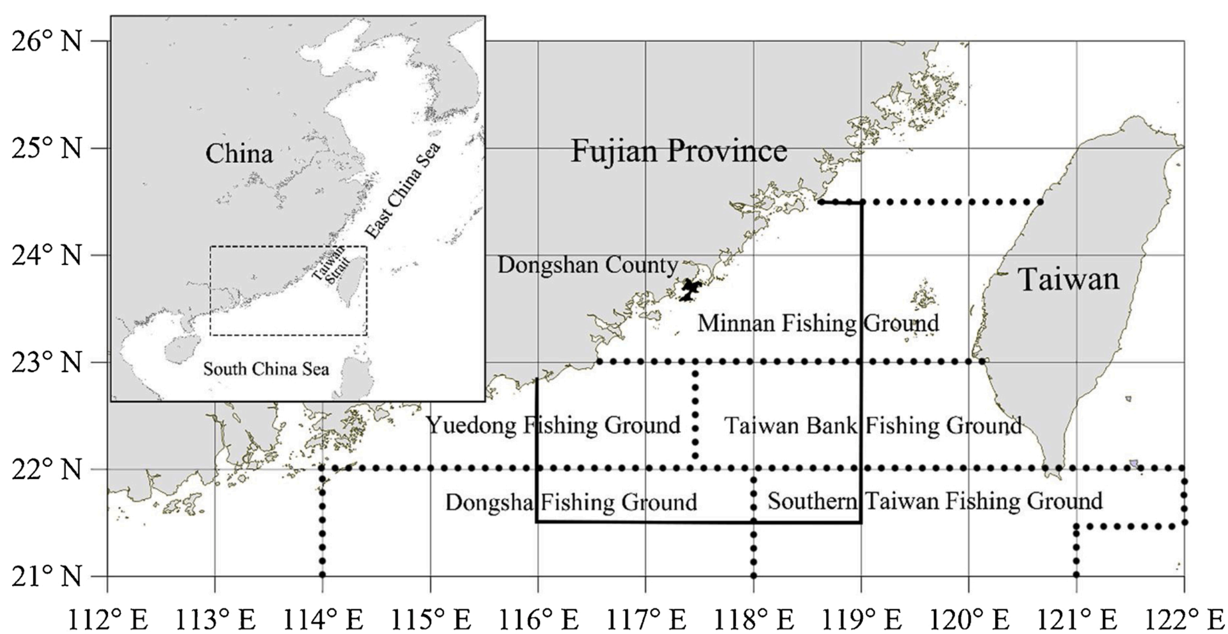

Fig. 2. Sampling site (Dongshan County, black area) and main fishing areas (black solid line area) for *Monomia haanii* in the southern Taiwan Strait, China, including the Minnan fishing ground, Taiwan Bank fishing ground, Yuedong fishing ground, Dongsha fishing ground and Southern Taiwan fishing ground (black dot line areas).

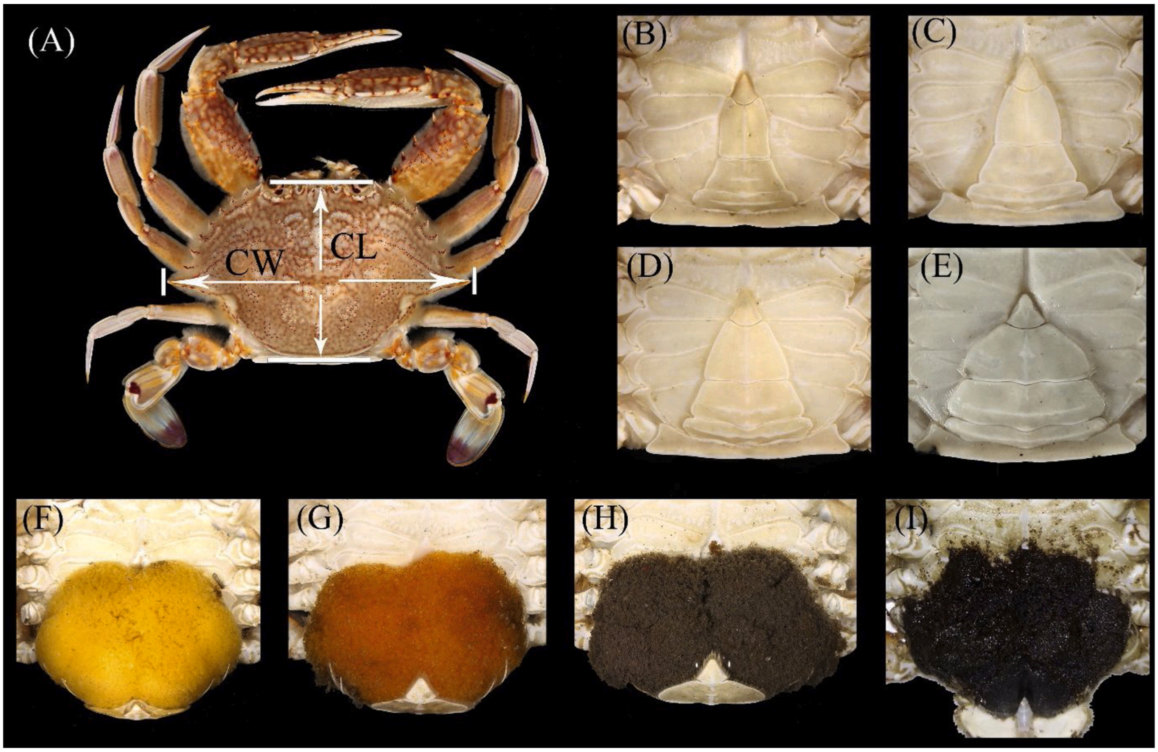

Fig. 3. (A) Dorsal view of *Monomia haanii* for carapace length (CL) and carapace width (CW) measurements. Male (B) and female (C-E) determination by abdomen morphology. Four egg colors with yellow (F), orange (G), brown (H) and black (I).

China to date (Fig. 2). Trawlers typically operate at sea for 3–9 days and keep catches fresh on ice before landing at Dongshan County.

2.2. Crab measurement and examination

For every *M. haanii* individual sampled, carapace width (CW, to 0.1 cm), carapace length (CL, to 0.1 cm), and body weight (BW, to 0.01 g) data were collected (Fig. 3A). Abdomen morphology and the occurrence of the 1st–2nd gonopods are used to determine the sex (Fig. 3 B–E). Females carrying eggs on abdominal pleopods were considered fully mature. In studied portunids (e.g. *P. pelagicus*, *P. trituberculatus*, *Scylla paramamosian*), the recently extruded eggs complete embryonic development through sequential yellow, orange, brown and black coloration, and the pre-hatched phases take over 8–30 days (Xue et al., 1998; Arshad et al., 2006; Hisam et al., 2018; Yao, 2008). We assumed embryonic development of *M. haanii* is similar to these portunids documented. Therefore, the four egg colors, yellow, orange, brown, and black, were assigned to embryonic developmental stages from early to pre-hatch in this study (Fig. 3F–I).

Female fecundity, defined as the number of eggs carried by a female, was estimated empirically. Briefly, pleopods carrying eggs were carefully removed from the body, dried with blotter paper, and weighted as an intact egg mass (to 0.0001 g). Furthermore, sub-samples (N = 5, approximate 0.02 g per sub-sample) were taken from different parts of each egg mass to a culture dish. The number of eggs per sub-sample were counted with a Leica M165FC fluorescence stereo microscope and Leica DFC550 digital camera. Next, estimates were upscaled to the entire egg mass, and the averages were employed for further analysis. Egg diameters (to 1 μm) from all four colors were measured using a Leica M165 FC fluorescence stereo microscope. We calculated the absolute fecundity (Fa) as: Fa = W * m / n, where W is the total weight of the whole egg mass for a female, n is the average number of eggs from the five sub-samples and m is the average weight of the five egg sub-samples (Johnson et al., 2010; Soundarapandian et al., 2013). The relative fecundity (Fr) was calculated as: Fr = Fa / CW and Fr = Fa / BW.

In the *M. haanii* processing factories, individuals (without the first paired claws) are usually steamed before meat processing, and the lump crabmeat and other body meat products are packed in cans for international trade. Therefore, the meat yield (%) was calculated as: mean yield (%) = Wm / BW * 100, where Wm is the total meat weight taken out from the cooked crab, BW is the body weight of the crab before cooking and without the first paired claws. The meat yield assessment was conducted in the laboratory and an experienced worker from a factory was invited to follow the standard procedures as the processing factories in Dongshan County.

2.3. Data analyses

Spawning months were determined by noting the percentage of females carrying eggs each month, irrespective of egg coloration: the number of females carrying eggs / the total number of females * 100. When the percentage of females carrying eggs increased substantially from past months, we assumed this corresponded to a peak spawning season.

The size at 50 % female maturity (CW_{50}) was determined by fitting a logistic regression (probity link) to the percentage of females carrying eggs vs. size (CW) class, using females from only what we determined as peak spawning months above.

Differences in sex ratio from 1:1 monthly and overall, in sizes of females and males monthly and overall, and the relationships of CW–BW and Fa–CW were analyzed by setting statistical significance to < 0.05. The statistical analyses were conducted using R (R Core Team, 2020), SPSS 13.1 and Microsoft Excel 2019 software.

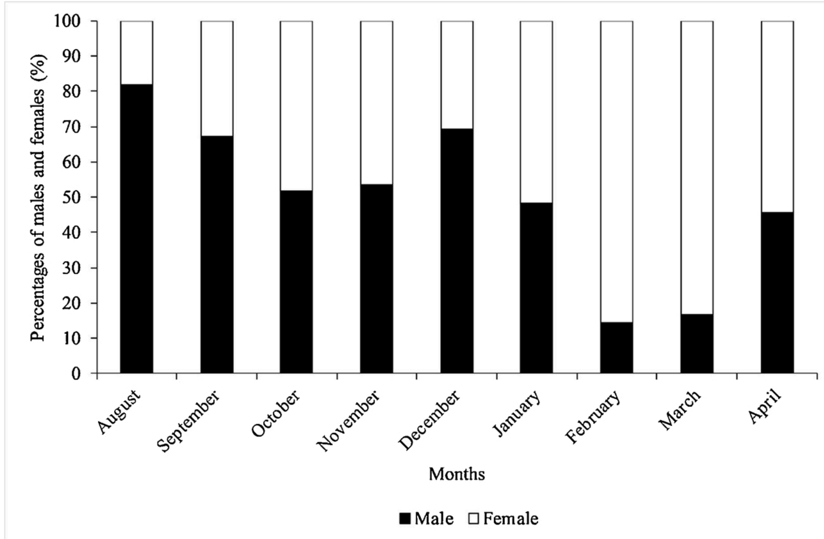

Fig. 4. Percentages of *Monomia haanii* males and females monthly from August 2018 to April 2019.

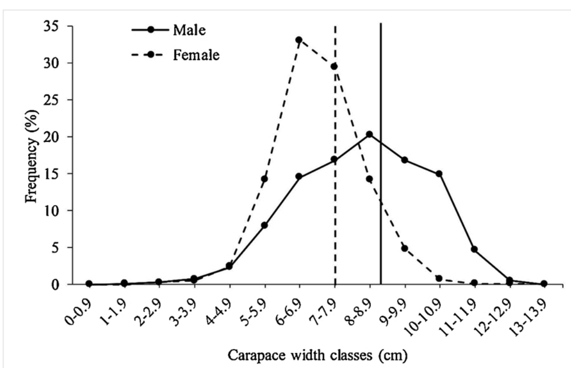

Fig. 5. Size (carapace width, CW) frequency (%) of *Monomia haanii* males (N = 1560) and females (N = 1662), collected from August 2018 to April 2019. Vertical lines indicate the average sizes of females and males.

3. Results

3.1. Sex ratio

A total of 3222 individuals with 1560 males and 1662 females were used in the analysis. The overall male: female ratio was 1: 1.07, with no significant difference from the 1: 1 ratio ($\chi^2 = 3.12$, df = 1, $p > 0.05$). Monthly variation in sex ratio was significantly different from the 1: 1 ratio ($p < 0.01$), showing a significant male-bias in August, September and December 2018, and a significant female-bias in February and March 2019 (Fig. 4).

3.2. Size distributions of females and males

The sizes ranged from 2.4 to 13.1 cm CW (7.0 ± 1.2 cm CW, mean ± SD, N = 1662) for females and from 1.8 to 12.3 cm CW (8.3 ± 1.7 cm CW, N = 1560) for males (Fig. 5). Females were mainly in size classes of 5.0–8.9 cm CW (90.85 %), and males in 6.0–10.9 cm CW (83.33 %), accumulating from the months with the frequency > 10 %. Males were significantly larger than females in CW ($t = 22.32$, df = 3,220, $p < 0.01$). Monthly variation in sizes of females (F = 48.03, df = 1,661, $p < 0.01$) and males (F = 39.91, df = 1,559, $p < 0.01$) were also significant (Fig. 6). Larger average sizes of females and males were found in October-December and September-December, respectively. The largest average sizes for both females and males were found in December, and the smallest average sizes in January.

3.3. Relationships between size and weight

In the CW–BW relationship, the exponential values 'b' were 2.9412 for females and 3.0336 for males. The b values significantly differ from 3 ($t = 21.15$ for females, t = 10.29 for males, $p < 0.01$), and also significantly differ between females and males ($t = 3.21$, $p < 0.01$) (Table 1, Fig. 7A). The CW–CL relationships were highly correlated for both females ($R^2 = 0.8897$, $p < 0.01$) and males ($R^2 = 0.9367$, $p < 0.01$) (Fig. 7B).

3.4. Spawning months

A total of 606 females carrying eggs were collected, throughout the entire sampling period (Fig. 8A). We determined a peak spawning season spanning February–April (Fig. 8B). Another spawning season seems to take place in and around August based on the high percentage of females carrying eggs. From August to October, the percentage of females carrying eggs decreased in a similar way to the ascending trend from March to April.

3.5. Sizes for female maturation

The minimum and maximum sizes for females carrying eggs were 4.6 and 10.6 cm CW, respectively (Table 2). The sizes of females carrying eggs were significantly different by month (F = 10.42, df = 605, $p <$ 0.01). There was no significant difference in the sizes of females carrying eggs in the two spawning seasons, February–April and August–September (t = 0.243, df = 561, $p > 0.1$). Smaller females carrying eggs (< 5 cm CW) were found in March and April. The dominant size classes for females carrying eggs were 7.0–7.9 (38.12 %) and 8.0–8.9 (30.26 %) cm CW. The CW_{50} was estimated as 6.3 ± 0.4 CW (to 0.5 cm CW interval) based on females sampled in peak spawning months of February–April (Fig. 9).

3.6. Fecundity

Fa were between 75,742 and 616,436 eggs (315,026 ± 128,131, N = 72) with female body sizes of 5.5–9.7 cm CW. Fr were between 13,153 and 66,284 eggs cm^{-1} CW (38,930 ± 11,724, N = 72), and between 3332 and 8321 eggs g^{-1} BW (5303 ± 1,213, N = 72). We found a typical

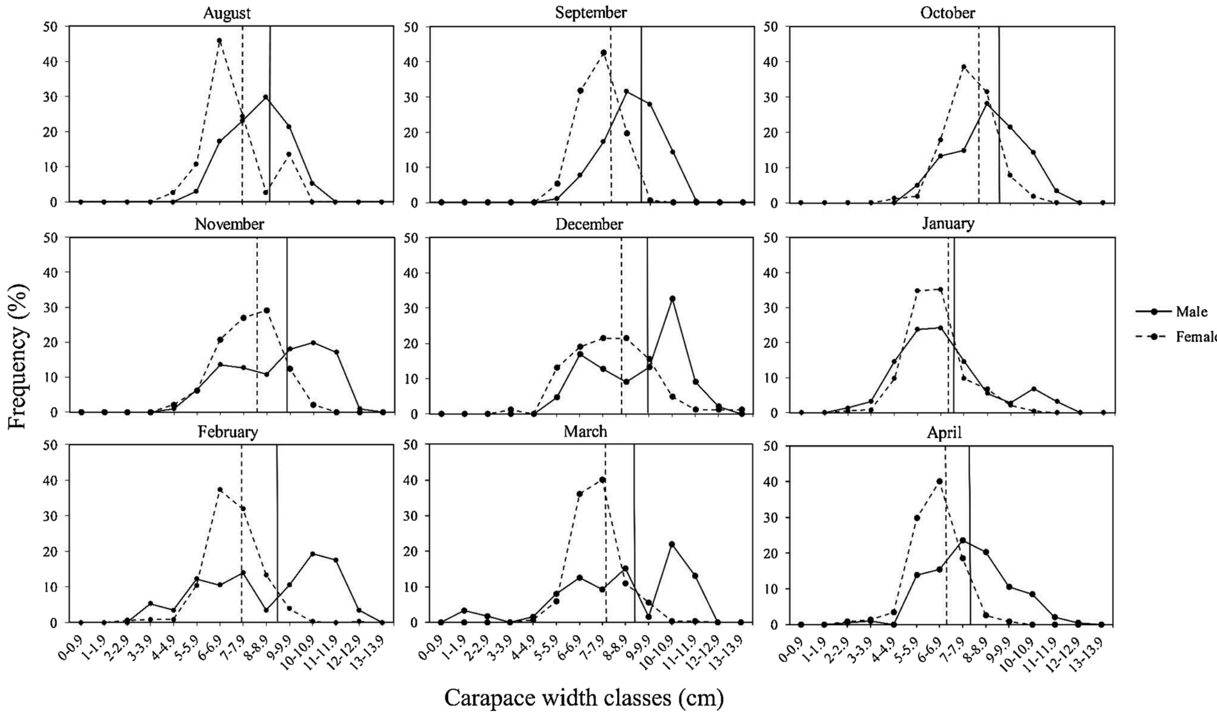

Fig. 6. Monthly size frequency of males and females, collected from August 2018 to April 2019. Vertical lines indicate the average sizes of females and males.

Table 1
Analysis of allometric and log-transformed equations of carapace width (CW)–body weight (BW) relationship in males and females of *M. haanii*.

Sex	X-variable (CW, cm)	Y-variable (BW, g)	Allometric equation	N	R^2 [a]	*b* (95% of *b*) [b]	SE *b* [c]	*t* (*b* = 3) [d]	AL [e]
Female	2.4–13.1	1.17–154.50	$BW = 0.1194\ CW^{2.9412}$	1662	0.8966	2.9412 (2.893–2.989)	0.0946	21.15	–
			logBW = 2.941 logCW–0.923		0.8966				
Male	1.8–12.3	0.71–223.70	$BW = 0.0971\ CW^{3.0336}$	1560	0.9419	3.0336 (2.996–3.071)	0.1352	10.29	+
			logBW = 3.034 logCW–1.013		0.9419				

[a] Coefficient of determination; [b] regression coefficient with 95 % confidence interval; [c] standard error (SE) of b; [d] Student's *t*-test for comparison between the b-value and 3; [e] allometric level (AL): (+) positive and (−) negative.

power relationship between Fa and CW ($p < 0.01$), and a logarithmic functional relationship between Fa and BW ($p < 0.01$) (Fig. 10).

3.7. Egg diameters

We randomly selected 14 females carrying eggs (5.5–9.7 cm CW) for egg diameter measurement; 5 individuals with yellow eggs, 4 individuals with orange eggs, 2 individuals with brown eggs and 3 individuals with black eggs. Egg diameters were 282–361 μm (313 ± 15, N = 368); 307 ± 103 μm from yellow eggs, 298 ± 39 μm from orange eggs, 314 ± 73 μm from brown eggs and 326 ± 252 μm from black eggs, showing a general increase of egg diameters from early to pre-hatching stage except from the orange eggs. Egg diameters were significantly different among four embryonic developmental stages (F = 109.71, df = 367, $p < 0.01$).

3.8. Meat yield

A total of 58 females (5.9–9.8 cm CW) and 35 males (6.0–11.4 cm CW) were randomly selected in April 2019 for meat yield assessment. The average meat yield was 18.49 % (10.79 %–32.01 %) for all females and males (N = 93) (Fig. 11). Specifically, we found an overall average of 18.12 % (10.79 %–32.01 %) for females (N = 58), 19.09 % (14.47 %–27.39 %) for males (N = 35), 18.60 % (10.83 %–32.01 %) for females carrying eggs (N = 19), and 17.14 % (10.79 %–26.84 %) for females without eggs (N = 39). Meat yields of females carrying eggs were generally low; however, there were no significant differences between females and males (t = 1.32, df = 91, $p > 0.05$), or between females carrying and not carrying eggs (t = 1.41, df = 56, $p > 0.05$).

4. Discussion

4.1. Sex ratio

A curious difference in *M. haanii* sex ratio over data from the past 20 years was identified. In this study, the overall male: female ratio of *M. haanii* (1: 1.07) was not different from 1: 1, although there was substantial monthly variation. Comparatively, an overall reported male: female ratio in 1992–1995 was nearly 2: 1 (Zhang, 1997). One possible explanation is the differences in fishing grounds over time and potential sexual segregation for parts of *M. haanii* life history. In 1992–1995, the fishing grounds for *M. haanii* (22°00′–24°30′ N and 117°30′–120°00′ E) were restricted to the Minnan and Taiwan Bank (Fig. 2). The fishing grounds for *M. haanii* (21°30′–24°30′ N and 116°00′–190°00′ E) in this study are shifted southwest and include adjacent fishing grounds such as Yuedong, Dongshan, and southern Taiwan (Fig. 2).

Marine crustaceans commonly have a skewed sex-ratio, and the existence of seasonal sex-specific habit segregation, single-sex migration and environmental parameters (e.g. water depth, temperature and salinity) may explain the phenomenon (Wenner, 1972; Young and Elliott, 2020). In other portunids, the same phenomenon is present. *Portunus pelagicus* females prefer higher salinity than males and often

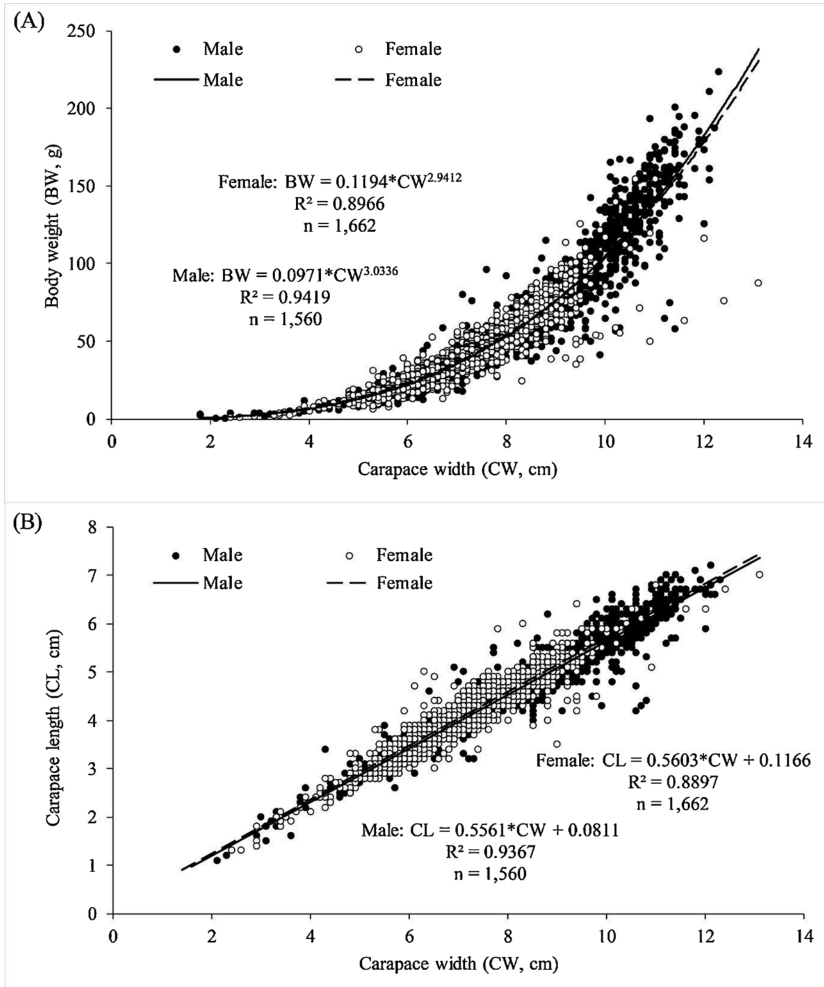

Fig. 7. (A) Carapace width (CW) and body weight (BW) relationship, and (B) carapace width (CW) and carapace length (CL) relationship for *Monomia haanii* females and males.

inhabit deeper waters (Campbell and Fielder, 1986), *Callinectes sapidus* females migrate to the nearshore continental shelf area for spawning (Ogburn and Habegger, 2015), *P. sanguinolentus* females move to shallow water for feeding after wintering offshore (Yang et al., 2014), and *Carcinus maenas* females prefer low salinity for spawning in May-August such as rivers or estuaries (Young et al., 2017). In this study, a strong female-bias occurred in February and March, the peak spawning season (Fig. 4), suggesting that *M. haanii* females may too migrate from deeper water to nearshore for spawning.

4.2. Variations in body size and spawning season

In large-size portunids, such as *P. sanguinolentus* and *P. trituberculatus*, females were significantly larger than males (Yang et al., 2014; Oh, 2011). By contrast, the size (CW) of *M. haanii* males were significantly larger than females both by month and with all samples combined (Figs. 5 and 6). Owing to *M. haanii* being a fast-growing species and under intense natural mortality and fishing pressure, it is suggested that very few individuals survive into their second year of life (Boenish et al., 2020). The spawning dynamics presented in this study indicate that males grow faster and reach a larger size than females. In *C. maenas*, after females begin to reach maturation, the size distributions of the two sexes diverge, and females dedicate more energy for gamete production in preparation for mating (Young et al., 2017). The same phenomenon also occurs in other middle-size swimming crab species, such as *Callinectes danae* (Sforza et al., 2010) and *C. sapidus* (Jivoff et al., 2017). Moreover, it may be the case that females stop growing after a 'terminal molt', but more laboratory studies are needed for confirmation of this hypothesis.

Although females carrying eggs were found in all sampling months from August 2018 to April 2019, two peak levels emerged: spring (February–April) and summer (August–September) (Fig. 8B). However, due to a lack of sampling in May–July because of the Chinese national annual fishing moratorium regulation, it is difficult to say whether the spring spawning season continues from February through the summer, or if there is a second 'peak' in August–September. In this study, peak spawning months were determined by the peak percentages of females carrying eggs instead of internal ovary morphology observation; the former can provide more precise determination on spawning timing. Moreover, we found high percentages ($>$ 50 %) of brown and black eggs carried by females in August and February–March, consistent with the peak spawning months determined and indicate the pre-hatching stage (Fig. 8A).

In southern China, there is a common crab spawning season found in February–April, e.g., for *M. haanii* (this study), *P. sanguinolentus* (Yang et al., 2014) and *P. pelagicus* (Liu et al., 2014). For all the aforementioned species, it is unclear to what extent spawning takes place in the summer months. For *M. haanii*, it may be equally plausible that there is a continuous Spring–Summer spawning period, or potentially there could be two distinct spawning seasons (e.g., *P. pelagicus* in the region exhibits two spawning seasons: March–May and August–September (Wang et al., 2001)). Past work supports a similar dynamic for *Charybdis natator* with

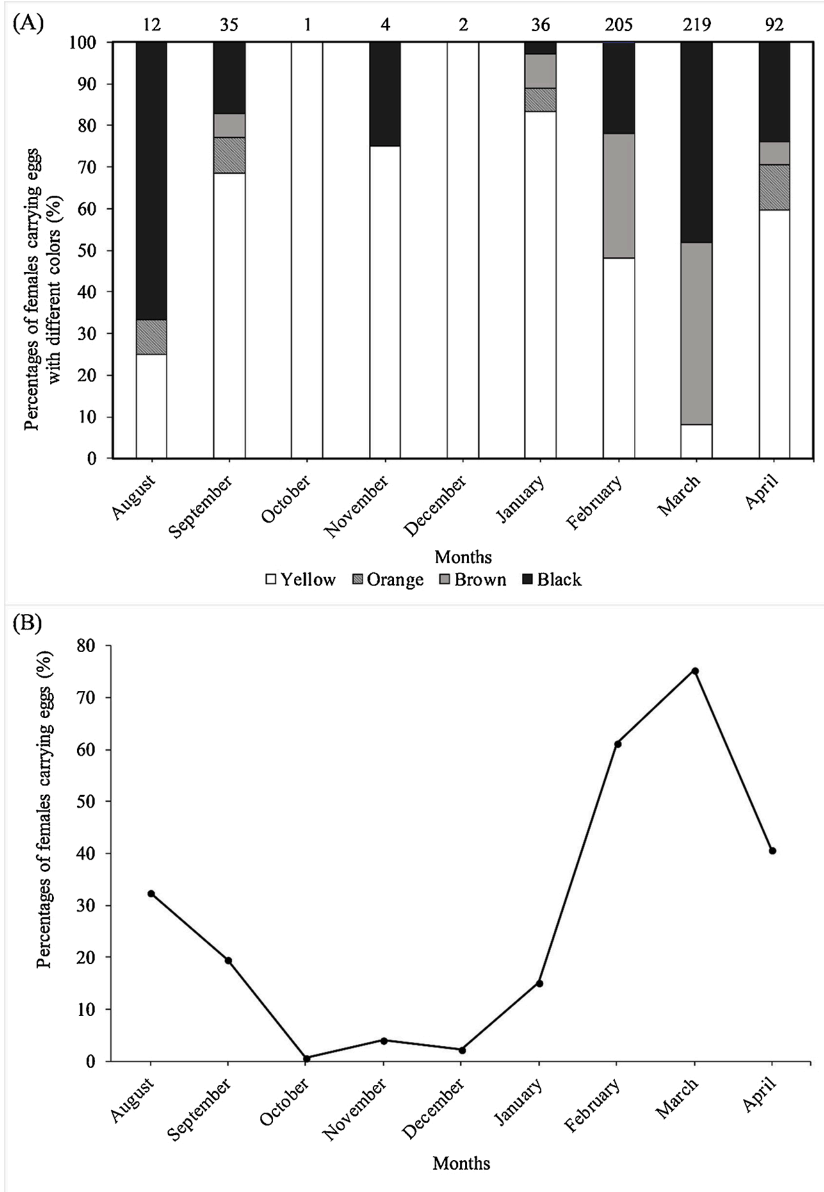

Fig. 8. (A) Percentages of *Monomia haanii* females carrying eggs (N = 606) by month and egg color (yellow, orange, brown, black), and (B) percentages of females carrying eggs (irrespective of egg coloration) by month from August 2018 to April 2019.

Table 2
Size variation of *Monomia haanii* females carrying eggs from August 2018 to April 2019.

Size (CW, cm)	August (2018)	September (2018)	October (2018)	November (2018)	December (2018)	January (2019)	February (2019)	March (2019)	April (2019)
Sample size	12	35	1	4	2	36	205	219	92
Average	6.7	7.2	8.2	8.9	7.3	7.6	7.2	7.2	6.4
Range	5.5–7.6	5.5–8.4	8.2	7.4–10.3	6.8–7.7	5.6–9.3	5.2–10.6	4.9–10.2	4.6–9.4

two spawning seasons in January–April and September–November (Sumpton, 1990). Given the rapid growth rate of *M. haanii*, two spawning seasons may correspond to two recruitment events. To resolve some of these questions, samples from the missing months (May to July), gonad development through histology and reproductive dynamics of this important species merit further study.

4.3. Fecundity

Fecundity of decapod crustaceans has a positive correlation with body size and weight (Erdman and Blake, 1988). In this study, we found that the female absolute fecundity had strong correlations with CW and BW. Similar correlations have also been reported for other swimming crabs (e.g., *P. sanguinolentus* (Yang et al., 2014), *P. trituberculatus* (Oh, 2011) and *P. pelagicus* (Johnson et al., 2010)). This study also found that

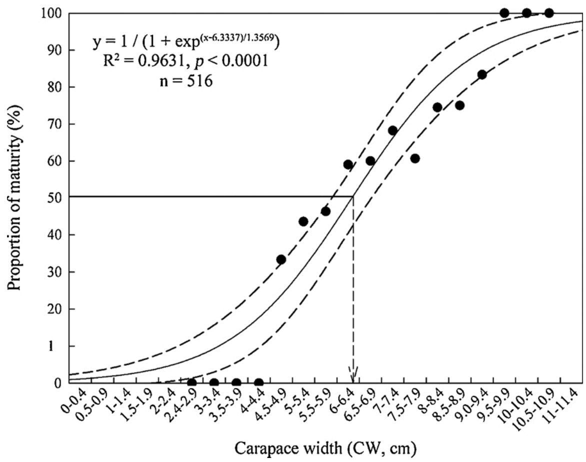

Fig. 9. Size (carapace width, CW) at 50 % female maturity for *Monomia haanii* based on all females sampled from peak spawning months (February–April 2019). Bootstrapped 95 % confidence intervals shown with dashed lines (N = 9999).

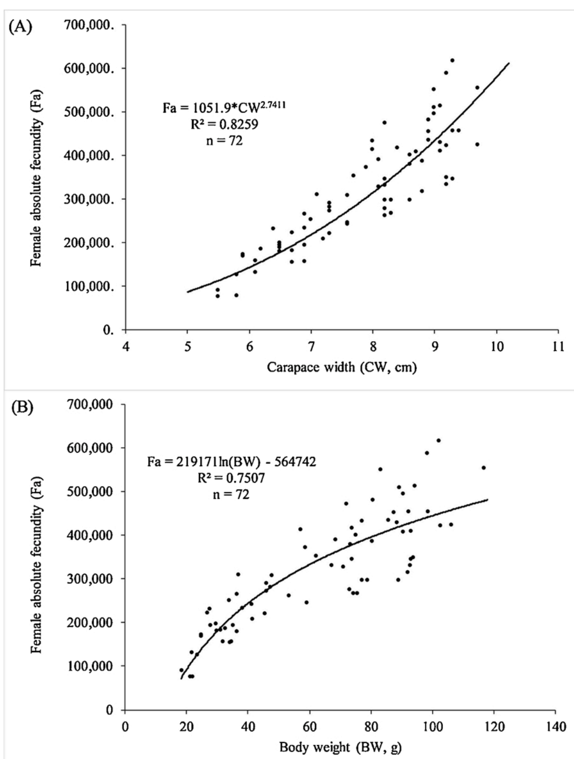

Fig. 10. (A) Absolute fecundity (Fa) and size (carapace width, CW) relationship, and (B) Fa and body weight (BW) relationship of *Monomia haanii* females carrying eggs (N = 72).

females having similar CW had large variation in the number of eggs carried (Fig. 9). This may be due to the number of batches during a spawning season (Wu et al., 2010), natural variation, catch storage conditions, or the embryonic developmental stage.

4.4. Meat yield

This is the first published laboratory examination of *M. haanii* meat yield. Such analyses will help researchers better understand crab processing and international trade sector dynamics. Unexpectedly, meat yields had no significant difference between sexes or size. The average meat yield was 18.49 % (10.79 %–32.01 %) in this study, which is higher than the approximate 15 % from processing factories (Fang M., personal communication). Meat quality and meat yield of *M. haanii* can be improved by storing the steamed crab body on board soon after harvest, a mode that some trap vessels follow (Liu and Lin, 2019).

Based on the meat yield obtained in this study, at least 40,000 mt of *M. haanii* were needed in Fujian annually to achieve lump crabmeat and frozen crab body productions for international trade in the past 10 years (China Custom Dataset, 2008–2018). This estimated *M. haanii* volume for meat processing is nearly equal to the total capture production of *M. haanii* in Fujian (Ocean Outcomes, 2018; OFBFJ, 2010–2018). Currently, due to the increasing demand in domestic markets for *M. haanii* consumption, *M. haanii* catches in Guangdong Province from the same fishing grounds (Fig. 2) are transported to Dongshan County for processing; international import of *M. haanii* from Vietnam was also reported (Liu and Lin, 2019).

4.5. Sustainable fishery

In 2018, a provincial regulation on the minimum catch size for *M. haanii* was set at 8.0 cm CW by the Oceanic and Fisheries Bureau of Fujian Province (http://hyyyj.fujian.gov.cn/). The setting size is larger than the CW_{50} determined in this study. In the regulation, the proportions of *M. haanii* catch individuals < 8.0 cm CW should not exceed 20 % of the total *M. haanii* catch per vessel per trip in 2020 and afterward. Under current operation mode, however, achievement of this regulation is challenging. The average proportion of *M. haanii* < 8.0 cm CW remained high, i.e., 80.7 % of the total catches per vessel per trip in January–April 2019 (N = 30) (Liu and Lin, 2019). Due to the demand of "feed-grade fish" in aquaculture facilities for carnivorous species, there is usually no discard of small-sized fishes and crustaceans by trawlers (Zhang et al., 2020). Meanwhile, there is no strict enforcement on mesh size; 1.0 cm mesh size is commonly used illegally in Chinese domestic trawl fishery (Liang and Pauly, 2017). Recently, the "one bite crab" product market has developed in China to utilize juveniles of *M. haanii* < 6.0 cm CW, mainly < 4.0 cm CW. A single management policy for fishery management will have difficulties achieving the laudable goal of sustainability. If the minimum catch size for *M. haanii* is strictly enforced, 62 % of *M. haanii* individuals from August 2018 to April 2019 would not be allowed to be landed in Dongshan County, which might result in lower income for the processing industries, from fishermen to processors and traders.

Increasing demand for *M. haanii* consumption in both international and domestic markets is subjecting this species to intense fishery pressure, responding to the general decline over the past 20 years in catch per unit effort (CPUE) of *M. haanii* in the southern Taiwan Strait (Liu and Lin, 2019). There is an urgent need to improve the knowledge of this species and revisit its stock assessment and management plan. This study provides the first comprehensive view on reproductive dynamics of *M. haanii* and provides robust allometric parameters (CW–CL, fecundity, maturity ogives), which can serve as foundational data to design management strategies and harvest regulations (Winger and Walsh, 2007). These outcomes will be significant for the future sustainable management of *M. haanii* stocks, one of the world's largest wild crab fisheries (Boenish et al., 2020).

CRediT authorship contribution statement

Bai-an Lin: Formal analysis, Investigation, Methodology, Writing - original draft. **Robert Boenish:** Formal analysis, Data curation, Methodology, Writing - review & editing. **Jacob P. Kritzer:** Conceptualization, Writing - review & editing. **Yan Jiang:** Investigation, Methodology. **Song-lin Wang:** Funding acquisition, Writing - review & editing. **Min Liu:** Funding acquisition, Investigation, Methodology, Supervision, Writing - review & editing.

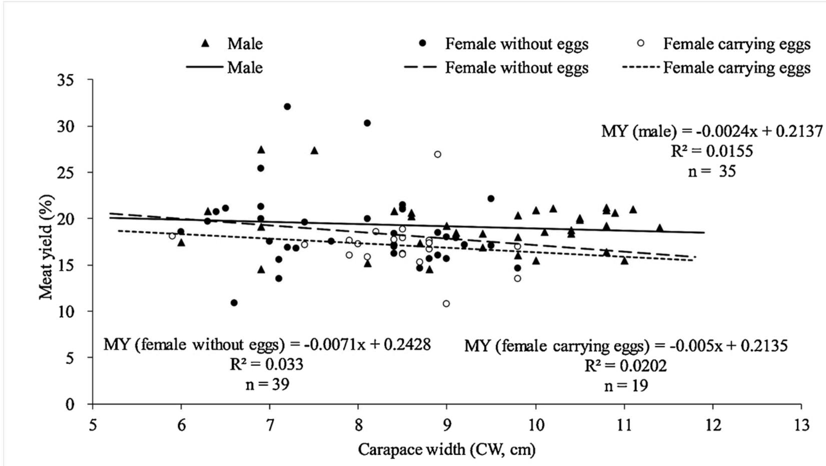

Fig. 11. Size (carapace width, CW) and meat yield (MY, %) relationships for *Monomia haanii* males (N = 35), females carrying eggs (N = 19) and females without carrying eggs (N = 39).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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