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Kleptoparasitism in *Arcotheres exiguus* (Burger, 1895): Symbiotic Dynamics and Reproductive Implications in *Paphia malabarica* from the Southwest Coast of India

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ABSTRACT

The present study conducted from April to September, 2024 along the southwest coast of Maharashtra, India, to investigate the host–symbiont relationship between the pinnotherid pea crab *Arcotheres exiguus* and its bivalve host *Paphia malabarica*. Integrated morphological and molecular techniques, including mitochondrial COI gene amplification, were employed to confirm the crab species. Morphological identification and morphometric measurements were performed using a stereo zoom microscope. Among 320 clams examined, 41.56% were found infested, with a predominance of ovigerous females, indicating a strong reproductive dependence on the host. Morphological analysis revealed distinct sexual dimorphism: males exhibited smaller, calcified carapaces, while females possessed broader, flexible carapaces and pleopods carrying between 611 and 3,750 eggs. The crabs occupied the mantle cavity of the bivalves, displaying kleptoparasitic tendencies by relying on host-filtered food, potentially compromising host health and immune function. Notably, no clam was observed to house both sexes simultaneously, suggesting that mating likely occurred externally. While *A. exiguus* benefited from shelter and reproductive conditions, the direct benefits to *P. malabarica* remain unclear. This study highlights the ecological role of *P. malabarica* as a critical reproductive habitat for *A. exiguus* and emphasizes the importance of conserving host bivalve populations. These findings contribute baseline knowledge on marine kleptoparasitism and underline the need for further research to evaluate the long-term ecological impacts of pinnotherid crabs on their bivalve hosts.

KEYWORDS: Pinnotheridae, pea crabs, *Paphia malabarica*, *Arcotheres exiguus*

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Data Availability Statement: Legal restrictions are imposed on the public sharing of raw data. However, authors have full right to transfer or share the data in raw form upon request subject to either meeting the conditions of the original consents and the original research study. Further, access of data needs to meet whether the user complies with the ethical and legal obligations as data controllers to allow for secondary use of the data outside of the original study.

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1. INTRODUCTION

Pea crabs, belonging to the family *Pinnotheridae*, are small, inconspicuous crustaceans that form symbiotic associations with various marine hosts including shrimps (Pearse et al., 1942), polychaetes (Gray, 1961; McDermott, 1962), gastropods (Geiger and Martin, 1999), bivalves (Stauber, 1945; Pearce, 1966), and echinoderms like sea urchins and starfish (Wells and Wells, 1961; Williams, 1984). Their widespread presence in marine ecosystems is due to their evolution of both ectosymbiotic (external) and endosymbiotic (internal) relationships. Despite their small size, pea crabs play a significant ecological role by contributing to the complexity of marine symbioses. Typically, pinnotherid crabs reside within the gill chambers, mantle cavities, or digestive tracts of their hosts, depending on the nature of their symbiotic relationship. One notable species, *Arcotheres exiguus* (Burger, 1895), formerly known as *Pinnotheres vicajii* (Chemnitz, 1782), infests the commercially important bivalve *Paphia malabarica*, widely consumed along India's southwest coast (Kumari and Rao, 1974). These crabs are difficult to detect due to their cryptic behavior and tendency to remain hidden within the gill chambers (Stauber, 1945; Pearce, 1966). *Arcotheres exiguus* exhibits kleptoparasitic behavior, feeding on food filtered by the host's filter-feeding system, thus reducing the bivalve's nutrient intake (Burger, 1895; Iyengar, 2008). This parasitism negatively affects the host's growth and reproductive capacity, and prolonged infestations can alter shell morphology, lowering the bivalve's commercial value (Kennedy et al., 1996; Kruczynski, 1975; Bierbaum and Ferson, 1986). Despite these adverse effects, the crab-host relationship reflects a delicate ecological balance: the pea crabs depend entirely on their hosts for shelter and nutrition, making host survival essential for crab persistence. Within the true crabs (Decapoda: Brachyura), the *Pinnotheridae* family contains about 320 recognized symbiotic species across 14 families (Castro, 2015). Determining whether some species are truly free-living or temporarily host-less remains challenging (Werding and Sanchez, 1989). Although among the most specialized symbiotic crabs (Serene, 1961), their functional adaptations for host association remain poorly understood due to their small size and cryptic lifestyle (Becker and Turkay, 2017; Palacios Theil and Felder, 2020).

Sexual dimorphism is common in pinnotherids, with generally larger, sedentary females and smaller, more mobile males, reflecting polygynandrous mating systems (Baeza and Thiel, 2007; Christensen and McDermott, 1958). Size variation between species often correlates with host microhabitat size (Becker and Turkay, 2017). The largest species, *Pinnaxodes gigas*, reaches a carapace width of 36 mm and inhabits geoduck siphons (Campos, 2016), while the smallest, *Nannotheres moorei*, measures only 1.5 mm and lives in hammer oysters (Manning and Felder, 1996) annother species, *Arcotheres pollus*, also inhabits hammer oysters (*Malleus albus*) (Manning and Felder, 1996). In India, *Pinnotheres vicajii* is known from *Paphia malabarica*, an economically important clam species (Kumari and Rao, 1974; Nagvenkar et al., 2014). Infestations cause gill erosion from crab mucus-collecting activity (Nagvenkar et al., 2014) and can induce fibrous mass formation due to abrasion (Stauber, 1945). Such infestations may reduce host body size by up to 30%, severely affecting commercial value (Trottier et al., 2012). Additionally, infested oysters show reduced gastro-somatic indices, indicating poorer health (O'Brien and Walker, 1999). Given the complex ecological interdependence between pinnotherid crabs and bivalve hosts like *Paphia malabarica*, this study was aimed to qualitatively assess infestation rates and the kleptoparasitic impact on host health and viability.

2. MATERIALS AND METHODS

2.1. Study area and sampling

A total of 320 clam specimens were collected from the Four Bungalows fish market in Mumbai between April and September 2024. The initial study objective was to observe the feeding behavior of bivalves. According to information provided by local vendors, the clams were most likely sourced from the Konkan coast via handpicking. During the acclimatization period in aquarium tanks, resident pea crabs were observed emerging from the clams;and the remaining clams were cut open to know the infestion and these crab-

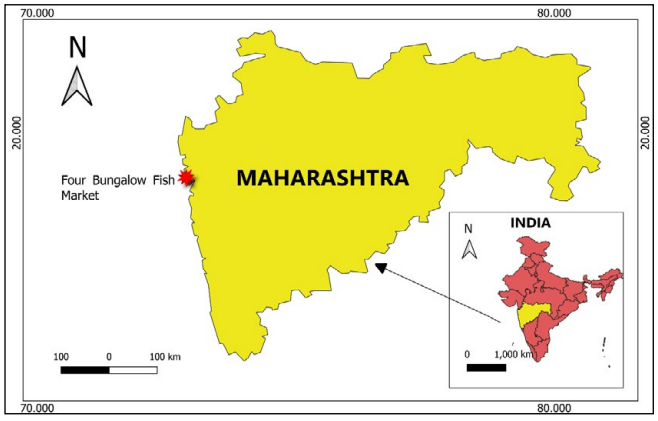

Figure 1: The map of the sample location

infested clam and crab specimens were subsequently taken for further taxonomic and molecular analysis.

2.2. Morphological identification

Specimens studied in the present work were collected alive from the market. When the clams were placed in the experimental tanks, the crabs which were present inside

the shells came out due to the change in water quality and associated stress. Specimens were morphologically identified with males and females distinguished by their abdominal structure. The crabs were preserved in 99.99% ethanol and photographed; morphometric measurements were taken using a stereo zoom microscope (Carl Zeiss, Stemi 508), and the specimens were identified to the lowest taxonomic level (Kumari and Rao, 1974). Morphometric measurements of clams were obtained using a Vernier caliper with an accuracy of 0.1mm and for crabs by using mosaic software.

2.3. Molecular identification

DNA was extracted using a DNeasy Tissue kit (QIAGEN). The 650bp COI gene fragment of mitochondrial DNA was amplified using LCO1490 and HCO2198 primers (Folmer et al.,1994). A total volume of 25µL polymerase chain reaction (PCR) mixture was prepared with 12.5µL of master mix (Promega), 0.8µL of LCO1490 and HCO2198 primers, 2µL of DNA template and 4.45µL of nuclease-free water. PCR application was performed in a Bio-Rad thermal cycler with the following conditions: 94˚C for 3 min, followed by 34 cycles of 94˚C for 30s, 44˚C for 1 min, 72˚C for 1 min, and a final extension at 72˚C for 10 min. The sequence generated was submitted to the NCBI Gene Bank with accession number: PQ471581

2.4. Taxonomic classification

Kingdom: Animalia

Phylum: Arthropoda Latreille, 1829

Subphylum: Crustacea Brunnich, 1772

Class: Malacostraca Latreille, 1802

Order: Decapoda Latreille, 1802

Infraorder: Brachyura Latreille, 1802

Superfamily: Pinnotheroidea De Haan, 1833

Family: Pinnotheridae De Haan, 1833

Genus: *Arcotheres Manning*, 1993

Species: *Arcotheres exiguus* (Burger, 1895)

3. RESULTS AND DISCUSSION

Arcotheres exiguus was identified as a small, soft-bodied pinnotherid crab exhibiting pronounced sexual dimorphism, wherein males were significantly smaller and morphologically distinct from females. This crab species possessed a smooth, flexible, and translucent carapace that was well-suited to its commensal lifestyle within the mantle cavity of its bivalve host, *Paphia malabarica* (Figures 2, 3 and 4). The crab's appendages, including walking legs and chelipeds, were morphologically specialized for efficient movement and manipulation of food within the limited space of the host cavity. Fine setae along the appendages assisted in collecting food particles filtered by the host, supporting the kleptoparasitic feeding behavior typical of the species. Detailed morphological examination under a stereomicroscope revealed that adult females had a

Figure 2: Crab (*Arcotheres exiguus*) and its host (*Paphia malabarica*)

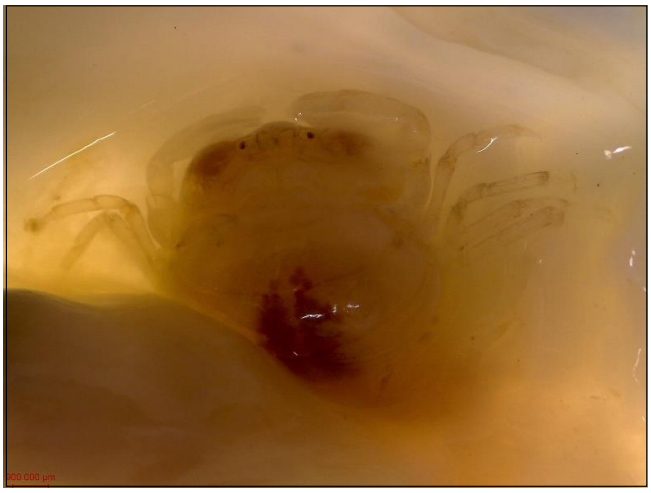

Figure 3: The occurrence of female crabs inside the host

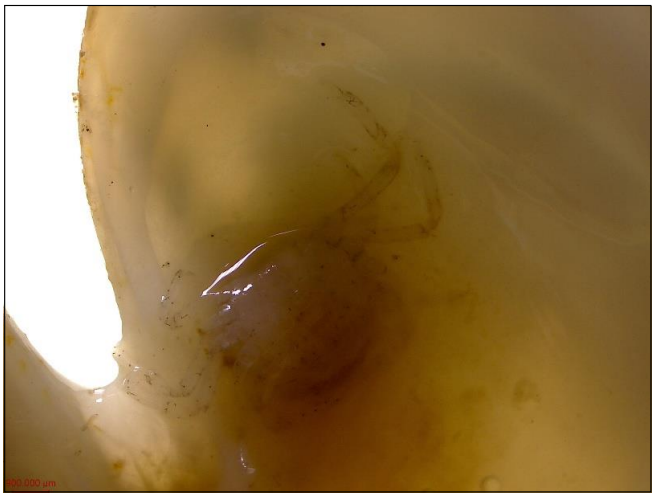

Figure 4: Occurrence of males inside the host

yellowish-brown, subquadrate carapace, where the width consistently exceeded the length, and were found carrying eggs ranging from 0.36 mm to 4.65 mm in diameter. The carapace was smooth, slightly convex, and demarcated by faint depressions forming subtle elevations. Female crabs possessed four pairs of walking legs, with the third pair being the longest and covered in fine setae. Their abdomen was broad and ventrally flexed to form a protective brood pouch that housed eggs, supported by four pairs of abdominal appendages (Figure 6). The fecundity analysis indicated that each female carried between 611 and 3,750 eggs, averaging 1,853 eggs per individual (Figure 7). The chelipeds were elongated and equipped with toothed dactyli to facilitate food handling and defense. Male crabs were distinctly smaller, possessing a hardened, calcified, circular carapace ranging from 3.0 to 4.3 mm in width, lacking the lateral flexibility seen in females. Their chelipeds had a prominent, bulging palm, and claw-like dactyli were curved and armed with a single tooth that fit precisely into a groove on the opposing claw, suggesting a role in mating. The walking legs were slender and elongated (Figure 5), with the third pair being the most extended. The male abdomen was narrow, snugly fitting into a ventral sternal groove, and bore blade-

Figure 5: Male crab (Dactylus broken of walking leg)

like copulatory pleopods used during external copulation. These morphological traits aligned with earlier descriptions provided by Kumari and Rao (1974), indicating consistency in species identification. Out of 320 *Paphia malabarica* specimens collected and examined, 133 individuals (41.56%) were infested with *A. exiguus*, indicating a notably high infestation rate. Among these, 57 individuals (43%) were male and 76 individuals (57%) were female, with most infested clams retrieved from buried intertidal substrates. The morphology of pea crab species associated with burrowing hosts exhibited significantly wider carapaces (higher aspect ratios) than those with non-burrowing

Figure 6: Ovigerous female

hosts, indicating host-driven convergent morphological adaptation (Hultgren et al., 2022). Importantly, no instance was recorded in which both sexes cohabited the same host individual, suggesting a strong host-exclusion behavior and indicating that *P. malabarica* did not support simultaneous colonization by a male and a female crab. This behavior also supported the hypothesis that mating occurred externally, likely during brief periods when the crabs left their hosts. In contrast two heterosexual crabs were present within a single host in a study Cuesta et al., 2019, suggesting they may form mating pairs inside the host. The presence of a high proportion of ovigerous females within hosts suggested a strong reproductive dependence on the host environment. *Paphia malabarica* thus served not merely as a shelter, but as a critical reproductive site for *A. exiguus*, offering both physical protection and a stable food source. However, the mutualistic or parasitic nature of this association remained ambiguous. While the crabs clearly benefited through reduced predation, enhanced food availability, and

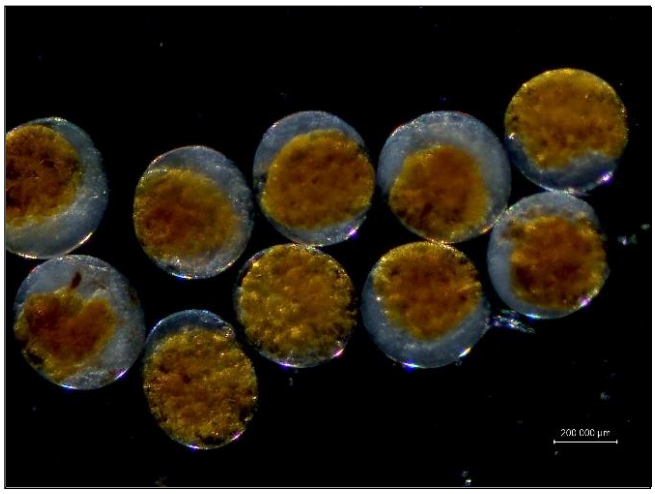

Figure 7: Eggs and yolk reserve

reproductive security, the host bivalves may have suffered physiological stress, reduced immunity, or decreased filtration efficiency because of the crab's presence. Despite this, the full extent of host detriment was not quantified in this study. Becker and Turkay confirmed this theory for hard stage males of *Pinnotheres pisum*, observing the lack of distal segments in their ambulatory legs, likely due to them having been squashed by the closing of their bivalve hosts and similar observation was observed in this study (Figure 5). The dependency of pinnotherid crabs on *Paphia malabarica* reinforced the ecological importance of conserving clam populations, as any disruption in host abundance or health could directly impact the symbiont's lifecycle. Earlier studies such as Gajbhiye and Khandeparker (2017) classified the male-host interaction as facultative, whereas the female-host relationship was considered obligatory, which was supported by the findings in the present investigation. Several studies suggested that host size, availability, and environmental conditions played pivotal roles in crab colonization success. The long-term presence of these crabs could potentially alter clam growth, energy allocation, or survival, as suggested by prior works of Kumar and Rao (1974) and Bierbaum and Ferson (1986). Host-switching and expansion tendencies were also evident from recent studies: Chryso et al. (2024) reported *Arcotheres placunae* in *Placuna quadrangular*, extending the known host range, while Trivedi et al. (2023) recorded the first Indian occurrence of *A. alcocki* in *Perna viridis* and *Pinnotheres pisum* was recorded for the first time in *Glossus humanus*, expanding its known host range to 34 taxa and confirming conspecificity across Mediterranean and Atlantic populations based on COI gene sequences (Marco-Herrero et al., 2023) demonstrating genus-level host plasticity. Hassan et al. (2022) reported habitat-driven host preferences in *Arcotheres* spp. in the Setiu Wetland Lagoon, emphasizing the importance of bivalve size and local environmental parameters. Furthermore, de Greef et al. (2023) underscored the influence of host trophic strategies and sediment type on symbiont establishment. These insights aligned with the present findings, where the stable burrowing nature and filter-feeding habits of *P. malabarica* created a favorable microhabitat for *A. exiguus*, facilitating both its survival and reproduction. The cumulative evidence suggested that kleptoparasitic crabs like *A. exiguus* were highly adapted to exploit host niches, and their success was intimately tied to the ecological health and availability of bivalve populations. These observations highlighted the necessity for further ecological and physiological studies on such host–symbiont systems to inform conservation and management of benthic communities in coastal ecosystems.

4. CONCLUSION

This study demonstrated that *Paphia malabarica* served as an essential reproductive niche for *Arcotheres exiguus*, especially for ovigerous females. The symbiotic relationship leaned towards parasitism, with potential implications for host fitness and commercial value.

5. ACKNOWLEDGEMENT

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