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Sexual Biology and Mating Behaviour in Decapod Crustaceans: A Case Study with Coral Reef-Dwelling Caridean Shrimps

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Abstract

Crustaceans have diversified sexual systems, incorporating various reproductive modalities such as gonochorism and a wide variety of hermaphroditism. In particular, the coral reef-dwelling caridean shrimps, living in symbiosis with other marine invertebrates, have developed unusual sexual systems that have given origin to a range of social systems, including the highly advanced eusociality. Protandric hermaphroditism, common among the caridean shrimps, has also reached a unique sexual condition, known as protandric simultaneous hermaphroditism in the genus Lysmata. Similarly, mating systems in the caridean shrimps are highly diverse and divergent. In addition, their occurrence in the coral reef shrimps is correlated to their lifestyle adaptations such as their commensal association with other invertebrates. Other ecological factors like the predation risk from outside of the host animals and differences in the host characteristics may also be the driving forces in determining mating associations. Furthermore, the transition from sexual monogamy to social monogamy under conditions of their symbiotic life led to a complex community living in several synalpheid shrimps. Understandably, the existence of various sexual and mating systems in these caridean shrimps has a dependence on the eco-social conditions prevalent in the coral reef biota.

Keywords: Alternative Mating, Eusociality, Monogamy, Protandric Hermaphroditism, Sexual System

1. Introduction

Crustaceans have an ancient origin about 500 million years ago during the Precambrian period[1] and have undergone dynamic species radiation, occupying diverse niches primarily in marine and freshwater ecosystems, with a few species venturing into land habitats. Decapods are the most species-rich and diverse group of Crustacea with an unrivalled diversity of sexual systems and mating behaviours to maximize mating success and fertilization accomplishment. Among the major groups of Decapoda, caridean shrimps (infra-order Caridea) found in the coral reef biota have developed unique sexual and mating systems, as a way of adaptation to living and reproducing in these precarious environmental niches. The majority of the caridean shrimps inhabiting the coral reef are found in commensal association with other marine invertebrates such as sponges, sea anemones, corals, and echinoderms. Although no precise tropic relationship between the shrimps and their invertebrate hosts has been established so far[2], the term symbiosis has been invariably used to refer to an association between the coral reef shrimps and their hosts, in as much as the former derive protection from predators and finds the host as a live shelter for breeding[3]. These shrimps show a wide variety of host-use patterns in which some species are found as solitary individuals, others as small structured or unstructured groups, and even others occurring as large loose aggregations in their respective hosts[2]. Following a symbiotic lifestyle along with other environmental factors, many of these symbiotic caridean shrimps reached complexity in their sexuality and mating behaviours, leading to communal

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living, and establishing an advanced social system, such as eusociality. This study attempts to review the origin and occurrence of different forms of sexuality and types of mating systems found in the coral reef-dwelling caridean shrimps.

2. Sexual Systems

Although a majority of crustaceans are gonochoristic, with individuals in a population expressing only one sex during their lifetime, a wide range of alternative sexual systems (from androdioecy to protandric simultaneous hermaphroditism) is witnessed in the vast assemblage of aquatic crustaceans. The occurrence of diversified sexual systems in crustacean taxa has an underlying relevance to different modes of sex determination and differentiation, habitat conditions, reproductive adaptations, and mating success. Among the caridean shrimps, the family *Hippolytidae* comprises many species that possess unique sexual systems, as a consequence of their adaptation to specialized habitat niches in the tropical coral reef environment[3]. Naturally, the occurrence of different types of protandric hermaphroditism has become the hallmark of sexuality in these caridean shrimps. Simultaneous hermaphroditism, in which the animal produces mature sperm and ova at the same time occurs mainly in lower crustaceans and the sessile barnacles with the ability to self- or cross-fertilize[4,5].

3. Protandric Hermaphroditism in Carideans

Although gonochorism is the principal mode of sexuality in Caridea, several alternative sexual systems comprising several forms of mixed-sex hermaphrodites exist in the coral reef-associated shrimps[3]. The most common sexual system is, however, protandric hermaphroditism, in which the individuals first mature as males and then, with an increase in size and age, change sex to females. Characteristically, protandric hermaphroditism in caridean shrimps exists in different forms. For example, in *Lysmata seticaudata,* all individuals in the population are reported to transform from males into females[6]. Later works however concluded that in all *Lysmata* species, the protandry was recognized to be another sexual condition namely protandric simultaneous hermaphroditism (see below). Nevertheless, in other protandric carideans, a variable proportion of the population matures as primary females without passing through a male phase. Thus, in *Thor manningi* of the family *Hippolytidae*, the population is composed of 50% primary males and 50% protandric hermaphrodites[7]. Furthermore, in the alpheid species, *Athanas kominatoensis* the population consists of both primary males and sex changers[8], whereas in yet another alpheid species *A. indicus* a mix of primary females, primary males and sex changers are reported[9].

4. Protandric Simultaneous Hermaphroditism

Protandric simultaneous hermaphroditism has been defined as the sexual pattern in which individuals first mature as a male and, with an increase in size, molts into a simultaneous hermaphrodite or ‘euhermaphrodite’, which can reproduce both as a male and female by outcrossing. Bauer[10] first described this sexual condition in the hippolytid genus *Lysmata* and rechristened it into protandric simultaneous hermaphroditism. This category of sexuality is also termed “adolescent protandry”[11]. Shrimps belonging to the Caridean genus *Lysmata* inhabit subtropical and tropical waters in the rocky bottom and coral reef crevices. They have striking colouration and, some species have fish-cleaning behaviours. Interestingly, protandric simultaneous hermaphroditism is found to be the only sexual system described so far in *Lysmata* genus[12,13].

In the *Lysmata* shrimp, a typical individual begins their reproductive life as a functional male and later transforms into a simultaneous hermaphrodite[14]. As in the protandric shrimps, the gonads are ovotestes, the ovarian portion of which is slower to mature than the testis part[13]. Protandric simultaneous hermaphrodites do not possess a mechanism for self-fertilization and, as a rule, *Lysmata* species are non-reciprocally outcrossing simultaneous hermaphrodites. The hermaphroditic *Lysmata* spawn successively and brood their embryos attached to the pleopodal hairs. Immediately after the hatching of the embryos, the hermaphrodite molts and becomes receptive to mating. This shrimp can mate with either a male or another simultaneous hermaphrodite. For the mating between two simultaneous hermaphrodites to occur, the female-acting individual should be the newly molted, pre-spawning, partner whereas the male-functioning shrimp could be in any stage of molting or spawning or in any stage of egg incubation. Understandably, female mating requires a fresh molt condition, during which it becomes receptive to males for depositing the spermatophores[3]. Observational data also reveals that pair formation more often occurs between two hermaphrodites rather than between a male and hermaphrodites, suggesting that hermaphroditic pairing will double their reproductive output by way of producing embryos as well as inseminating their sexual partner, in comparison with hermaphrodites paired with males. Sex allocation, referring to parental investment in the respective male and female gamete formation, is female-biased in these simultaneous hermaphrodites, making egg formation and embryo development in the brood, a priority[15].

5. Mating Systems

Mating brings about the union of both male and female gametes, culminating in fertilization and the production of a diploid zygote with the potential to develop into an adult. The most primitive form of this process occurs in marine invertebrates like corals, polychaetes and echinoderms, which release their gametes into the open sea, where random mating (fusion of male and female gametes) takes place. This type of fertilization does not require body contact between males and females. Conversely, internal fertilization involves a simple or elaborate mating process, preceded by mutual attraction and prolonged courtship[16]. Although crustaceans have originated in the sea and have undergone adaptive radiation in different marine environments, they are never known to practice free spawning, except penaeid shrimps, which release their fertilized eggs into the seawater for direct development. Most of the other crustacean species however brood their fertilized eggs attached to pleopodal hairs, sometimes forming a brood chamber. Furthermore, decapod crustaceans possess atypical, non-motile spermatozoa, making them unsuitable for broadcast fertilization in the seawater medium. Consequently, crustaceans have contrived sperm transfer mechanisms using sperm packets, called spermatophores[16]. In primitive insects and Cryptozoic soil arthropods, spermatophore transfer occurs by indirect, contact-free methods, whereas in crustaceans, sperm transport via spermatophore is always direct, involving true mating[17].

In crustaceans, mating behaviour has evolved around the percept that molting in the adult female is an intervening factor for reproductive activities, such as spawning. In many decapods, reproductive activities alternate with molting cycle, sometimes in quick succession, so that mating, fertilization and egg laying are relegated to the post-molt stage when the female gonopores are soft and accessible to intromittent organs for copulation. Hartnoll[18] distinguished this type of mating as “soft-female mating” as against the “hard-female mating” in which the female copulates during the intermolt stage. In addition, several other factors such as the low operational ratio between females and males, availability of receptive females as well as male mating behaviour impose restrictions on the structuring of mating systems in crustaceans. In addition, males are equipped with powerful chelae, which are useful in female defence and guarding during mating[4]. In general, mating systems in Crustacea are classified in terms of the number of mates per male or female, and male mating behaviour has evolved primarily in response to the spatial and temporal distributions of receptive females in the population[19].

Basic mating systems found in Crustacea consist of monogamy and polygamy, although other mating practices like mate guarding and pure searching are prevalent among various decapods. Emlen and Oring[20] opined that polygamy is the optimal male mating strategy, whereas monogamy coupled with mate choice is the optimal female mating strategy. Furthermore, in many crustaceans, mating systems involve dramatic premating behaviour on the part of the male, such as courtship signalling, fighting among males or defence of females before mating. Other influencing factors on the evolution of mating systems in Crustacea relate to life history patterns, ecological influence, functional morphology of copulation and insemination, and social determinants of both male and female behaviors[21].

6. Mating Systems in the Coral Reef Caridean Shrimps

Caridean shrimps inhabiting the coral reef ecosystem have evolved a dazzling array of mating systems, in response to their peculiar lifestyle of symbiotic living with other marine invertebrates. Accordingly, mutualistic living with live host animals has promoted different mating associations such as pair-living monogamy or host-switching polygynandry. In addition, habitat (host) characteristics have a profound influence on shaping mating strategies into social systems in symbiotic shrimps. The complexity of evolved social structures in them could match only the social systems found in insects and higher vertebrates like birds. In addition to symbiotic shrimps, the coral reef carideans also include many species that are free-living and gregarious. They too have adopted distinct mating strategies, suited to their lifestyle. Different mating systems existing in coral reef caridean shrimps are listed in Table 1.

Table 1. Common mating systems in coral reef-associated shrimps

1.1 Short Courtship Type of Mating (Pure Searching)		
Species	**Host Organisms**	**References**
Heptacarpus picta	Free living	48
Heptacarpus paludicola	Free living	49
Athanus nitescens	Free living	23
Alpheus dentipes	Free living	23
1.2 Pair Bonding Monogamy Type (Heterosexual Pair)		
Apopontonia dubia	*Spongia* sps.	50
Onycocaris amakusensis	The sponge *Callyspongia elegans*	51
Onycocaris oligodendata	purplish sponge	51
Onycocaris spinosa	Small sponges living at the base of the branching corals	51
Onycocaridella prima	*Mycale sulcata*	52
Onycocaridella monodoa	Pavaesperella hidentata	52
Onycocaridites anornodactylus	Sponges	53
Orthopontonia ornatus	*Jaspis stellifera*	54
Periclimenaeus stylirostris *Periclimenes brevicarpalis*	Sponges and ascidian tunicates Sea anemone *Stichodactyla haddoni*	55 56
Typton dentatus	Coral actinaria, *Reniera* sps.	55
Periclimenes brevicarpalis	*Stichodactyla haddoni*	57
Dasycaris zanzibarica	black coral, sea whips	58
Periclimenes colemani	Asthenosoma intermedium	59
Periclimenes ornatus	*Entacmaea quadricolor, Heteroactis malu, Parasicyonis actinostroides*	57
Anapontonia denticauda	*Galaxea fascicularis*	60
Coralliocaris superba	Staghorn coral, *Acropora tubicinaria and* 15 other sps. of *Acropora*	28
Jocaste lucina	Acropora tubicinaria	28
Jocaste japonica	*Acropora* sp., *Acropora humilis, Acropora variabilis, Acropora tubicinaria, Acropora nasuta*	2

Table 1 to be continued...

Ischnopontonia lophos	*Galaxea fascicularis*	2,28,52
Periclimenes koroensis	*Fungia actiniformis*	61
Philarius imperialis	Acropora sp., Acropora *Millepora*	55
Vir philippinensis	*Plerogyra sinuosa*	61
Ctenopontonia cyphastreophila	*Cyphastrea microphthalma*	62
Paratypton siebenrocki	*Acropora hyacinthus* and other 6 sp. of *Acropora*	28
Stenopus scutellatus	Free living	63
Stenopus tenuirostris	Free living	64
Stenopus zanzibaricus	Free living	58
Lysmata debelius	Pisces	25,58
Lysmata grabhami	Pisces	63,65
Thor amboinensis	Actiniaria, Scleractinia	66
Stenopus hispidus	Pisces (Morays, tangs, grunts, groupers)	24; 67
Lysmata debelius	Free living	25
Hymenocera picta	Free living	26
Alpheus angulatus	Free living	23
Alpheus heterochaelis	Commensal with *Panopeus herbstii*	23
Alpheus armatus	*Bartholomea annulata*	23
Alpheus roquensis	*Bartolomea lucida, Bartholomea annulata*	23
1.3 Eusociality		
Synalpheus rathbunae	*Xestospongia rosariensis*	68,69,70
Synalpheus paraneptunus	*Hyattella intestinalis, Oceanapia sp., Pachypellina podatypa, Xestospongia cf. proxima*	68,71,72
Synalpheus regalis	Sponges Xestospongia cf. subtriangularis and *Hyattella intestinalis*	36,38
Synalpheus filidigitus	*Xestospongia*	36,73
Synalpheus chacei	Demosponges *Niphates amorpha* and *Lissodendoryx colombiensis*	74
Synalpheus elizabethae	Sponge *Hyattella intestinalis*	36,69
Synalpheus neptunus	Neopetrosia proxima	75,76
1.4 An Alternative Type of Mating		
Rhynchocinetes typus	Free-living	32
Athanas kominatoensis	Purple sea urchin	8
Rhynchocinetes durbanensis	Free-living	45

7. Pure Searching

Many caridean shrimps live in congregation in the coral reef niches. Shrimp families belonging to *Alpheidae* and *Hippolytidae* include several small-male species, practising promiscuous mating systems with little precopulatory interaction between males and females[3]. In these free-living swift-moving shrimps, the male mating tactic is "pure searching", in which the males are continuously on the prowl for a receptive female and, when one is encountered, she copulates with minimum premating interactions. The male then sets off to search for another receptive female. Unlike other mating systems in Crustacea, the males do not fight for or defend females, keeping the intra-male competition to the rapid and efficient searching for receptive females[22]. Pure searching could be considered a primitive mating system in as much as the males do not invest in guarding the female partner beyond spawning. High population density and high frequency of spawning in the free-living caridean shrimps favour the evolution of a pure searching mating strategy rather than the energy-expensive female guarding strategy by males. The males are small in size and do not possess any weaponry such as the large chelipeds, characteristic of mate-guarding shrimp species. Small body size in males increases their agility in finding the potential mating partner and renders them less conspicuous to predators[21].

Pure search mating behaviour is also found in symbiotic caridean shrimps; in such cases, it is termed pure search polygynandry. In this mating system, males roam among hosts in search of receptive females and, once mated, the males leave the female in search of others. The female gets the benefit of mating with different males, thereby enhancing the genetic diversity of their offspring. Another deviation from pure search mating is found in the shrimp species of the genus *Athanas*, which leads to a solitary symbiotic life on sea urchins. Adult males change their hosts in search of receptive females living solitarily in other sea urchin hosts and, when they find one, they form heterosexual pairs[5]. After mating, however, the males depart the female in search of other mates. If the males have limited chances of getting extra females for mating, due to low population density, then the male attends to the female for a longer period, resulting in monogamy[23].

8. Monogamy

Adoption of a symbiotic lifestyle represents one of the important environmental adaptations found in the caridean shrimps of the coral reef ecosystem. The macro-invertebrates that harbour the symbiotic shrimps are chiefly sponges, corals and sea anemones. Depending on the host characteristics such as ecology, morphology, abundance, and spatial distribution, the caridean shrimps have evolved different mating systems. Among them, the most commonly found is monogamy, in which a heterosexual pair live and reproduce together inside a host animal. According to Emlen and Oring[20], monogamy in vertebrates would evolve when females are dispersed, owing to scarce and/or widely dispersed resources, or when young are dependent on care from both parents. On the other hand, monogamy has evolved in the symbiotic shrimps under circumstances when hosts are relatively rare and are small enough to support only a few individuals, and the predation risk away from the hosts is high[21]. In the pair-bonding species of caridean shrimps, males cohabit with females, independent of their reproductive status or developmental stage in brooded embryos. Examples of such stable pairing among caridean shrimps are the banded shrimp *Stenopus hispidus*[24], the scarlet cleaner shrimp *Lysmata debelius*[25], the harlequin shrimp *Hymenocera picta*[26] and several species of snapping shrimps such as *Alpheus angulatus*, *A. heterochaelis*, *A. armatus* and *A. roquensis*[23]. These monogamous symbiotic shrimps are territorial, and cooperatively defend their host and hence are called resource-defence monogamy.

Furthermore, the symbiotic living of caridean shrimps with invertebrate hosts has also given origin to different forms of monogamy. Shuster and Wade[19] described a variant of pair bonding, termed "persistent pairs" in the sponge shrimps *Sponigocola* and *Spongiocaris*, which form pairs within the hexactinellid sponges. Juvenile shrimps enter the sponge through its basketlike body wall, and soon grow too large to escape the sponge and remain imprisoned for their entire adult lives within the rigid spongocoel[27]. Interestingly, the death of one member of the breeding pair results in the sterility of the other member. Another example of persistent pairs is found in the pontoniin shrimp *Paratypton siebeurochi* which lives in association with the scleractinian coral *Acropora*.

In this case, a male and female form a cyst within the corallum of the coral and get permanently incarcerated together for their entire life[28].

9. Social Monogamy

An important variant of monogamy in the coral reef caridean shrimps is social monogamy, meaning the togetherness of two heterosexual adults as a social system[26]. This type of monogamy in the symbiotic shrimps has originated from the long-lasting heterosexual pairing, bolstered by behavioural traits such as territorial cooperation and extended mate guarding by the male partner. Social monogamy has been described in two *Alpheus* species, *A. armatus* and *A. imaculatus*, both of which live symbiotically outside of their sea anemone host, *Bartholomea annulata*[29]. Whereas the males of *A. immaculatus* stay close to their female partners, the males of another species, *A. armatus,* would frequently leave their female partners to find and mate with other solitary females. It is posited that lower predation pressure in *A. armatus* would have allowed males to wander from their anemone host and their female partner, thereby becoming polygynous. The males of *A. armatus* have bigger snapping claws than *A. immaculatus* males and have more colourful uropods to meet the challenges of competition for solitary receptive females. On the contrary, high predation pressure in the habitat of *A. immaculatus* has favoured a "forced" sexual fidelity in the males. Social monogamy is also seen in the sponge-dwelling symbiotic species belonging to the genus *Lysmata.* In these shrimps, social monogamy is formed between a male and a simultaneous hermaphrodite or more, frequently between two simultaneous hermaphrodites[16]. As for these symbiotic shrimps, monogamy is advantageous in the coral-reef environment, where sponge refuges are discrete, scarce, relatively small, and when predation risk is high outside of this refuges[15].

Mating strategies in the caridean shrimps not only differ among species but also the deviation occurs at the intraspecific level. The protandric simultaneous hermaphrodite *Lysmata pederseni* living inside the tube sponge *Callyspongia vaginalis* shows monogamy in the population on the southeast Caribbean coast, whereas the same species inhabiting the same sponge in the coral reef at Florida Keys, Florida, USA, lives solitarily or in groups inside the sponge tube. They do not form heterosexual pairs inside their living host but practice polygynandrous mating[30]. This intraspecific difference in mating behaviour is attributed to the environmental heterogeneity and the host ecology inherent to these two coral reefs. The host sponge in the Caribbean Island is a scarce resource, and the predation risk for the shrimp is high, thereby favouring monogamy. On the contrary, in the Florida Keys, the host sponge population consists of more abundant, but smaller individuals than the population of the central and south Caribbean[15]. The solitary *L. pederseni* found in the sponge tube is also seen to brood embryos of different developmental stages. The high sponge host abundance in the Florida Keys is conducive for the males and/or the hermaphrodites to roam among the host individuals seeking solitary hermaphrodites, resident in the sponge tube. This condition leads to the abandoning of monogamy by the males and adopting a promiscuous polygynandrous mating system in the Florida Keys population. The assumption of mating association in these symbiotic *Lysmata* shrimps is not genetically programmed but is liable to changes due to variations in the host characteristics such as density, abundance and spatial distribution[15].

10. Precopulatory Mate Guarding

In crustaceans, mate guarding has evolved as a male's competitive strategy to monopolize a female for copulation, and to ensure his priority of access to the female when the latter becomes receptive[31]. Among the coral reef free-living caridean shrimps, the rock shrimp, *Rhynchocinetes typus* shows the atypical mode of mate guarding by caging the female between the chelipeds, until the latter becomes receptive for mating. In these rock shrimps, the males exist in three morphotypes, and only the dominant robustus morphotype is engaged in precopulatory female guarding, while the female-like typus and intermedius types mate stealthily and deposit the spermatophores without prior mate guarding[32].

As for the symbiotic shrimps, the host organism constitutes a critical resource and hence the males increase their chances to mate by monopolizing the hosts. Host defence in these symbiotic shrimps has also led to guarding the female partner in the monogamous mating system. For example, in the partially protandrous shrimp *Athanas kominatoensis*, monopolization of hosts allows males to defend their refuges and potential mating partners on them[8]. In the caridean shrimps, mate-guarding behaviour along with predation pressure in the symbiotic species have become the selective forces towards the advancement of social monogamy. This is in contrast with the other behavioural factors such as the biparental care of the offspring as well as the territoriality, which would have constituted the driving forces of social monogamy in birds and mammals[33].

11. Eusociality

Wilson (1971)[34] defined eusociality as the condition of multiple generations organising into groups using an altruistic division of labour. In social insects, like the honey bee and termite ants, this condition extends further into cooperative care of offspring, and reproductive skew, by which reproduction is restricted to a single mother queen. As for aquatic animals, crustaceans have the unique distinction of having evolved such complex social systems only in the coral reef-associated caridean shrimps[35]. Duffy[36] first reported the discovery of eusociality in *Synalpheus regalis* from the lifestyle description of this sponge-dwelling alpheid shrimp species. *S. regalis* lives inside large sponges in colonies of up to 350 individuals with only a single breeding female, the queen, as well as a small number of male mates. The queen lacks the characteristic snapping claw, and bears two minor chelae, as found in juveniles. The colony members of *S. regalis* exhibit behavioural differentiation too. The large sub-adults, with their powerful chelae, defend the colony against intruders, allowing the juveniles and the queen to feed and grow unmolested. The sub-adults, whose reproductive potentials are suppressed, are analogous to the sterile worker honeybees[37]. In addition, the genetic relatedness of colony members, as revealed from allozyme data, together with demographic evidence of natal philopatry, would further indicate that colonies in this species represent close kin groups, which form a necessary prerequisite for evolution into eusocial condition[38]. These eusocial shrimps have direct development and, hence, the offspring never leave the sponge nest and remain with the parent shrimps.

Additional observations indicate that *Synalpheus* species display varying levels of social development, ranging from colonies containing multiple queens to a single egg-laying queen. For example, in *S. longicarpus*, hundreds of heterosexual pairs cohabit in a sponge host with multiple breeding females[39]. In another species, *S. chacei*, the colonies are much smaller, but genetically heterogeneous, indicating the presence of multiple queens in the colony. The females of this multi-queen colony are not only smaller but possess snapping claws. Bornbusch *et al.*,[40] analysed the energy allocation strategies in the queen towards reproduction (fecundity) and defence (fighting claw) as related to the evolution of eusociality. This study also analysed the reproductive success of the reproductive queen in terms of several eggs laid versus colony size. When multiple reproducing females occur within a less-evolved eusocial colony, an intra-sexual competition within the colony is created, favouring the development of a large major chela in the queens. On the other hand, in the highly evolved eusocial species, more energy is invested in egg production by the single queen, with less need to maintain defensive weaponry, such as the development of a large chela. Further studies on the ecology and behaviour of Synalpheid species would unravel the influence of extrinsic factors that affect the morphology and reproductive potentials of the queen in shaping the eusocial status of the colony. Social monogamy in different forms appears to be the important precursor to the evolution of eusociality in sponge-dwelling symbiotic shrimp for the reason that it fosters the formation of close kin groups and long-term parent-offspring associations[38,39].

12. Alternative Mating Strategy

Alternative mating strategies in males arise on account of variations in the spatial and temporal distribution of sexually receptive females, together with changes in female life history[40]. In Crustacea, sexual dimorphism in body size and morphology, such as the occurrence of different male morphotypes, has resulted in alternative mating strategies. The intense intrasexual selection also favours alternative reproductive tactics in the subordinate males[41]. In the classical example, the sponge-living isopod *Paracerceis sculpa* has three genetically discrete male morphotypes, α-male, β-male and γ-male[42]. The α-male is large and dominant, and defends harems inside the spongocoel, whereas the smaller β-type, resembling the females in size, invades the spongocoel by mimicking the behaviour of females. The γ- morphotype is tiny and secretive and enters the harem by stealth. The relative fertilization success is high in the dominant α-morphotype and the two subordinate types have to resort to alternative strategies such as sneak mating. However, in caridean shrimps, such as the freshwater prawn *Macrobrachium* and the rock shrimp *Rhyncocinetes* the male morphotypes arise from developmental conversion and behavioural polyphenism[19]. In the caridean rock shrimp, *Rhynchocinetes typus* and *R. brucei*, living in the coral crevices, the males undergo remarkable changes during their ontogeny: they become sexually mature in the typus morphotype, which is female-like in size and morphology, then pass through several intermedius types, before finally reaching the terminal molt stage, termed robustus morphotype[43,44]. Among them, the robustus is the dominant morphotype with hypertrophied maxillipeds and major chelipeds. This dominant male engages in mate guarding of receptive females, thereby preventing access to subordinate males. The hinge-back shrimp *R. durbanensis*, having wide distribution in Indian waters, has recently been reported to have male morphotypes, similar to other *Rhynchocinetes* species[45]. Laboratory study has indicated that the mating behaviour in all three morphotypes (touching, overlapping and holding) is similar (Figure 1). However, only robustus and intermedius types appeared to fertilize the broods of the female successfully. Robustus females were faster in approaching the receptive females and transferring the spermatophores. On the other hand, approaches of the female-like typus morphotypes were often rejected by

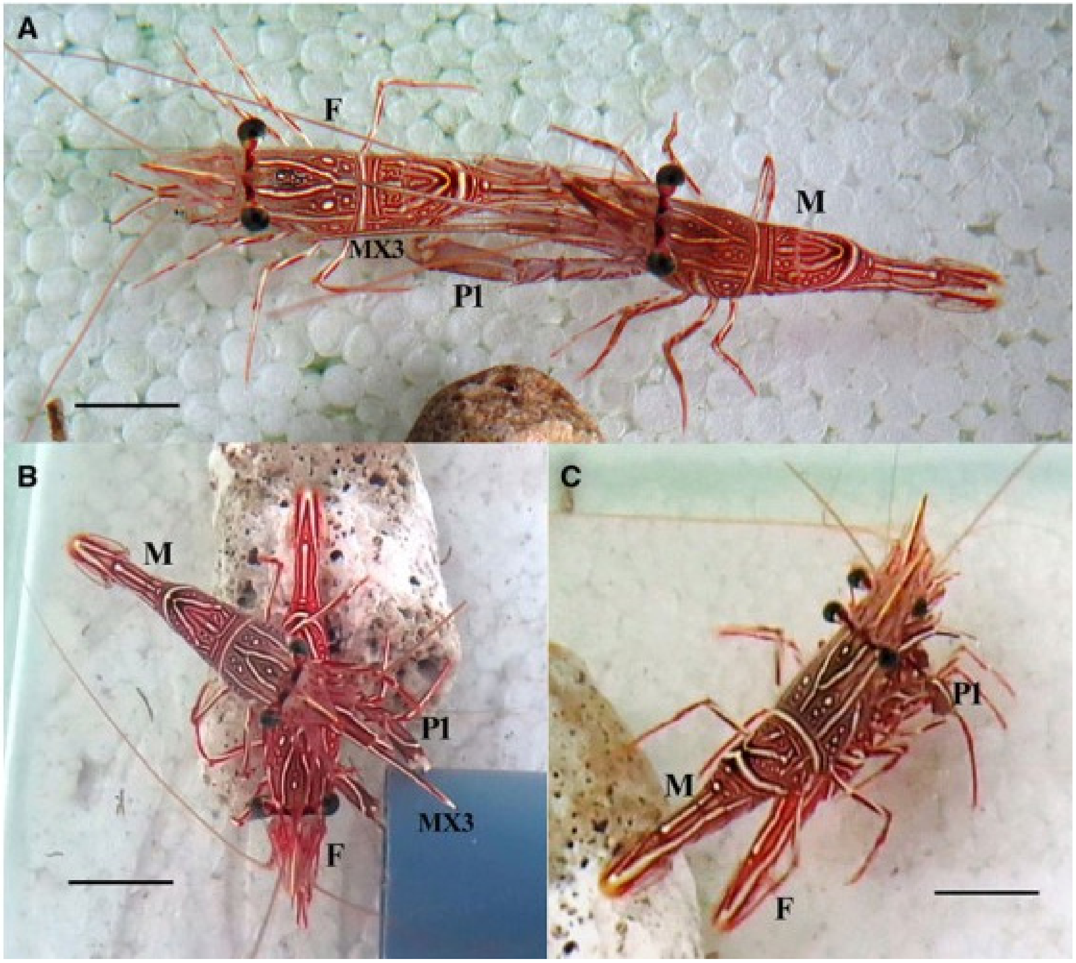

Figure 1. Mating events of *R. durbanensis*. **(A).** Initial contact of robustus male with female using antenna, extended third maxilliped and major chelipeds (touching behaviour). **(B).** Overlapping. **(C).** Holding behaviour. Scale bars A = 1 mm; B, C = 0.5 mm. Reproduced from Prakash, *et al*[45].

the females and resulted in unsuccessful spermatophore transfer. A dominance hierarchy exists in these shrimps in which females appear to prefer mating with the large males.

Alternative mating strategies have also been reported in the partially protandric alpheid shrimp *A. kominatoensis* in which two male morphotypes, small and big, are reported[8]. However, only the small and subordinate males change sex to females, whereas the larger ones remain males throughout their lives. As the small males have low mating success in the presence of big males, they adopt the alternative reproductive strategy of changing sex to females[4].

13. Conclusion

Unlike their terrestrial counterpart, insects, the predominantly aquatic crustaceans have developed unique sexual systems and a multitude of mating systems, thanks to their successful adaptation to varied environmental conditions. Coral reefs in the tropical and subtropical seas are a vibrant, dynamic, species-rich ecosystem inhabited by representatives from all animal groups. Shrimps belonging to the caridean families, *Hippolytidae* and *Alpheidae*, as well as the subfamily *Pontoniinae,* dominate the crustacean fauna in the coral reef[2]. Many species living in symbiosis with other invertebrate hosts have evolved dual sexuality by which the production of male and female gametes rests with a single individual. The occurrence of different categories of sequential hermaphroditism among the caridean species gives insightful information to trace the evolution of hermaphroditism among these aquatic invertebrates. Ghiselin[46] advanced the size advantage theory to explain the adaptive significance of protandric hermaphroditism, in which the male phase precedes the female phase. In *Lysmata wurdemanni* the sex change from the male phase to the larger simultaneous hermaphrodite female phase is variable. Below a certain minimum size, individuals are males and cannot function as females, due to wanting enough energy resources to produce large yolky eggs and, hence, the sex change of males has a threshold size[12]. The underlying physiological mechanism of the sex change in sequential hermaphrodites is known to be the involvement of the androgenic gland, which produces a male sex hormone. The androgenic gland appears to be active during the male phase and atrophies during the sex change to the female phase[4]. However, the status of androgenic gland activity in protandric simultaneous hermaphrodites, possessing a gonad, containing active testis and ovary has not been investigated so far in the *Lysmata* shrimps.

The assumption of peculiar mating systems in the coral reef-associated caridean shrimps is correlated with the adoption of lifestyle strategies in response to their habitation in diversified environmental niches. A special feature of interest in their mating behaviour is monogamous mating, which has evolved in response to their symbiotic living with other large invertebrates, providing residence and mating sites to the shrimps. This monogamous pair-bonding, bolstered further by other limiting factors such as predation risk outside the host organisms, led to an advanced condition called social monogamy, as well as community living when the invertebrate host is large enough to accommodate many individual shrimps to form colonies. In the synapses of shrimp species, such social monogamy has given rise to a highly structured colony formation. Furthermore, species such as *Synalpheus regalis* have reached the pinnacle of complexity in sexuality and peculiar mating behaviours, establishing advanced social systems such as eusociality. The complexity of evolved social structures of these symbiotic shrimps could only match the social systems found in insects and vertebrates like birds. Recent work is also beginning to unravel the astounding armoury of chemical messengers to bolster communication and interaction among the members of the colony[47]. Because of their ability to colonize every conceivable environmental niche both in water and on land, crustaceans have evolved complex sexuality and mating systems that have given origin to advanced social behaviours, as exemplified in the coral reef-dwelling caridean shrimps.

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