Mating Behaviour in Different Size Males of *Macrobrachium idae* (Heller, 1862)

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Abstract

Twenty seven commercial *Macrobrachium* species are found in Asia and the Pacific Ocean. Most of them are inhabited in freshwater except few are exclusively marine oriented. Few species live in brackish water especially in the mouths of rivers. A close examination of *M. idea* reveals that three distinct morphotypes based upon size ranking, the ratio of claw length to body length (relative claw length) which included small male (SM), medium sized male (MS) and bigger sized male (BS). The mating behaviors of three different males 4 experiments were conducted by (1) 3 BS males (90-100 mm) vs. female (50-75 mm); (2) 3 MS males (60-75 mm) vs. female (50-75 mm); (3) 3 SM males (45-55 mm) vs. female (50-75 mm); (4) 1BS male, 2 MS males and 3 SM males vs. female (55-75 mm). The mating behaviour of *M. idae* was divided into four phases such as (I) Contact: When the male recognize the pre-mating female, it moves towards the female and starts approaching her. (II) Guarding: During this behaviour, the male encircled the female with his second pereiopods in a way that her tail region. (III) Mounting: After shell getting slightly hardens; the male grasps the female and begins to mount the female. After that using third and fourth pereiopods male started to clean the brood chamber to deposit the spermatophore. (IV) Mating: Took place when the female turned on her back, so that her ventral side was up. Next moment the spermatophore was ejected and deposited on the ventral median thoracic region of the female. After mating the pair was separated and again the male protects the female until the shell hardens completely. The 89.46% of the females were successfully fertilized in the presence of BS males and only 4.56% failed to become berried. In the cases of MS and SM males, successful fertilization was happened in 34.5% and 38% of the females and infertility was recorded for 34.37% and 40.99% of the females, respectively. The reproductive success of the BS male was significantly higher than that of the other two morphotypes (P<0.05).

Keywords: *M. idea*; Act of pairing; Morphotypes; Reproduction; Population dynamics

Introduction

In crustaceans there is a competition for mating especially among the males. The aggressive and dominant males win over less aggressive and subdominant males [1-5]. The male reproductive success depends on male-male competition and aggression. This is very common in polygamous species. The individuals who are at a competitive disadvantage sometimes adopt an entirely different group of reproductive behaviours [6]. The present study evaluates the relative reproductive potential of three different size males of *M. idae* by examining their mating strategy in close quarter in an aquarium and to arrive at a qualitative evaluation of each of these morphotypes (representing three different developmental stages) according to each type's specific physical characteristics, typical behaviour and probability of achieving successful fertilization.

Materials and Methods

Collection

The animals were collected from Ponnanthittu (Lat.11°28'41"N; Long. 79°45'30"E) waters which is located 2 km south to Parangipettai and connected with Vellar estuary. The prawns were caught by the fisherman with the help of trap, line and hand-net and scoop net. The specimens collected from the fisherman were ranged from 30 to 110 mm in length. Totally 150 specimens were collected and transported to the laboratory in live condition by keeping them in bucket containing freshwater and aeration. After reaching the laboratory they were washed carefully with distilled water to remove the dust and algal particles.

Selection of three different sized males

A close examination of *M. idae* males reveals that three distinct morphotypes based upon size ranking and the ratio of claw length to body length (relative claw length). Three male categories include (a) small males (SM) (b) medium sized (MS) males and (c) bigger sized (BS) males (Table 1). The selection of males was performed according to the morphologically distinctive characteristics of the three male categories and females were based on their state of sexual maturation as determined by gonad development [7]. The females used in each experiment were sexually matured and mostly in the size range of 45 to 80 mm.

Experimental setup

Mating probability of SM, MS and BS males was examined in separate glass aquarium by stocking each of these morphotypes together with a female. In other set of experimental group all three different sized males (SM, MS and BS males) were stocked together with a female in glass aquarium. The rate of female fertilization by the subordinate SM, MS and BS males in separate glass aquarium and female fertilized in the glass aquarium where stocked with all three different sized males indicates that the actual probability of SM and MS males to achieve a

S. No	Category	BS male	MS male	SM male
1	Body size	Large	Medium	Small
2	Relative claw length (cm)	16-17.5	11.5-13	4-5
3	Mobility	Mainly resting and self-grooming	Mainly resting and self-grooming	Mainly exploring
4	Agonistic competition	Aggressive and dominant	Aggressive and subdominant	submissive
5	Courtship	Protecting and grooming	Never observed courting	Never observed courting
6	Copulatory attempts	Must turn over	Must turn over	Sneaking while turning itself underneath

Table 1: Qualitative comparison of physical and behavioral characteristics of the three male morphotypes of M. idea.

successful copulation in a situation more similar to that prevailing in nature where BS males are guarding and protecting receptive females.

The following stocking combinations were tried in the present study.

1. 3 BS males (90-100 mm) vs. female (50-75 mm).

2. 3 MS males (60-75 mm) vs. female (50-75 mm).

3. 3 SM males (45-55 mm) vs. female (50-75 mm).

4. 1BS male 2 MS males and 3 SM males vs. female (50-75 mm).

One glass aquarium (for a close observation) and two fiber glass tanks were kept for each stocking combinations. Whenever a male went through a morphotypic transformation, died, or suffered from physical injury (such as lost of claws while moulting or fighting), that was replaced by another male of a similar morphotype. Altogether, all males in each aquarium were replaced 3-4 times due to injuries within the entire observation period. In addition to the males, a female with ripe gonads was present at any given time in each aquarium. Whenever a female became berried, it was replaced by an equivalent female, and was transferred into a separate aquarium to observe the embryonic development. When a receptive female in an observation aquarium either did not became berried, or lost all eggs within 48 hours from the pre-mating moult, it was replaced by another female and failure of fertilization was recorded.

Experimental conditions

Observations were carried out in glass aquarium (58 × 58 × 37 cm) equipped with aerators to satisfy the need of dissolved oxygen (5 ppm) and also temperature control devices to maintain optimum temperature (27-28°C) throughout the experiment. In each aquarium six or seven plastic pipes was placed (3 cm in diameter and 5-15 cm long) which served as shelters for newly moulted individuals. All experimental animals were fed daily with chopped fish and clam meat. Uneaten feed was removed daily from each aquarium and fiber glass tanks by siphoning. Glass aquarium was checked daily for moults, male morphotypic transformations and berried females. Berried females were kept isolated in fiber glass tanks (45 × 30 × 37 cm) which also equipped with aerators and temperature control devices to maintain conducive environment.

Observations and measurements

Behavioural observations were carried out especially when a female entered into pre-mating moult. Special attention was given to the relative position of each individual in the aquarium to the male-female interactions (protecting and mating) and to the typical male-male interactions (agonistic behavior). Whenever a female was removed, some 48 hours after a pre-mating moult, its physical state was recorded, i.e., lost appendages, broken antennae and other signs of physical injury. Embryonic development was observed two weeks later by a microscopical examination of eggs sampled from the females

abdomen and served as the ultimate proof of successful fertilization. The percentages of successful fertilizations, failures to fertilize, female mortalities due to physical injuries made by males soon after pre-mating moult and other female mortalities unrelated to interactions with males were calculated.

Results

General mating behaviour

The mating behaviour of *M. idae* was divided into four phases in general as given below.

Contact

When the male recognizing the pre-mating female, it moved towards the female and started approaches her with his shoulders perked up. With his first antenna stretched forward gently grasps her uropod, pleopods etc., with his first pereiopods.

Guarding

After male contacts the newly moulted female, the male guards the female. During this behaviour, the male encircled the female with his second pereiopods in a way that her tail region faces his head region. This was continued for 1.30-3 hours until the shell slightly hardens.

Mounting

After the shell gets slightly harden, the male grasps the female and begins to mount the female. In the mean time he begins to search for the sternum of the female using the dactylae of his third and fourth pereiopods on which his spermatophore is to be deposited. The male supports female body with his long second and fifth pereiopods throughout mounting and mating. When he was recognizing her sternum near the bases of her last three pairs of pereiopods he began to turn her upside down using his first, third and fourth pereiopods. After that using third and fourth pereiopods male was started to clean the brood chamber.

Mating

Mating took place when the female was turned on her back, so that her ventral side was up. Immediately after this the male strongly bends backwards with a vigorous beating of pleopods. Pressing down from above, he brought his genital pores very close to the female's ventral thoracic region without touching the sternum. Next moment the spermatophore was ejected and deposited on the ventral median thoracic region of the females. After mating the pair was separated and again the male protects the female until the shell hardens completely.

Experimental setup 1

In this setup 3 BS males (90-100 mm) were stocked with a matured female. When the males encountered the pre-mating female there was a strong competition between the males for mating. The stronger male started to court the female from other males. Once he was won over

than he tried to contact the female and eventually mounted her. After mounting, the male turned over the female and started grooming the female brood chambers to remove the dust and other algal particles from brood chamber before the deposition of the spermatophores.

Experimental setup 2

In this setup 3 medium sized (MS) males (60-75 mm) were stocked with a matured female. When the males met with the pre-mating female there was a fight between the males for mating. At last the male which won the competition was turning over the female and finally went for mating without cleaning the brood chamber and courting was totally absent.

Experimental setup 3

In this experimental setup 3, small sized (SM) males (45-55 mm) were stocked with a matured female. When the males encountered the pre-mating female there was a competition between males. The successful male started attracting by contact and mounting the female, then tried to turn over the female. Since the males are smaller than the female it was very difficult for him to turn the female. So the male tried to mate the female by sneaking while turning it underneath of the female and started mating without cleaning the brood chamber of the female. The small males failed to court the female and occasionally injured by the continuing attempts of the several SM males to approach her at the same time.

Experimental setup 4

In this setup, 1 BS male, 2 MS and 3 SM males were stocked with a matured female. When the bigger, medium and smaller sized males were approached the pre-mating females for mating, major behavioural differences were visible between BS, MS and SM males. The BS males showed all the characters like courting, mounting and turning the female and subsequently tried to attach its spermatophore. In the BS male's territorial area the MS males were immobile. Although MS males were attracted by the female, they were easily chased away by the dominant BS male. In many instances after one or two agonistic encounters the MS males ignore the mating couple. But when the BS male was absent a series of agonistic encounters among the MS males were resulted in

dominant male trying to capture the female prior to mating. BS male spend most of its time resting and grooming themselves, or actively courting and protecting the receptive female while displaying agonistic behaviour towards all other males. The SM males were highly mobile. They were the first to react to the introduction of food and were strongly attracted to receptive females. They usually avoid physical contact with superior BS and MS males by retreating into the water column whenever closely threatened by the BS and MS males. However, there were always few SM males continuously hovering around the female whether the female was alone or protected by the BS male. Occasionally SM males were attempted to sneak under the female and attached its spermatophore to the female's abdomen. The successful aggressive BS male turned the female and attached their spermatophore.

Reproductive potential of the three male morphotypes

Comparison between the relative frequencies of successful fertilizations by the three male morphotypes was presented in Table 2, experiments 1, 2 and 3 showed that the reproductive advantages of BS male were dominant over MS and SM males. The female was successfully (89.46%) fertilized in the presence of BS males and only 4.56% female was failed to become berried. In the cases of MS and SM males, successful fertilization was 41.69% and 34.66% and the infertility was recorded 34.37% and 40.99% respectively. The reproductive success of the BS male was significantly higher than that of the other two morphotypes ($P<0.05$) (Table 3).

In addition to high probability of achieving a successful fertilization, BS proved to be better guards of receptive newly moulted females than SM and MS males. Only BS males were observed to protect the females during courtship activity. Moreover, only 3.18% of the females died as a consequence of male aggression whenever BS males were present, whereas females stocked with MS and SM males, had a mortality rate of 18.74% and 19.09% respectively.

Reproductive potential of SM and MS males in the presence of a dominant BS male

In the experiment-4, where SM and MS males were kept together with BS males (Table 2), 70.33% of the females were successfully

Experiments	Stocking combinations	Successful fertilization (%)	Failure of fertilization (%)	Mortality due to inflicted injuries (%)	Natural mortality (%)
1	3 BS	89.46 ± 1.76	4.56 ± 0.42	3.18 ± 2.76	2.77 ± 4.81
2	3 MS	41.69 ± 5.06	34.37 ± 2.12	18.74 ± 4.24	5.18 ± 1.73
3	3 SM	34.66 ± 2.75	40.99 ± 0.86	19.09 ± 2.18	5.20 ± 2.44
4	1 BS male, 2 MS males and 3 SM males	70.33 ± 5.12	17.89 ± 4.35	7.39 ± 2.31	4.36 ± 4.12

Table 2: Reproductive potential of the three male morphotypes when held separately and in combination with female (values are mean of three values ± SE).

Parameters	Source of variation	SS	df	MS	F	P-value	Sig
Successful fertilization	Between Groups	5846.169	3	1948.723	124.7414	4.68E-07	
	Within Groups	124.9768	8	15.6221			P<0.05
	Total	5971.146	11				
Failure of fertilization	Between Groups	2431.406	3	810.4687	132.8111	3.66E-07	
	Within Groups	48.81933	8	6.102417			P<0.05
	Total	2480.226	11				
Mortality due to inflicted injuries	Between Groups	584.4189	3	194.8063	21.78889	0.000332	
	Within Groups	71.525	8	8.940625			P<0.05
	Total	655.9439	11				
Natural mortality	Between Groups	11.65053	3	3.883511	0.313206	0.815595	
	Within Groups	99.19387	8	12.39923			P<0.05
	Total	110.8444	11				

Table 3: One-Way ANOVA for the reproductive potential of the three male morphotypes (%) when held separately and in combination with females.

fertilized, indicating that females may readily become berried, under these experimental conditions, depending only on the ability of the male morphotypes present to complete successful mating. All reproductive relative behaviour is statistically significant (Table 3).

Discussion

Many scientists worked on alternative mating strategies world over [8-12]. These approaches have focused primarily on behavioural or developmental differences among individuals. Raanan and Sagi [13] described three male morphs representing successive growth stages in freshwater prawn, *M. rosenbergii* [14]. Kuris et al. [15] demonstrated that developmental path among the male morphs in *M. rosenbergii* are determined by feeding schedule and social interactions among individuals. Barki et al. and Kurup et al. suggested that in fact, four morphs are identifiable [16,17] and that dominance hierarchies among the morphs exist, wherein removal of larger individuals induces smaller individuals to grow. However, not all individuals responded equally to this stimulus, as expected if males vary in their responsiveness to social and nutritional cues [15,18]. Other *Macrobrachium* species also appear to exhibit male polymorphism, *M. dayanum*, *M. idae*, *M. malcolmsonii* and *M. scabriculum* reviewed in [15]. In the present study *M. idae* also showed dominance hierarchies among the males as in *M. rosenbergii* [19,20]. The different male morphotypes were defined on the basis of colour and spination of the chela, behaviour and growth characteristics [21,22]. Kuris et al. [15] have summarized operational allometric criteria to recognize the morphotypes and describe the transition between morphotypes. The *M. idella idella* were classified mostly based on the size of the chelate, behaviour, and growth characteristics but not the colour of the chelate legs as in *M. rosenbergii* [23]. In the present study also *M. idae* was classified on the size of the chelate, behaviour and growth characteristics not the colour of the chelate legs.

Mating is initiated only after a female experienced the pre-mating moult. Necessity of pre-mating moult in decapods has been described by several workers. Atema [24] suggested that inter-moult females get rejected by the males, because they lack of proper sex pheromone. Antheunisse et al. [25] observed that the female *Palaemonetes* with ripe ovaries moult into "breeding dress", which is characterized by the presence of extra setae for egg attachment, enlargement of abdominal brood pouch and development of periodic chromatophores etc. Following the moult into "breeding dress", females became attractive and receptive to males. It is inferred that the pre-mating moult is the preparatory step for breeding purposes. In the present study, *M. idae* males were also preferred the permating females and rejected inter-moult females. Just like *M. idella idella* [23] the females of *M. idae* also had ripe ovaries and enlarged brood pouch with extra setae for egg attachment.

In the present study the bigger (BS) and smaller (SM) sized males may represent two alternative ways of mating while the medium sized (MS) males may be considered an intermediate developmental stage between these two, with a relatively low mating probability as such, in the presence of a BS male. This notion is supported by the fact that both SM and BS males hardly increase in body size while MS males are characterized by a rapid growth rate [22,26], thus, investing relatively little energy, if any, in reproduction during this stage of development. The BS mating strategy may rely on superiority in threatening display towards the other males, while investing a great deal of energy in developing its weaponry (large, massive claws).

In many crustaceans male's exhibit highly developed fighting structures (chelae, pereiopods). Males of these species may overtake females and hold them in a firm mating grip making it difficult to detect females have preferences. Despite these difficulties several studies indicate that females are capable of exerting preferences for certain males by exhibiting resistance to the advances of some males. For example, female tanner crabs resisted mating attempts from one-clawed males [27] and female crayfish resisted mating attempts from small males more efficiently than those from larger males [28]. In many species of females offer little resistance to males because it may be costly and dangerous, sometimes even leading to the death of the female [13]. Instead of showing overt choices, females may exert their preferences for certain males in subtle, often cryptic, behaviours that are difficult to observe or quantify. It is for these reasons that female preferences are often little known in crustacean species with coercive male mating behaviour. In the three spot crab *Portunus sanguinolentus*, small male invaded the breeding territories of larger male. Since the larger male had bigger chelate which displayed aggressive interaction with small male and chased away and finally placed himself in the cradle carry position. The female crab avoided the small crab and accepted the bigger crab for its aggressive interaction and eventually successful mating was happened [29]. In all of these populations, extreme sexual dimorphism involving large size and elongated chelae in males suggests that competition for mates is intense [30]. Moreover, relatively long lived individuals appear to obtain information and respond appropriately with respect to their future mating opportunities, to nutritional and social cues during development [15]. Populations of the same species appear to vary in the proportions of individuals exhibiting different male morphologies [31,32]. In the present study the bigger sized males dominated over the other medium (MS) and small sized (SM) males and the females preferred BS males than other two sizes because the bigger sized males court and protect the female by his bigger chelate leg from other males. Whereas the courting behaviour is absolutely absent in medium and small sized males.

Courtship display is an important pre-mating behaviour in carideans. Heckenlively [33] and Ameyaw-Akumfi [34] suggested that courtship reduces aggressive tendencies in the female. Antennal contact by the male with a receptive female appears important in recognizing the sexual receptivity [35]. Hamano [36] suggested that the antennal contact created a mutual understanding between the mating pairs. As in *Palaemonetes pugio* and *P. vulgaris*, the male can recognize a receptive female only after antennal contact with any surface of the female [37]. The recognition mark may be a non diffusible coating of the integument of the female [38]. However, Ling [39] suggested that the ripe female *M. rosenbergii* secretes a substance which attracts male. Gleeson [40] reported the presence of pheromone in the urine of pre and post-pubertal moulted female blue crabs. *Callinectes sapidus* which is elicits courtship behaviour in mature males. Similarly, males of the small shrimp, *Heptacarpus paludicola* respond to matable females from a distance with increased levels of activity such as, walking and swimming [41], the females may emit a water-soluble pheromone which attracts males. The presence of pheromone is not tested in the present study. However, it is clear that antennal contact is unavoidable and such contact elicits an immediate response from the female. Precopulatory mate guarding is widespread among crustaceans [42,43]. The explanation for this tendency in many species is moulting initiates female receptivity and chemical cues present in female urine or present on females themselves prior to this moult allows males to locate, guard and inseminate females as soon as they become receptive. Mate guarding reduces the ability of females to mate more than once, thus a male who guards a female successfully fertilizes all of her ova. If a

male unsuccessfully guards his mate, or if he leaves her in search of other females before her receptivity is complete, the males fertilization success with that female will be eroded due to matings by other males. Sperm competition is reported to be an alternative mating strategy in crustaceans [43-45]. The guarding behaviour is an act of protecting the newly moulted female from aggression by other individuals. In the present study, *M. idae* showed this behaviour before and after mating until the females shell hardened as in *M. idella idella* [23]. Unfortunately Chow et al. [46] did not observe any such behaviour in *M. rosenbergii* whereas, Ling (1969) [39], Ling (1962) [47] reported such behaviour in *M. rosenbergii*, in which the pre-mating moulted female was promptly and tenderly protected by a mature male from the attack of other individuals.

Males in a wide range of crustacean species that engage in mate guarding exhibit flexibility in guarding duration in response to local sex ratios, as well as in their responses to female body size, reproductive condition, parasitemia and resistance to male guarding attempts [43,48]. Variability in guarding duration in response to sex ratio shows a consistent pattern in several pericardia [43]. Such behavioral flexibility is consistent with the hypothesis that mate guarding evolves as an adaptation to prevent multiple mating. Flexibility in mate guarding behaviour is evidently under strong sexual selection because males who guard ineffectively lose fertilizations to other males. Thus, the expression of this behavioural trait is consistent with the predictions of threshold inheritance of behavioral phenotypes [45]. The present study was also evident for the above reasons. Genetically variable characters likely to influence behavioural liability include individual sensitivities to crowding and to circulating hormone levels [49-51]. Other characters likely to influence mating behavior may include heritable sensitivities to pheromone concentrations [52], to the density of mating competitors [53], or to the perception of mating behavior by other individuals [54]. In *M. rosenbergii,* the BC (Blue claw male) males seem to enjoy most of the benefits which contribute to male reproduction success, namely, high attractiveness for females, advantage in agonistic encounters with other males, and high survival (85-100%) probability of fertilized females following mating. The main costs associated with BC mating strategy involve energy expenditure in defending a territory, reduced flexibility to readjust to changing environmental conditions, and the reduced ability to moult and thereby regenerate lost limbs, resulting in a relatively short life span [13]. In the present study the BS males also showed similar behaviour as in BC males of *M. rosenbergii* and BS males of *M idelle idella* [23]. The bigger chelate male crab of *P. sanguinolentus* enjoyed all sexual related activities and ultimately succeeded in mating with females [29].

In many species, small males invade the breeding territories of larger males by avoiding direct competition altogether. Once inside breeding territories, these "sneaker" or "satellite" males surreptitiously mate with receptive females, as occurs in isopods (*Paracerceis sculpta*, [55], amphipods (*Microdeutopus gryllotalpa* [56], *Jassa marmorata* [57] and in many decapods, *Macrobrachium* spp [13], sand bubbler crabs, *Scopimera globosa* [58], spider crabs, *Libinia emarginata* [59] and rock shrimp, *Rhynchocinetes typus* [60]. In each of these species, stolen matings appear to yield unconventional males but a tiny fraction of the fertilization success gained by males. That is, satellite males appear to "make the best of a bad job" [11]. In the present study unconventional males took fertilizations away from males whose fertilization success is already disproportionately large; satellite males are more successful at siring offspring than territorial males who secure no mates at all. SM males, on the other hand, were less attractive to females. However, their ability to readjust quickly to changing conditions, together with

the ever-present option to shift to the MS rapid growing phase, and its associated chance of becoming a BS male, may balance the lower probability of fertilizing females while being a SM male (only 34.66% under the present experimental conditions).

In the present study the males mating strategy in *M idae* is dependent primarily on the individual's size ranking within the population. A direct relationship between relative size and mating behaviour was also described in the cases of *M. rosenbergii* [13], dung flies, *Sepsis cynipsea* [2] and *Scatophaga stercoraria* [61]. In the above cases most of the size variation was attributed to environmental causes. Constantz [5] suggested that a highly competitive environment, in which there is a high frequency of large males, may favour small, sneaking males, since territorial males primarily will be occupied with agonistic behaviour that consumes a significant fraction of their time and energy. At an evolutionary stable strategy, the relative proportions of the two male types in the population should be at an equilibrium in which the fitness of both is equal [62]. The signals by which any individual determines its relative position within the size hierarchy, and the mechanisms by which these signals are translated to mating behaviour and to the regulation of growth rate are presently unknown.

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